NESTING ECOLOGY OF THE GREY-HEADED FISH-EAGLE AT PREK TOAL, TONLE SAP LAKE, CAMBODIA

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ABSTRACT.—Little is known about the ecology of the Grey-headed Fish-Eagle (GHFE; *Ichthyophaga ichthyaetus*) despite it being a globally near-threatened species in apparent decline. We here present the first quantitative information on nesting ecology of this species, in a regionally significant population at Prek Toal, part of the seasonally flooded swamp forest surrounding the Tonle Sap Lake, Cambodia. We found that GHFE selected trees as nest sites that had an open crown structure and were relatively tall. Grey-headed Fish-Eagles preferred nesting closer to permanent water than expected, but the timing of breeding did not differ according to distance to permanent water: we suggest that their preference for nests near water may reflect an advantage based on prey availability. Water snakes, known prey of GHFE, were significantly more abundant at a site in permanent water than at a temporarily flooded site, in December. We also found that human habitation was negatively correlated to GHFE nest-site occupancy rates. This may reflect indirect effects of human exploitation of GHFE food supplies, which may be exacerbated in the future by changes to the Tonle Sap ecosystem resulting from upstream dam construction.

KEY WORDS: *Grey-headed Fish-Eagle*; Ichthyophaga ichthyaetus; *flooded forest*; *human disturbance*; *hydropower*; *nest site*; *water snake*.

ECOLOGÍA DE ANIDACIÓN DE *ICHTHYOPHAGA ICHTHYAETUS* EN PREK TOAL, LAGO TONLE SAP, CAMBOYA

RESUMEN.—Se conoce poco sobre la ecología de *Ichthyophaga ichthyaetus*, a pesar de ser una especie casi amenazada a nivel global en declive aparente. Aquí presentamos la primera información cuantitativa sobre la ecología de anidación de esta especie. Estudiamos una población regionalmente significativa en Prek Toal, que es parte del bosque de pantano estacionalmente inundable que rodea al lago Tonle Sap,

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Camboya. Encontramos que *I. ichthyaetus* seleccionó árboles como sitios de anidación que tenían una estructura de copa abierta y que eran relativamente altos. Los individuos de *I. ichthyaetus* prefirieron anidar más cerca del agua permanente que lo esperado, pero el momento de anidación no difirió de acuerdo a la distancia al agua permanente: sugerimos que su preferencia de anidar cerca del agua puede reflejar una ventaja basada en la disponibilidad de presas. Las serpientes de agua, presas conocidas de *I. ichthyaetus*, fueron significativamente más abundantes en un sitio en agua permanente que en un sitio inundado temporalmente, en diciembre. También encontramos que la presencia humana estuvo negativamente correlacionada con las tasas de ocupación de sitios de anidación de *I. ichthyaetus*. Esto puede reflejar los efectos indirectos de la explotación humana de las fuentes de alimento de *I. ichthyaetus*, lo que podría incrementarse en el futuro por cambios en el ecosistema de Tonle Sap resultantes de la construcción de una represa río arriba.

[Traducción del equipo editorial]

Little is known about the ecology of the Grey-headed Fish-Eagle (GHFE) (*Ichthyophaga ichthyaetus*) despite it being a formerly widespread species throughout Indo-Malaya (Ferguson-Lees and Christie 2001) in apparent decline (Samant et al. 1995, Grimmett et al. 1998) with a conservation status of globally near-threatened (IUCN 2008). Several researchers have suggested that causes of population decline (BirdLife International 2001, Baral and Inskipp 2004) may include deforestation, pesticides, and anthropogenic disturbance, but few of these are based on anything more than anecdotal evidence. If the apparent population decline is to be addressed through effective conservation planning, however, then it is essential that conservation decisions are based on a thorough understanding of the species' ecological requirements. Some of the first quantitative data on the GHFE, gathered at Tonle Sap Lake in Cambodia, have been reported earlier by Tingay et al. (2006). Here, we extend those findings with more detailed results, which may contribute to more informed conservation decisions in this regionally important aquatic ecosystem, the largest freshwater lake in Southeast Asia (Campbell et al. 2006).

We previously documented (Tingay et al. 2006) a high-density breeding population of GHFEs in the seasonally inundated swamp forest at Prek Toal. This population appears to be regionally significant, considering the reported declines in neighboring Thailand, Malaysia, Myanmar, Laos, and Vietnam (Wells 1999, Robson 2000, Fuchs et al. 2007). The breeding cycle of GHFE at Prek Toal begins when the floodwater begins to rise in September and ends when the floodwaters are fully receded in March (Tingay et al. 2006, S. Visal unpubl. data). This population is at least partly dependent on water snakes as prey and may be threatened by the unsustainable mass-harvesting of water snakes by the local human population (Tingay et al. 2006), because an estimated 6.9 million snakes are removed annually from the lake for human and captive-crocodile consumption, as well as for the medicinal wildlife trade in Southeast Asia (Brooks et al. 2007). GHFE at Prek Toal may also be threatened by the upstream construction of hydropower dams in China, Laos, Thailand, and Cambodia, which have the potential to alter drastically the Tonle Sap Lake flood cycle (Kummu and Sarkkula 2008).

In this report, we present analysis of features of nest-site selection by GHFE at Prek Toal. First we examine whether GHFE preferentially place nests in the tallest trees with an open canopy structure, as this will minimize the risk of nest-flooding and allow unencumbered parental access: studies of other tropical fish-eagle species have documented selection of such traits (Berkelman et al. 2002, Hollamby et al. 2006). Next, we consider whether GHFE preferentially nest closer to permanent water, because this should allow access to a more prolonged aquatic food supply, given that floodwaters recede in the latter part of the breeding cycle. We also test whether a known component of the diet, water snakes, are more abundant in permanent water than in temporary water when floodwaters are receding (typically, during the nestling-rearing phase). Finally, we examine whether GHFE nest site distribution is influenced by proximity to human habitation.

METHODS

Study Area. The Tonle Sap Lake (12°25′ to 13°25′N; 103°25′ to 104°40′E; Fig. 1) covers 2500 km² in the dry season (January to May), expanding to 12 000 km² during the wet season (June to October; Rundel 2000; Fig. 1). The Tonle Sap River connects the Tonle Sap Lake to the Mekong River, making the lake a highly productive wetland ecosystem (Campbell et al. 2006) that supports one of the largest freshwater fisheries in the world (Hortle et al. 2004). The dominant floodplain habitat is de-
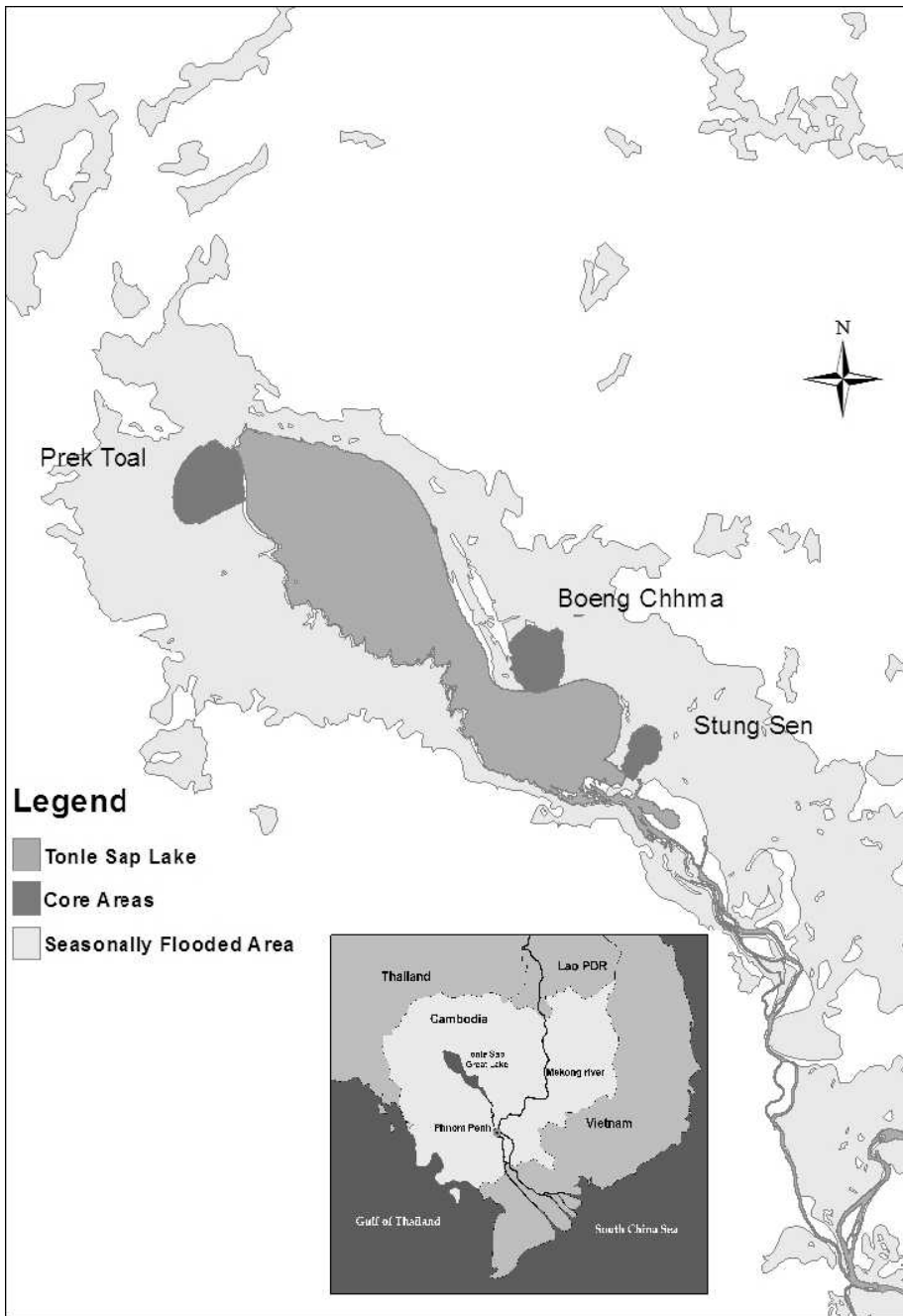
Figure 1. Location of the three Core Areas on Tonle Sap Lake, Cambodia, and the extent of the floodwater.

scribed as freshwater swamp forest and is characterized by the seasonality of the flooding, as opposed to the permanent flooding of the classic swamp forest of Southeast Asia (Rundel 2000). This unique ecosystem forms a large vegetation belt 7–40 km wide surrounding the open water surface and is estimated to cover approximately 3600 km² (Rundel 2000). It is adapted to withstand seasonal water-level variation of up to 10 m and is of relatively simple floristic composition, comprising three main vege-

tation types: short-tree scrublands, gallery forest, and aquatic herbaceous vegetation. The short-tree scrublands cover approximately 80% of the floodplain and consist of dense, fairly homogenous stands of short trees and scrub 2–4 m in height. Typical species include *Vitex holadenon*, *Acacia spiralis*, and *Corbretum trifoliatum*. The gallery forest covers approximately 10% of the floodplain and is primarily found close to the shoreline and rivers, consisting of 7–15-m-tall trees dominated by *Barringtonia acutangula* and *Diospyros cambodiana* (Campbell et al. 2006). The Tonle Sap Lake contains three designated core protected areas: Prek Toal (21 342 ha), Boeng Chhma (14 560ha) and Stung Sen (6355 ha). The Prek Toal Core Area (13°07′N, 103°39′E), where our study was based, is situated at the northwestern end of Tonle Sap and is considered one of the most intact areas of freshwater swamp forest around the lake (Chan et al. 2004).

Surveys. We conducted our study over three years: 3–13 December 2005; 30 November–7 December 2006; 1 October–31 December 2007 (Fig. 2). We defined an occupied GHFE site according to previously described criteria (Rabarisoa et al. 1997), which included any sign of use such as the presence of green leaf nest-lining material, eggs or nestlings, or incubating or brooding adults. In 2005 we conducted a systematic survey via boat-based north–south transects 1 km apart, between 4.5 km and 8 km in length, in which we recorded all occupied and unoccupied nest sites (Tingay et al. 2006). In subsequent years, the study area was expanded (Fig. 2), including areas we searched for previously unrecorded sites and all previously identified nest sites (and their vicinity), with retention of the original criteria of nest-site occupation. The location of all occupied and unoccupied nest sites was recorded by handheld Geographical Positioning System (GPS) accurate to <10 m resolution.

In each year, whenever possible, we recorded the stage of breeding according to the two major phases of the breeding cycle: pre-hatching (=late breeders) and post-hatching (=early breeders). We based this on direct observations into the nests (eggs or nestlings) where possible, or, where access was limited, by indirect inference from observations, including adult posture on the nest (i.e., bird sitting low in the nest equals incubation; bird sitting high in the nest equals brooding nestlings). The validity of this inference was tested during a subsequent breeding season (2009), when predictions based on adult posture ($n = 42$) were verified by climbing

to each nest to inspect the contents. Predictions were correct in all but one nest, where we had predicted nestlings but the eggs were just in the early stage of hatching (R. Tingay unpublish. data).

Nest-site Characteristics. In 2006, we recorded the following at each occupied nest site: nest-tree species, nest-tree height, height of nest in tree, nest-tree crown density, nest aspect, position of nest in canopy, distance to next-nearest tree, next-nearest tree species, next-nearest tree height, and next-nearest tree crown density. Tree height was measured by tree depth below water (telescopic pole of known length) + height of observer eye level to water level (using a clinometer) + observer eye level to treetop (using a clinometer). Distance of observer to tree was calculated with a 200 m rangefinder (Leica DISTO™ A5, Milton Keynes, Bedfordshire, U.K.), positioned at 10, 15, 20, or 25 m from the tree to facilitate direct use of the built-in clinometer scales. Height of nest in tree was calculated in the same way, with the measurement taken at the base of the nest. Crown density was visually estimated as the amount of light that was blocked by branches and foliage, using four categories: 0–25%, 26–50%, 51–75%, and 76–100%.

Nest-site locations were entered as a layer into a Geographical Information System (GIS, ArcView). Permanent water bodies and the location of Prek Toal village were entered as additional layers in the GIS via a digitized 1:50 000 map of Prek Toal (Defense Mapping Agency Topographic Center, Washington DC, Sheet 5735 III) captured during the dry season (Tingay et al. 2006), thereby allowing estimation of distances between these features and nest sites.

Food Availability. To evaluate food availability (water snakes) in permanent and temporary floodwater, we set out traditional water snake gill nets (Brooks et al. 2007) in the two contrasting habitats: Site 1, permanent river channel (Prek Da), water depth 3.75 m; Site 2, temporarily flooded forest 1 km west of Prek Da, water depth 5.20 m. The identical nets (three sections × 70 m length, 1.5-m depth, 2-cm mesh size) were set simultaneously in an unbroken line (210 m) on a north–south axis at both sites on the afternoon of 2 December 2006 and checked daily at 07:00 H for the following four days. Water snakes were removed each morning and a tape measure was used to collect morphometric data, including snout to end-of-tail measurements. Snakes were not weighed because mass would be dependent on whether the snake had just eaten or not.
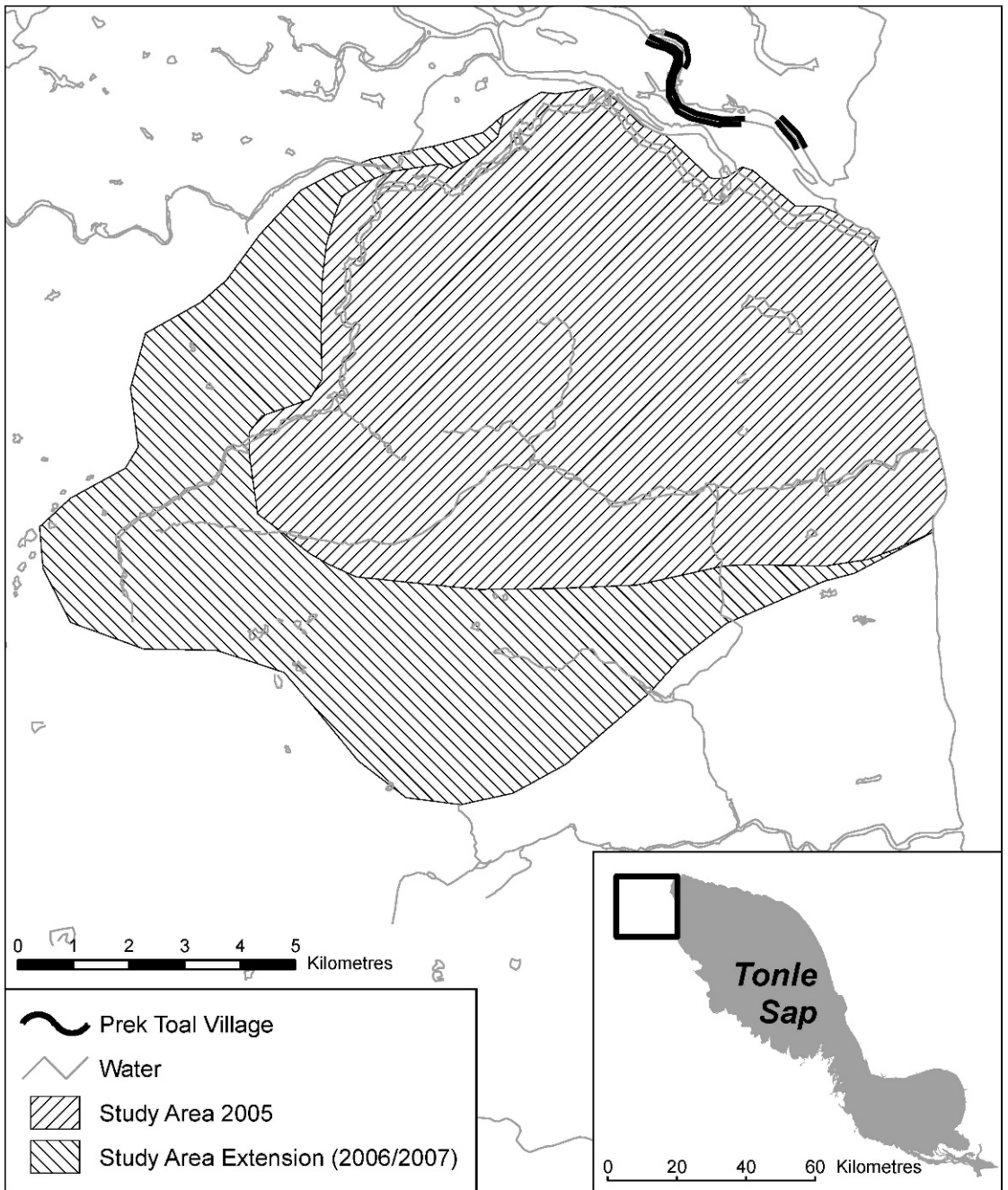
Figure 2. The flooded swamp forest study site at Prek Toal, illustrating survey areas in 2005 and 2006/2007, with Prek Toal village highlighted in black.

Table 1. Results of binomial GLM investigating the relationship between presence and absence of a GHFE nest site (response variable) with tree height and crown density as explanatory terms; df = 63.

EXPLANATORY TERM	ESTIMATE	SE	Z	P
Tree height	0.46	0.17	2.7	0.006
Crown density	−2.11	0.59	−3.6	<0.001

Statistical Analyses. To analyze features associated with nest site trees we used presence/absence of a nest site, based respectively on measures from trees that contained a nest and from the next-nearest tree without a nest but which were paired through their location with each nest tree. Hence, we employed a binomial GLM (logit link function) to test for factors associated with the presence or absence of a nest. Although we took several measures of nest-site characteristics, the only two that we could employ by way of comparison with trees where no nests were present were tree height and crown density. As we had no *a priori* biological reason to expect that these two variables would interact (confirmed by an exploratory model run) our analysis simply included both crown density and tree height as main explanatory terms, assigned as continuous variables.

Distances to permanent water of occupied nest sites were compared to distances as expected from the distribution of all points in the study areas, using two-sample Kolmogorov-Smirnov tests, because there was no *a priori* expectation that either the frequency distributions of either nest site distances or points within the study area would be normally distributed (confirmed during data exploration). Distances were classed into 100-m categories, censored to the largest distance category recorded (for study area: 1.8 km) and analyzed separately by year (2005 and 2006) because, for nest sites, the records could not be considered independent, and study area varied by year. Frequency records for each distance class were converted to percentages to maintain comparability between the nest site and study area data.

We tested whether birds that nested closer to permanent water initiated breeding earlier by contrasting measures of distance to permanent water for the two "timing of breeding" classes (early and late) using a Mann-Whitney test, considering each year (2005 and 2006) separately.

To test for the effect of distance to human habitation on nest-site occupancy, data from 2005, 2006,

and 2007 were used to estimate occupancy across the three study years, but only within the 2005 study area because here we had the greatest confidence that all possible alternative nest sites had been discovered. Hence, we could be reasonably sure here that the absence of a pair of birds or other signs of occupancy was genuine and that birds had not moved to an alternative nest site within the same territory. We analyzed only the lower 50 percentile of all nest site records, ranked by distance to Prek Toal village (equivalent to <7 km from Prek Toal), as we did not anticipate that the village's influence would extend to all of the 2005 study area. We used a three-class site occupancy index as a response variable (0 = not occupied in any year, 1 = occupied in one or two years, 2 = occupied in all three years), and distance to Prek Toal (square-root-transformed) as an explanatory variable. Because disturbance may have been greater closer to permanent water bodies (rivers are used for human transport corridors) or, alternatively, nest sites close to permanent water may have been preferred by fish-eagles (see Results), we also included distance to permanent water (square-root-transformed) as an additional explanatory variable. Our initial model was a saturated Poisson GLM (log link function; i.e., including both main explanatory variables and their interaction).

The comparison of water snake catches between site 1 and site 2 (permanent water and temporary floodwater, respectively) was achieved using paired samples tests.

RESULTS

In the binomial GLM examining tree features associated with presence or absence of a nest, both crown density and tree height were significantly associated with the presence of a nest, negatively and positively, respectively (Table 1). Hence, GHFE nests were more likely to be found in relatively tall trees with an open crown structure. In 2006, 28 nests (82%) were in Ptol trees (*Diospyros cambodiana*), and three nests (9%) each were in Chrakeng (*Mallotus anisopodus*) or Taor (*Terminalia cambodiana*) trees. All nests in 2006 were orientated away from the south/southeast.

The distribution of distances from nests to permanent water differed significantly from that expected based on the "availability" of all points within the study area, both in 2005 (Kolmogorov-Smirnov $Z = 4.39$, $P < 0.001$) and in 2006 (Kolmogorov-Smirnov $Z = 5.16$, $P < 0.001$; Fig. 3). This was
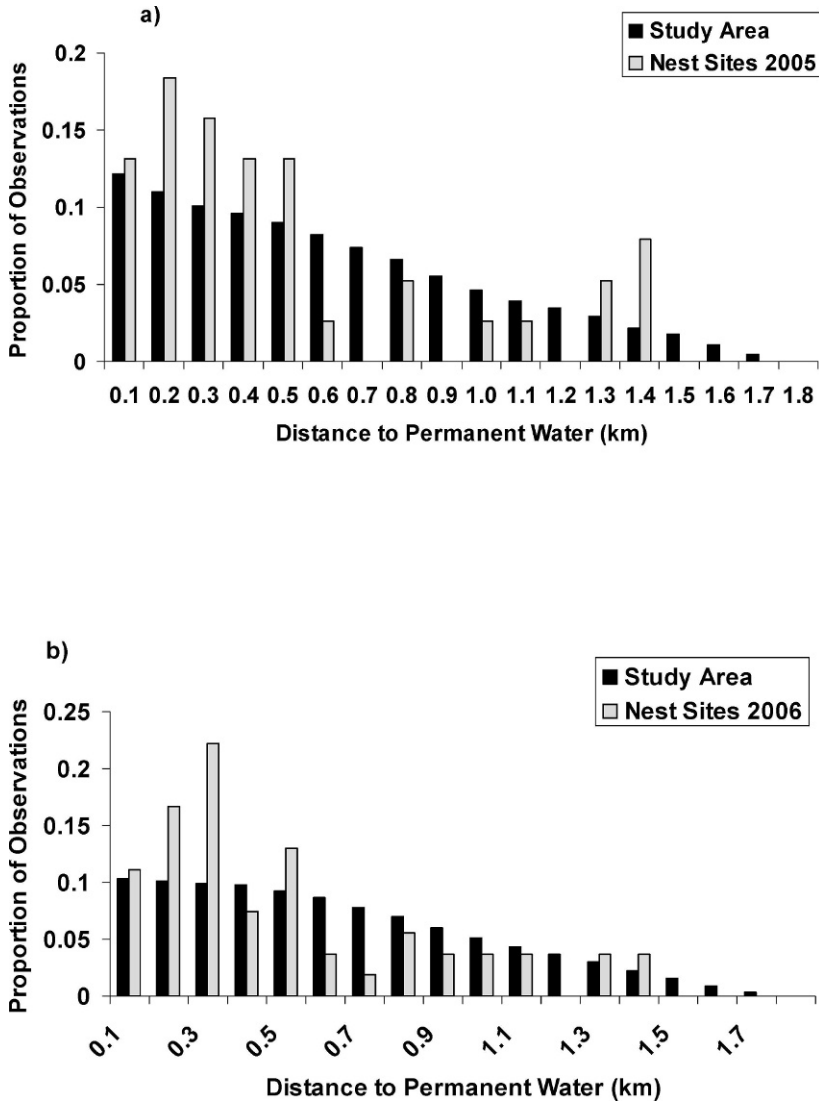
Figure 3. Distribution of distances to permanent water for occupied GHFE nest sites and all points within the study area (as estimated by an overlay of a 50-×-50-m grid in the GIS) for (a) 2005 and (b) 2006.

largely due to nest sites being closer to permanent water than expected (Fig. 3). A secondary peak in nest site distribution in 2005 at 1.3–1.4 km from water was potentially an artifact resulting from our inability to discriminate all permanent water using the available digital maps and the more restrictive 2005 study area (lower 50 percentile), but may still have influenced the test for 2005. Censoring 2005 data to 1 km removed this possible influence on the test and illustrated that observed and expected distributions still differed significantly (Kolmogorov-

Smirnov $Z = 5.65$, $P < 0.001$), confirming that fish-eagles were more likely to nest close to permanent water.

Median values of distance to permanent water for "early" and "late" breeders were, respectively, 0.32 km ($n = 6$) and 0.32 km ($n = 7$) in 2005 and 0.28 km ($n = 9$) and 0.34 km ($n = 8$) in 2006. There was no significant difference between 'early' and 'late' breeders according to distance to permanent water, either in 2005 (Mann-Whitney $U = 21$, $P = 1.00$) or 2006 (Mann-Whitney $U = 33$, $P = 0.81$). This sug-

Table 2.   Results of Poisson GLMs (log link function) investigating potential relationships between an index of GHFE territory occupancy (response variable) and distance to permanent water and distance to Prek Toal village (both variables square-root-transformed) as explanatory terms. Respectively, df = 13, 14, and 15 for the three models.

MODEL	EXPLANATORY TERM	ESTIMATE	SE	Z	P	AIC
1	Distance Perm Water	−2.60	6.14	−0.42	0.672	
	Distance Prek Toal	0.30	1.80	0.17	0.868	
	Interaction	1.27	2.79	0.46	0.649	55.5
2	Distance Perm Water	0.17	0.64	0.26	0.793	
	Distance Prek Toal	1.09	0.48	2.27	0.023	53.7
3	Distance Prek Toal	1.10	0.48	2.29	0.022	51.8

gested, although sample sizes were limited, that birds that started breeding earlier were not more likely to breed closer to permanent water.

In our initial saturated Poisson GLM neither explanatory variable (distance to permanent water and distance to Prek Toal) nor their interaction was significant, so we dropped the interaction term in a second model, which then revealed distance to Prek Toal as a significant positive term (Table 2). Our subsequent and best model (as judged by AIC) dropped distance to permanent water and retained only distance to Prek Toal, as a significant positive term (i.e., nest-occupancy was lower closer to the village; (Table 2, Fig. 4).

There was no significant difference in the mean length of snakes caught at sites 1 and 2 (t = 0.73, df = 107, P = 0.468). The number of snakes and the total length of all snakes caught at site 1 was significantly greater than at site 2 (paired samples tests: t = 10.08, df = 3, P = 0.002; t = 8.89, df = 3, P = 0.003, respectively), indicating that snakes were more abundant in the permanent water site than in the temporarily flooded water site. The species
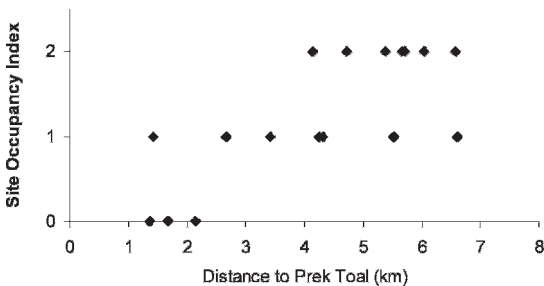

Figure 4.   Index of GHFE territory occupation (0 = not occupied in any year, 1 = occupied in one or two years, 2 = occupied in all three years) in the 2005 study area as a function of distance of the territory to the village of Prek Toal.

composition of snakes, however, did not appear to differ between the permanent and temporarily flooded sampling sites (Table 3).

DISCUSSION

We found that GHFEs at Prek Toal selected relatively tall trees with an open crown structure as nest sites. Although GHFE preferred nesting closer to permanent water than expected, there was apparently no difference in timing of breeding according to distance to permanent water. Water snakes were significantly more abundant at a site in permanent water than in a temporarily flooded site (although see below for discussion on study limitations). We also found that human habitation had a negative effect on GHFE nest-site occupancy.

Grey-headed Fish-Eagle selection of relatively tall nest trees with an open crown structure is consistent with results from other fish-eagle species (Andrew and Mosher 1982, Shiraki 1994, Berkelman et al. 2002, Hollamby et al. 2006). This preference likely reflects ease of access, in addition to maximizing increased visibility for territorial defense. Due to our study's limitations we could not map tree characteristics at a landscape scale, but subjectively, our strong impression was that features of trees selected by GHFE for nest sites did not vary by distance to permanent water. This impression was confirmed by scrutiny of aerial photographs of the study area (R. Tingay unpubl. data). Our opinion, therefore, is that GHFE were not more likely to nest near permanent water due to nest-site availability. We suggest, based on our documentation of differences in water-snake abundance between permanent and temporarily flooded sites, consistent with the results of Karns et al. (2000), that GHFE prefer nesting close to permanent water because food abundance is greater here. Further research on GHFE diet, however, is required to test our suggestion rigorous-

Table 3. Snakes captured using gill nets and proportional contribution to total catch per site in permanent water (Site 1, n = 81) and temporary water (Site 2, n = 28) at Prek Toal Core Area, Tonle Sap Lake.

COMMON NAME	SCIENTIFIC NAME	SITE 1	SITE 2
Puff-faced water snake	*Homalopsis buccata*	0.037	0.035
Rainbow water snake	*Enhydris enhyrdris*	0.59	0.43
Tentacled water snake	*Erpeton tentaculatum*	0.025	0.035
Tonle Sap water snake	*Enhydris longicauda*	0.33	0.5
Bocourt's water snake	*Enhydris bocourti*	0.012	0

ly. Tingay et al. (2006) documented water snakes as GHFE prey items, but their importance and potential seasonal availability is currently unknown; thus, our limited study may not account for seasonal variation in water snake abundance or GHFE prey preferences. Similarly, we have also recorded fish as GHFE prey (R. Tingay unpubl. data), and, based on studies elsewhere (Junk et al. 1989), we would predict fish abundance to be greater in permanent water, but research on fish ecology at the Tonle Sap is still in its infancy and currently is confined to the main lake (Campbell et al. 2006).

If GHFE prefer to breed closer to permanent water due to proximity to an abundant prey source, then any advantage accrued apparently did not translate into an earlier start to breeding. As all birds seem to commence breeding in early September when the flood waters are rising (toward the end of the rainy season), then when floodwaters are at their peak (October/November) most nests should contain nestlings or have eggs nearing hatch; peak food demands would therefore coincide with potential peak food abundance. However, the factors influencing breeding seasons in tropical fish-eagles are poorly understood. Our study season precluded documentation of reproductive success of birds by proximity to permanent or temporarily flooded habitats, and practically it would be difficult to access temporarily flooded areas at the end of the breeding season once waters have receded. Nevertheless, we speculate that differences in breeding success, due to enhanced prey availability, may explain the propensity for GHFE to nest near permanent water; further research on reproductive rate is required.

We can offer no single causal explanation for why GHFE avoided the proximity of human habitation, as several are possible and our results offered no means of discrimination. Potential explanatory candidates would include direct (albeit potentially unintentional) disturbance of nesting attempts through increased human activity close to Prek Toal village or indirect impacts through depletion of GHFE food supplies, given the intense human exploitation of potential GHFE prey (Campbell et al. 2006, Brooks et al. 2007).

If GHFE at Prek Toal already face potential difficulties from intense harvesting of their prey (Campbell et al. 2006, Brooks et al. 2007), then additional pressures from the change to the lake's hydrological regime induced by the construction of upstream hydropower dams (Kummu and Sarkkula 2008) may add to these problems. We have highlighted gaps in knowledge of GHFE biology at Prek Toal, and recommend research efforts to fill these gaps. We also recommend extending the research to other areas of the swamp forest surrounding Tonle Sap Lake. It is known that GHFE breed in the Boeng Chhma Core Area (Fig. 1; S. Visal unpubl. data), but the distribution and status of GHFE there, and in other areas of the swamp forest, is currently undocumented. Given the regional significance of the Prek Toal GHFE population, and the variety of potential threats to this population's stability (Tingay et al. 2006), our information on GHFE nesting ecology can be used to facilitate a rapid assessment throughout the Tonle Sap Lake swamp forest. In conjunction with filling these knowledge gaps, in light of the potential future changes to this unique ecosystem, we also recommend long-term monitoring of the high-density GHFE population at Prek Toal, as large raptors are excellent bioindicators of the health of ecosystems (Sergio et al. 2005, 2006).

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