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ORIGINAL ARTICLE

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Small-clawed otters (*Aonyx cinereus*) in Indonesian rice fields: latrine site characteristics and visitation frequency

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Abstract Latrine sites, or areas where otters scent-mark and deposit feces, are a habitat feature that serve an important role in communication for many otter species. The small-clawed otter (*Aonyx cinereus*) inhabits both natural and rice field landscapes in Southeast Asia. However, latrine site use by small-clawed otters in rice field landscapes is largely unknown. Based on a 53-week field survey and landscape analyses, we investigated latrine site use by small-clawed otters in rice field landscapes in West Sumatra, Indonesia. Using land use and/or local environmental variables as predictors, we performed generalized linear model analyses to explain the spatial patterns of latrine site occurrence and otter visitation frequency to latrine sites. We determined that small-clawed otters use some latrine sites repeatedly over time; 10 latrine sites were still in use more than 7 years after their initial discovery. Generalized linear model analyses revealed that an intermediate number of rice field huts was the single most important predictor of latrine site occurrence, whereas distance to the nearest settlement, distance to the river, and mean water depth of the rice field adjacent to the latrine site were important predictors of otter visitation frequency to latrine sites. These results indicate that the latrine site preferences of small-clawed otters in rice field landscapes are strongly associated with intermediate levels of rice farming activities. Indonesian rice fields are being degraded or disappearing at an accelerated rate because of land conversion and modernization of agriculture. We emphasize an urgent need for design and implementation of otter-friendly rice farming to conserve small-clawed otters.

Keywords Scent marking · Otter spraint · Habitat preference · Satoyama · Rice paddy field

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Introduction

Many mammals use scent marking for communication (reviewed in Ralls 1971; Johnson 1973), and areas where mammals scent mark with feces are called latrine sites. Latrine communication is common among many mustelid species such as polecats, minks, martens, badgers, and otters (reviewed in Hutchings and White 2000).

Despite their semi-aquatic nature, otters use latrine sites on dry land (Kruuk 1992). Otter latrine sites serve multiple functions, including territorial marking, sexual attraction, and communication among conspecific individuals or small groups (Hutchings and White 2000). Otters also use latrines for activities other than scent marking; for example, the latrine sites of North American river otters (*Lontra canadensis*) are used to delineate territories and serve as meeting places or social information hubs among small groups (e.g., Melquist et al. 2003; Green et al. 2015; Barocas et al. 2016). Therefore, latrine site surveys have become a standard method for assessing occurrence, identifying habitat preference, and/or constructing species distribution models of otters (Swimley et al. 1998; Reuther et al. 2000; Stevens et al. 2011).

Unlike other mustelid carnivores, which frequently visit and defend territorial boundaries, otters intensively use and defecate in core areas that are important for foraging, grooming, and constructing holts (dens) (Kruuk 1992; Hutchings and White 2000). Therefore, frequently used latrine sites provide a relative measure of the intensity of use of different latrine sites and their associated habitat characteristics (Hutchings and White 2000). For this reason, researchers have studied otter visitation at latrine sites to assess habitat quality (Prenda and Granado-Lorencio 1996) and fish prey availability (Crait et al. 2015), and to determine the locations of latrine sites relative to the home range of otters (Barocas et al. 2016).

The small-clawed otter (*Aonyx cinereus*) is distributed in South and Southeast Asia, and has been designated a vulnerable species by the International Union for Conservation of Nature (IUCN) (Wright et al. 2015). Although small-clawed otters are common in zoos, their basic ecology is largely unknown in the wild (Wright 2003). Small-clawed otters are carnivores that primarily prey on aquatic animals, such as crabs, fish, frogs, arthropods, mammals, and snails (Kruuk et al. 1994; Aadrean et al. 2010; Hon et al. 2010). Small-clawed otters use a variety of natural and human-altered habitats, including rivers, streams, peat swamps, mangrove forests, rice fields, ditches, and fish ponds (Hussain et al. 2011).

In a protected wetland area in India, small-clawed otters prefer shallow, narrow streams and high-elevation areas rather than deep, large rivers and low-elevation areas (Perinchery et al. 2011; Raha and Hussain 2016). When small-clawed otters use human-altered landscapes, such as coffee and tea plantations adjacent to protected areas, latrine site occurrence is associated with riparian vegetation and the availability of potential refuges (e.g., boulders and fallen logs) (Prakash et al. 2012). Although environmental characteristics of the small-clawed otter latrine sites have been reported for human-altered landscapes (e.g., Prakash et al. 2012), such characteristics have yet to be investigated based on visitation frequency.

In rice field landscapes of some Southeast Asian countries, such as Malaysia, Thailand, the Philippines, and Indonesia, small-clawed otters use rice fields as foraging and latrine sites (Foster-Turley 1992; Aadrean et al. 2010; Gonzales 2010; Kanchanasaka and Duplaix 2011). A previous study in the Malay Peninsula demonstrated that the latrine sites of small-clawed otters occurred in rice fields adjacent to a mangrove mudflat (Foster-Turley 1992). In addition, a preliminary descriptive study in Indonesian rice fields reported that the latrine sites of small-clawed otters were located near rice field huts or trees (Aadrean et al. 2010). However, these previous reports were primarily descriptive studies that only highlighted the potential importance of specific landscape components to latrine site occurrence. Furthermore, these studies did not assess the relative importance of such landscape features relative to other environmental factors. Even though small-clawed otters are a common inhabitant of Satoyama landscapes (a landscape mosaic of secondary forests, grassland, rice fields, cropland, and streams surrounding villages) in Southeast Asia, little information exists concerning their latrine site characteristics in such landscapes.

In this study, we sought to determine which land use factors are important for explaining the occurrence of latrine sites of small-clawed otters in Indonesian rice fields. Because the frequency of visitation to latrine sites may differ depending on local environmental conditions, such as prey availability (Crait et al. 2015), we subsequently investigated which land use and local environmental factors best explain the visitation frequency of small-clawed otters to latrine sites. This study is the first to document the visitation frequency of small-clawed otters to latrine sites. Rice fields differ from natural wetlands in that landscape components and local physicochemical environments are influenced by farming activities. We hypothesized that the occurrence and visitation frequency of latrine sites are related to land use and local environmental factors specific to rice field landscapes. Based on the results, we discuss the importance of developing otter-friendly farming in the face of agricultural modernization and land use changes, which in turn lead to loss of potential otter habitats.

Methods

Study area

The study site was located in rice field landscapes along the Batang Anai River drainage in the Padang Pariaman Regency, West Sumatra, Indonesia (longitude 0°38′00″S–0°40′40″S, latitude 100°17′10″E–100°20′20″E, altitude 25–50 m; Fig. 1; Fig. S1). Climate data from BPS-Statistics Indonesia (2010–2013) indicated that the Padang Pariaman Regency has an average temperature of 25.4 °C (range 22.7–27.3 °C), average humidity of 87.0% (range 82.3–91.2%), and average monthly rainfall of 372.3 mm (range 138.0–853.2 mm), all of which are characteristic of the tropical climate in this region. The substrate of the Batang Anai River adjacent to the study site is dominated by gravel, whereas that of downstream areas is dominated by sand. Gravel and sand mining is regularly conducted along the Batang Anai River by local people. High precipitation and steep slopes, which are typical characteristics of West Sumatra, contribute to high water level fluctuations of the river.

The rice fields included in this study are irrigated by the Anai Dam, which irrigates 13,640 ha of farmland along the river drainage. Prior to construction of the Anai Dam, farmland in this area was irrigated by the Batang Anai River and rainwater via earthen canals and ditches. After the dam and concrete canals were constructed in 1996, both the area of farmland and cropping intensity increased in the entire drainage area. In this study, we only used data from an upper area of the irrigated farmland (Fig. S2), because this area has been surveyed since 2008 (Aadrean et al. 2010). In recent years, many rice fields in the lower areas have been drained and converted to dry farmland (i.e., corn fields

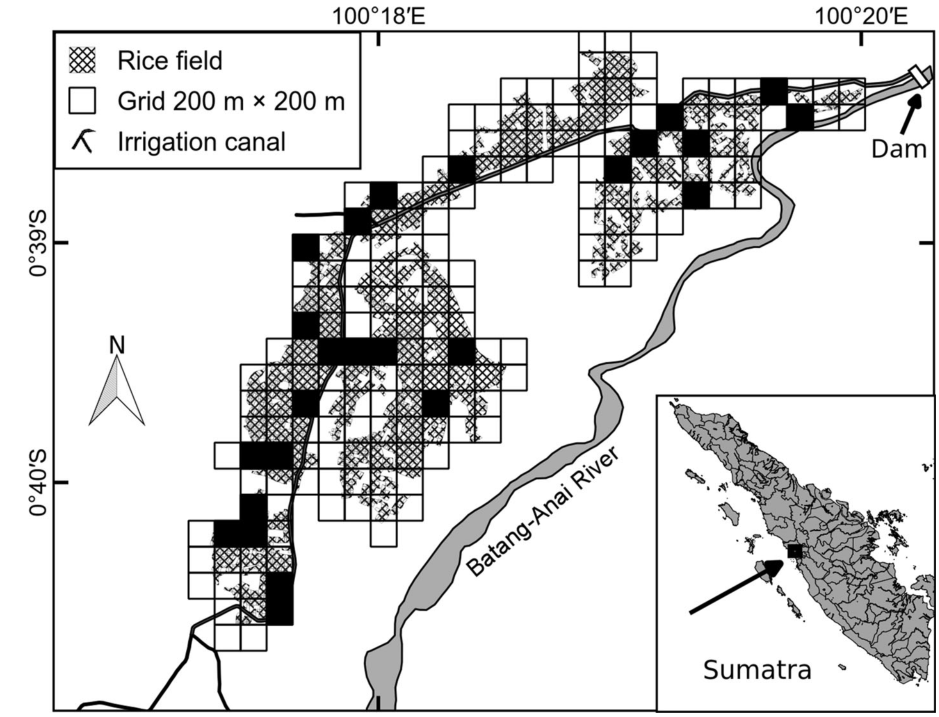

Fig. 1 Study site in the Batang Anai River drainage area in West Sumatra, Indonesia. Each grid is 200 × 200 m. *Filled grids* represent areas where latrine sites of small-clawed otters were found in the 2015 survey (conducted over 53 weeks from April 12, 2015 to April 10, 2016). Small effluent ditches flowing from the rice fields to the river are not shown

and palm oil plantations) or human settlements. Potential otter habitats have presumably been eliminated because such land use changes are associated with the draining of wetland habitats.

In the Batang Anai River drainage, rice fields are planted 2–3 times a year. Farmers can start a new planting cycle any time of year at their discretion. Consequently, different planting phases can be found across the entire landscape throughout the year. Owners of rice fields are smallholder farmers. Most farmers use chemical pesticides and fertilizers, although a few use a mixture of organic and chemical fertilizers. For plowing, farmers use fuel-operated hand tractors. Planting, harvesting, pesticide and fertilizer application, and other farming activities are conducted manually.

Among the four otter species (*Lutra lutra*, *L. sumatrana*, *Lutrogale perspicillata*, and *Aonyx cinereus*) that occur in Sumatra, only small-clawed otters inhabit the study area (Aadrean et al. 2010). Potential food items of small-clawed otters in the rice fields include fish (e.g., *Anabas testudineus*, *Puntius binotatus*, *Clarias batrachus*), mollusks (e.g., *Melanoides tuberculata*, *Tryonia clathrata*, *Pomacea canaliculata*), and frogs (e.g., *Fejervarya cancrivora*, *F. limnocharis*). Although small-clawed otters reportedly feed heavily on *Potamon* and other unidentified crabs (Kruuk et al. 1994; Hon et al. 2010), crabs are absent from earthen ditches and rice fields in the study area. In the Batang Anai River drainage, non-indigenous golden apple snails (*Pomacea canaliculata*) provide an important food source for small-clawed otters (Aadrean et al. 2011).

Field surveys

The occurrence of latrine sites of small-clawed otters was first studied in 2008 and 2010 by walking along ditches and levees adjacent to rice fields (Aadrean et al. 2010). Otter footprints left in the mud of the rice fields also provided guidance to the latrine sites. Owing to the conspicuous smell of spraints (otter scat) and damage to the vegetation of levees or occasionally the rice plants adjacent to latrine sites, local farmers are often aware of latrine site locations; thus, information regarding latrine site locations was also provided by farmers encountered during the field surveys.

The first preliminary survey was performed over a 17-day period between July and December 2008. In 2010, a second preliminary survey was performed over a 19-day period between April and September. These preliminary surveys were only conducted along main levees throughout a wide geographical area in the upper Batang Anai River drainage. In 2015, a thorough, systematic survey was performed over a 32-day period from February–April and August–September throughout the rice fields within a subset of the preliminary survey areas (Fig. 1). In the 2015 survey, we surveyed every individual rice field in the study area along one side of the levee at least once. Because rice fields are arranged in blocks, this procedure allowed us to check, on average, two or more sides (levees) of each rice field. We were also careful to re-survey the old latrine sites. Some of the old latrine sites had been converted to shrubland or roads;

thus, we were only able to re-survey 16 of the 19 old latrine sites in 2015.

During the latrine site survey in 2015, we ground-checked land use classifications with the aid of printed satellite images (see subsection "Land use analysis"). We also used the satellite images to confirm that every individual rice field was surveyed at least once. In addition, we recorded the locations of rice field huts (called "dangau" in the Minangkabau and Bahasa languages) during the field survey because a preliminary study identified several latrine sites adjacent to a rice field hut (Aadrean et al. 2010).

To record the visitation frequency to latrine sites by small-clawed otters, we monitored latrine sites weekly over the 53 weeks from 12 April 2015 to 10 April 2016. Of 29 latrine sites, we removed four newly discovered latrine sites from the visitation frequency analysis, as these four latrines were discovered after August 2015, and therefore could not be monitored all 53 times; these four latrine sites were only used in the occurrence analysis. At each visit, two trained field crews recorded the presence of new spraints. We considered spraints that were located at a certain site in a given week to be one otter visit regardless of the size and number of spraints. To verify that the spraints were new, we collected and removed old spraints when each latrine site was surveyed. The spraints of small-clawed otters are slimy and sticky, and otters smear their spraints when they defecate (Aadrean et al. 2010). When removing spraints, we attempted to avoid removing substrate to retain spraint slime, thereby minimizing artificial disturbances to latrine site use by small-clawed otters.

In the rice field adjacent to each latrine site, we also recorded the mean water depth and golden apple snail biomass as measures of local environmental conditions. All latrine sites were located within 2 m of the nearest rice field. Water depth (cm) was measured from the levee using a ruler at one location along the first row of rice plants near the latrine site. If the bottom of the rice field was uneven, we measured water depth at several points along the levee, and the average value was used to represent water depth. Golden apple snails were collected by first placing a 2-m long rope along the levee and then placing two 20-cm sticks perpendicular to the levee to delineate a quadrat (20×200 cm). Wet weights of golden apple snails were determined using a digital scale to the nearest 0.1 g. Local environments of the rice fields fluctuate along with planting cycles. To infer average annual environmental conditions, water depth and snail weight from the rice field adjacent to each latrine site were each averaged over the 53-week period.

Land use analysis

Before starting the field survey in 2015, we digitized and classified Google Earth satellite images (Google Inc., California, USA) into the following land use types: rice fields, dry farmland, settlement, tree patches, irrigation canals, roads, and other. Although the satellite images allowed us to delineate farmland borders, we could not differentiate rice fields and dry farmland. Therefore, we printed the images and subsequently verified the land use classifications in the field during the latrine site surveys in 2015.

In the land use dataset, we only included areas with tree patches and settlements that were > 225 m^2. We considered roads (width ≥3 m; either gravel or paved) to be those that could be driven by cars. For irrigation canals, we only digitized primary and secondary concrete channels (width > 4 m). For logistical reasons, we were unable to digitize the complex network of earthen ditches and small tributaries of the Batang Anai River. In this paper, we only use maps that were verified in the field.

We conducted geographical information system (GIS) analysis using QGIS ver. 2.6.1 (QGIS Development Team 2014). To calculate the nearest distance from each latrine site to the respective land use, we used the plugin NNJoin ver. 1.2.2 (Tveite 2015).

Data analysis

We constructed statistical models of latrine site characteristics in two steps. First, we modeled the occurrence of latrine sites along the Batang Anai River using grid-based analysis (hereafter, the "occurrence model"). Prior to analysis, we divided the map of the study area into 200×200-m grids. We determined grid size based on the average distance to the nearest latrine sites (230.9 m ± 142.7 SD). Only grids that contained surveyed rice fields were selected; consequently, 189 grids were selected for further analysis. Although the grids were added to maps after the field survey was performed, we were able to determine the presence or absence of latrine sites in each grid based on the individual rice field survey data from 2015. We used a generalized linear model (GLM) to model the occurrence of latrine sites (response variable) with seven land use variables as predictors (Table 1). We treated the response variable as having a binomial distribution with logit link. Because we used the satellite map from 2015, we only used the latrine site occurrence data from the 2015 field survey in the occurrence model.

Second, we modeled the visitation frequency of small-clawed otters to the latrine sites using a point-based analysis (hereafter, the "frequency model"). We defined otter visitation frequency to latrine sites as the number of times spraints were found in a certain location during the 53-week period. We used the number of visitations as the response variable and the land use and local environmental variables as predictors (Table 1). We treated the response variable as having a negative binomial distribution and a log link.

In both models, we initially checked the normality assumption for each predictor using the Shapiro–Wilk normality test. When the normality assumption could

Table 1 Predictor variables used in two generalized linear models to investigate the occurrence of small-clawed otter latrine sites (the occurrence model) and visitation frequency of small-clawed otters to the latrine sites (the frequency model)

Variable	Description	Mean	SD	Range	Transformation
Occurrence model					
ricefieldprop	Proportion of rice field area in the grid	0.45	0.30	0.00–1.00	$\arcsin(\sqrt{x})$
treeprop	Proportion of tree patch area in the grid	0.09	0.10	0.00–0.42	$\arcsin(\sqrt{x})$
streetsettleprop	Proportion of street and settlement areas in the grid	0.13	0.19	0.00–1.00	$\arcsin(\sqrt{x})$
canalprop	Proportion of canal area in the grid	0.02	0.04	0.00–0.16	$\arcsin(\sqrt{x})$
dryfarmprop	Proportion of dry farmland area in the grid	0.04	0.06	0.00–0.32	$\arcsin(\sqrt{x})$
hutnumber	Number of rice field huts in the grid	0.75	1.10	0–6	None
gridriverdist	Nearest distance (m) from the centroids of the grids to Batang Anai River	1141	564.1	15.6–2377.0	None
Frequency model					
Landscape factors					
dryfarmdist	Linear distance (m) to the nearest dry farmland	132.5	95.5	32.8–421.2	$\log(x)$
treedist	Linear distance (m) to the nearest tree patch	74.8	68.0	0.0–257.8	$\sqrt[4]{x}$
streetdist	Linear distance (m) to the nearest street	170.3	77.7	52.4–304.4	None
riverdist	Linear distance (m) to the Batang Anai River	1204.0	595.5	82.2–2258.0	None
canaldist	Linear distance (m) to the nearest irrigation canal	162.0	142.5	9.3–555.0	$\sqrt[4]{x}$
settlementdist	Linear distance (m) to the nearest settlement	97.1	77.1	0.0–292.6	$\sqrt{x}$
hutdist	Linear distance (m) to the nearest rice field hut	73.2	79.6	0.0–243.1	$\sqrt[4]{x}$
Local environmental factors					
watermean	Mean water depth (cm) of an adjacent rice field (over 53 weeks)	1.66	0.80	0.79–4.51	$\frac{1}{x}$
snailweightmean	Mean weights (g) of golden apple snails in an adjacent rice field (over 53 weeks)	8.06	6.77	0.63–21.32	$\sqrt[4]{x}$

Transformation refers to the type of data transformation used to normalize the predictor variable

not be met, we performed arcsine-square-root, log, fourth-root, square-root, or multiplicative inverse transformations (Table 1). Appropriate data transformations for predictors used in the visitation model were determined based on Box–Cox log-likelihoods (Dormann 2011). The predictors of the visitation model were subsequently standardized by scaling and centering. We checked for collinearity among predictors in all models; no predictors were highly inter-correlated (Pearson correlation analyses: all $r < 0.7$). When necessary, we included polynomial degrees of a predictor variable based on scatter plots.

We selected the best model using backward stepwise selection based on Akaike's Information Criterion correction for small samples (AIC_c). The model with the smallest AIC_c was considered the best model. When two or more models had small differences in AIC_c values from the model with the smallest AIC_c ($\Delta AIC_c < 2$), we selected the most parsimonious model (i.e., fewest parameters) (Burnham and Anderson 2004).

We performed Moran's I test to examine whether spatial autocorrelation existed in the residuals of the respective best models (Dormann et al. 2007). For all cases, there was no evidence of spatial autocorrelation (Moran's I: $P > 0.1$).

We assessed model performance using explained deviance (D^2), calculated as 1 − (residual deviance/null deviance) (Guisan and Zimmermann 2000). When more than one predictor was retained in the refined model, we compared D^2 for the models that excluded each predictor to that of the full model to infer the relative contributions of predictors to the response variable (expressed as ΔD^2).

We conducted all statistical analyses using R freeware (R Core Team 2016). We used the MASS package to compute and plot profile log-likelihoods for the parameters of the Box–Cox power transformation, and to fit the negative binomial GLM (Venables and Ripley 2002). We also used the spdep package to compute Moran's I statistics to test for spatial autocorrelation (Bivand and Piras 2015) and the MuMIn package to calculate AIC_c values (Bartoń 2016).

Results

Latrine sites

Of the 29 latrine sites, 13 were newly discovered in 2015, and 16 were old latrine sites from the 2008 or 2010 surveys (10 sites from 2008 and six from 2010). The average number of visitations by small-clawed otters to the latrine sites was 11.9 ± 10.0 SD (range 0–29, $N = 25$). One old latrine site was no longer used, and four old latrine sites were only visited once each during the 53 weeks. The visitation frequency to the latrine sites did not significantly vary with the year of first discovery of the latrine sites (Kruskal–Wallis rank sum test: $\chi^2 = 0.72$, $P = 0.70$; Fig. S3).

Occurrence model

We found latrine sites of small-clawed otters in 25 of 189 grids (Fig. 1). Based on model selection among nine candidate models using AIC_c in the GLM, the number

Table 2 Parameter estimates of the best occurrence models and frequency models

Model covariate	Estimate	SE	z value	P value	K[a]	AIC$_c$	ΔAIC$_c$	Weights
Occurrence model								
Occurrence ~ canalprop + hutnumber – hutnumber^2					3	139.43	0	0.3405
Intercept	−3.0196	0.4359	−6.927	< 0.0001				
canalprop	2.6434	1.5319	1.726	0.0844				
hutnumber	1.7100	0.5601	3.053	0.0023				
hutnumber^2	−0.3507	0.1646	−2.131	0.0331				
Occurrence ~ hutnumber – hutnumber^2					**2**	**140.16**	**0.73**	**0.236**
Intercept	−2.7612	0.3899	−7.082	< 0.0001				
hutnumber	1.7100	0.5563	3.074	0.0021				
hutnumber^2	−0.3636	0.1639	−2.219	0.0265				
Occurrence ~ canalprop + treeprop + hutnumber – hutnumber^2					4	140.26	0.83	0.2245
Intercept	−3.4852	0.6285	−5.545	< 0.0001				
canalprop	2.9589	1.5666	1.889	0.0589				
treeprop	1.3812	1.2244	1.128	0.2593				
hutnumber	1.9210	0.6095	3.152	0.0016				
hutnumber^2	−0.3999	0.1781	−2.246	0.0247				
Frequency model								
Frequency ~ settlementdist – watermean – riverdist					**3**	**174.85**	**0**	**0.4649**
Intercept	2.2309	0.1643	13.578	< 0.0001				
settlementdist	1.0690	0.2559	4.178	< 0.0001				
watermean	−0.4438	0.1708	−2.598	0.0094				
riverdist	−0.5639	0.2308	−2.444	0.0145				
Frequency ~ settlementdist – watermean + hutdist – riverdist					4	176.51	1.66	0.2032
Intercept	2.1992	0.1590	13.835	< 0.0001				
settlementdist	1.1558	0.2673	4.324	< 0.0001				
watermean	−0.4683	0.1645	−2.847	0.0044				
hutdist	0.2207	0.1611	1.370	0.1706				
riverdist	−0.6534	0.2330	−2.804	0.0050				

Bold-faced font indicates the best model based on the lowest ΔAIC$_c$ (Akaike's Information Criterion correction for small samples) and the most parsimonious model (fewest variables among models with ΔAIC$_c$ < 2). Note that the watermean was inverse-transformed ($1/x$) using Box–Cox transformation; a negative value in the estimate represents a positive value in the actual relationship. See Table 1 for abbreviations of the predictors

[a]Number of parameters

of rice field huts was the sole variable that explained the occurrence of small-clawed otter latrine sites (Table 2; Table S1). Latrine site occurrence exhibited a non-linear relationship with the number of huts; occurrence was positively associated with the number of huts, but negatively associated with the squared number of huts. Consequently, latrine sites had the highest probability of occurring with an intermediate number of huts (two or three) (Fig. 2). D^2 of the best model was 0.09.

Frequency model

Based on model selection among 10 candidate models, distance to the nearest settlement, distance to the Batang Anai River, and mean water depth of the rice field adjacent to a latrine site were the most important predictors that explained the visitation frequency of small-clawed otters to the latrine sites (Table 2; Table S2). The visitation frequency to the latrine sites was positively associated with distance to the nearest settlement and mean water depth, but negatively associated with distance to the Batang Anai River (Fig. 3). D^2 of the best model was 0.41. Among the three predictors, distance to the nearest settlement exhibited the highest contribution to D^2 (ΔD^2 = 0.31), followed by mean water depth (0.16) and distance to the Batang Anai River (0.14).

Discussion

Effects of land use and local environmental factors on latrine site occurrence and visitation frequency of small-clawed otters

We found that the small-clawed otter latrine sites were related to both landscape- and local-level environmental characteristics of rice fields. According to the occurrence model, the number of rice field huts was non-linearly related to latrine site occurrence, with latrine sites occurring with the highest probability in the presence of an intermediate number of huts. The number of rice field huts was the sole important variable that explained latrine site occurrence. Furthermore, nine of 25 (36%) latrine sites were located near a rice field hut (distance < 3 m). In Sumatra, rice field huts are used by farmers as shelters; to guard rice from wildlife; to rest or have lunch; and/or to temporarily store fertilizers, pesticides, and farming equipment (Kato 1978). Rice field huts are usually built near earthen irrigation ditches, which may

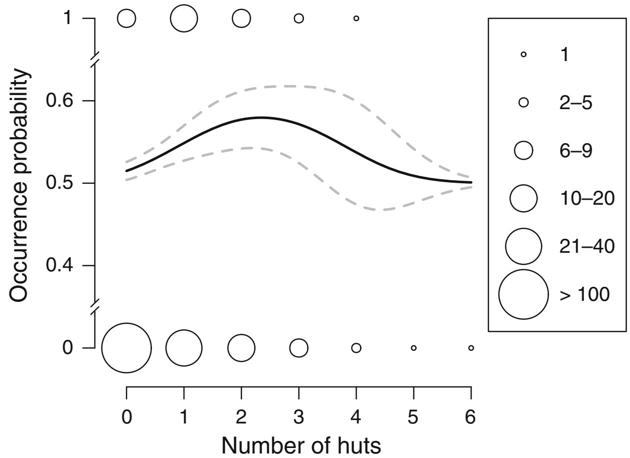

Fig. 2 Relationship between the number of huts and latrine site occurrence of small-clawed otters. The *solid line* indicates the predicted value. *Grey dashed lines* indicate approximate 95% confidence limits (±2 standard errors of the generalized linear model fit). *Open circles* indicate the distributions of raw data. *Circle* size is proportional to sample size (number of grids)

provide foraging sites for small-clawed otters. Moreover, the raised floors of rice field huts may provide temporary refuge for otters against sudden encounters with humans, and serve as an equivalent to fallen log refuges in natural habitats (Swimley et al. 1998; Anoop and Hussain 2004; Prakash et al. 2012). In addition, open grassland areas around rice field huts may provide suitable locations for grooming sites (Shenoy et al. 2006). Therefore, rice field huts may serve as important foraging, refuge, and grooming sites for small-clawed otters. However, a trade-off exists between larger numbers of huts and the intensity of human activities; that is, large numbers of rice field huts indicate intense human activities in these landscapes. Therefore, a landscape that contains an intermediate number of rice field huts may be an ideal location for small-clawed otter latrine sites.

Bridges are another land use feature that serve as important latrine sites for small-clawed otters (Reuther et al. 2000). Therefore, bridge surveys have become a standard survey method for otters (Gallant et al. 2008; Stevens et al. 2011; Just et al. 2012). A hut survey could also serve as a standard survey method for assessing the occurrence of small-clawed otters in rice field landscapes where large bridges are absent or rare.

The frequency model revealed a positive relationship between the visitation frequency of small-clawed otters to the latrine sites and mean water depth of the adjacent rice field. Annual mean water depth is an indicator of water availability in the rice field. Because small-clawed otters generally feed on aquatic animals (Kruuk et al. 1994), dry rice fields may be unsuitable as foraging sites. These results are consistent with the findings of Prenda et al. (2001), who reported that Eurasian otters in Mediterranean streams are usually found at sites inundated by water during the dry season.

The visitation frequency of small-clawed otters to the latrine sites was also positively associated with distance to the nearest settlement. In Eurasian otters (*Lutra lutra*), sprainting activities, which were assessed by the number of spraints found along a transect, tend to be low in urban areas where land conversion or other human activities are intense (Prenda and Granado-Lorencio 1996). Although our study was conducted in human-altered landscapes, small-clawed otters appear to use sites that are relatively distant (approximately 300 m) from settlements frequently to avoid direct encounters with humans (Fig. 3). Light emitted by settlements may also disturb otter behavior, as these animals are generally crepuscular or nocturnal (Hussain et al. 2011).

Another landscape factor that was strongly associated with latrine visitation frequency by small-clawed otters was distance to the river. Because small-clawed otters typically prefer narrow streams to wide rivers (Perinchery et al. 2011; Raha and Hussain 2016), we hypothesize that small-clawed otters use the river as a corridor to travel across rice field landscapes rather than

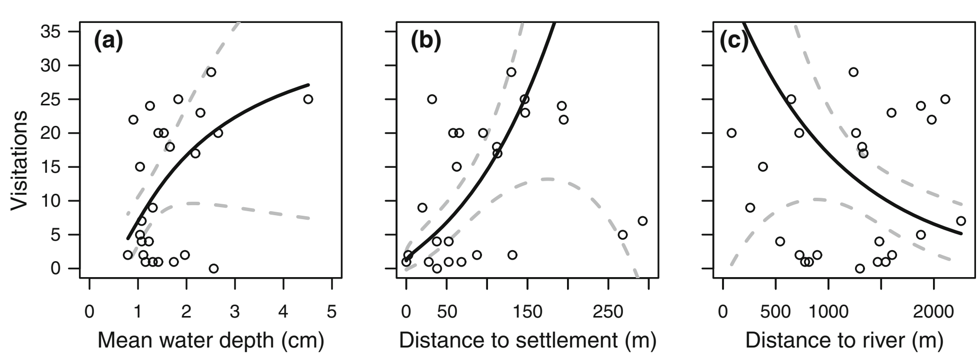

Fig. 3 Relationships between small-clawed otter visitation frequency to latrine sites and mean water depth of the rice field adjacent to the latrine site (**a**), distance to a settlement (**b**), and distance to the Batang Anai River (**c**). The *solid lines* indicate predicted values. *Grey dashed lines* indicate approximate 95% confidence limits (±2 standard errors of the generalized linear model fit). The predicted value and confidence limits for each predictor were calculated from the parameter estimates of the best model when the remaining predictors were set to the mean values. Note that the predictors were back-transformed to show the actual associations with the response variables. *Open circles* indicate raw data

as a primary habitat. Because we have no information about the home range of small-clawed otters, this hypothesis should be tested in the field using telemetry.

A limitation of this study was the predictive performance of the occurrence model. Although various land use factors were included in the occurrence model, the D^2 of the best model was only 0.09. However, both linear and squared terms for the number of huts showed significant associations with latrine site occurrence ($P < 0.05$) in the GLM (Table 2). We hypothesize that the occurrence of latrine sites might be more significantly associated with finer-scale land use factors, such as the network of earthen ditches, small tributaries of the Batang Anai River, small patches of native shrubs, or the presence of swamps or abandoned fish ponds; none of these features could be quantified using the current coarse resolution maps. Choosing an appropriate spatial scale to determine latrine site occurrence may also be important, as species responses to landscape or land use factors are scale-dependent (e.g., Usio et al. 2017). These points warrant further exploration in future studies using finer-scale satellite or aerial maps, along with field evaluations and multi-scale land use analysis. Furthermore, although we ensured that we surveyed each grid, we cannot eliminate the possibility of pseudo-absence, because new latrine sites might have appeared after the one-time survey took place. To minimize or avoid the influence of pseudo-absence, presence-absence surveys should ideally be performed multiple times at each sampling unit (grid) (MacKenzie et al. 2006), or a presence-only modeling technique, such as Maximum Entropy Modeling (MaxEnt; Phillips et al. 2006), should be used.

Latrine site fidelity of small-clawed otters

We revealed that small-clawed otters tend to use some latrine sites over long periods of time, as 10 latrine sites were used for more than 7 years. This was rather surprising, because landscape features change dramatically over the year based on rice cultivation cycles.

In captivity, latrine sites of small-clawed otters are first chosen by the alpha male (Alana Dewar, *pers. comm.*). After the alpha male dies, the group continues to use the latrine site, and his position is filled by another male in the group. Even though spraints are regularly removed and cleaned, the group still uses a similar location as the latrine site, but the exact location changes gradually over time. The otter latrine sites are even likely passed on to the next generation, as several latrine sites of African clawless otters (*Aonyx capensis*) discovered in 1972 were still used after more than 40 years (Rowe–Rowe 1992; Kubheka et al. 2013). Therefore, records of the exact locations of latrine sites may be useful for future monitoring of latrine site use by small-clawed otters in rice field landscapes, unless drastic environmental changes take place.

Implications for otter conservation

Rice fields may serve as an alternative wetland habitat for various types of aquatic and semi-aquatic wildlife, including endangered species (Bambaradeniya and Amarasinghe 2002; Usio and Miyashita 2014). Our study indicates that rice fields provide important latrine sites for small-clawed otters. Nevertheless, how and to what extent modernization of agriculture, such as intensive use of agrochemicals and large machinery, affects small-clawed otters remains unknown. Modernization of agriculture in paddy-dominated landscapes has dramatically increased agricultural production (Food and Agriculture Organization of the United Nations 2000); however, such agricultural intensification has caused severe declines in biodiversity in rice field landscapes (Natuhara 2013). For example, in Japanese Satoyama, overuse of agrochemicals, farmland consolidation, and cementing of the bottom and sides of irrigation ditches have led to losses of aquatic biota from rice field landscapes and accelerated biological magnification of toxic chemicals (Miyashita et al. 2014). Such combinations of multiple stressors, in turn, have led to extinctions of the crested ibis (*Nipponia nippon*) and Oriental white stork (*Ciconia boyciana*), which were once widely distributed throughout Japan (Usio and Miyashita 2014).

Indonesia is currently experiencing human overpopulation; hence, increased food production through agricultural modernization is unavoidable. Natural wetlands have been disappearing at an accelerated rate because of their conversion to palm oil plantations (Margono et al. 2014). In addition, changes in land use or farming practices have led to losses of aquatic and semi-aquatic organisms that use rice fields as foraging or refuge sites. Furthermore, the System of Rice Intensification (SRI), in which less water is used during rice cultivation, is being promoted in Indonesia (Wardana et al. 2015). Although the SRI protocol encourages the use of organic pesticides and fertilizers, shallow-flooding practices may produce detrimental effects on aquatic biodiversity, including small-clawed otters. Given these threats, we emphasize the need for the design of otter-friendly rice-farming practices before small-clawed otters completely disappear from the region.

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