Occupancy estimation of wild species in a palm oil plantation using unstructured data

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Abstract

In 2020-2024, plantation workers at a large oil palm plantation in West Kalimantan recorded

sightings of wild species of several species groups. They did not use a standardized field

method and produced no comprehensive reports, but recorded only one or a few species per

visit. Such unstructured data are generally viewed as challenging for statistical analysis. Here,

we used occupancy models to estimate what proportion of spatial units (both non-natural and

forest) a given species occupied annually in the plantation. Models with different covariates

were tested for species for which most data were available: 13 birds, 7 mammals, among

which the iconic Orangutan *Pongo pygmaeus,* and 3 reptiles. For each species, the model

which best fitted the data was selected. Two shortcomings in our data complicated the

analyses. First, occupancy models require detection and non-detection records, but because

no fixed species lists were used, there is no unique way to generate non-detections. We

generated non-detection records in several ways and ran the models again to evaluate the

consequences for occupancy estimates. Second, imbalances in sampling may occur because

of a lack of sampling design to select study sites. Most concerning are sites were surveyed

only once in 2020-2024. We ran the models without those sites to examine whether results

were different. Although the shortcomings mentioned turned out not to distort our results, the

occupancy estimates were imprecise for many study species because of low detection rates,

and extra efforts are needed to improve that.

Introduction

The expansion of oil palm (*Elaeis guineensis* Jacq.) plantations in tropical areas affects wildlife negatively (Fitzherbert *et al.* 2008; Meijaard *et al.* 2018; Marsh *et al.* 2025). Over time, the palm oil industry has been increasingly willing to mitigate the negative effects by taking protection and management measures. Examples are setting aside areas with High Conservation Values (HCV-areas) which are protected against illegal logging, burning and land-clearing (HCV Resource Network 2017) and the protection of "forest islands" within plantations (Paterno *et al.* 2024).

Effective biodiversity protection and management measures require detailed knowledge about local wildlife, but collecting sufficient local data is often hard in tropical areas (Maharani *et al*. 2025). Furthermore, protection and management measures are more likely to succeed if there is considerable support among plantation workers and other stakeholders. We believe that both obtaining more data and increasing support can go hand in hand by encouraging plantation workers and others to collect sighting records of wild species.

For these two reasons, in 2019, the Indonesian oil palm company Austindo Nusantara Jaya (ANJ) launched a special program, called PENDAKI which is the Indonesian acronym for Care for Biodiversity, to stimulate the recording of sightings of wild animals and plants by plantation workers in their concessions (Maharani *et al*. 2025). One of these areas is the KAL ("Kayung Agro Lestari") oil palm estate in West Kalimantan. This estate contains hundreds of production blocks planted with oil palms and several small forest islands (total area 9583 ha; Fig. 1). The estate also includes several large HCV-areas (together 3845 ha) with remnants of the original tropical moist forest. Since 2019, many observers have participated in the program to collect wildlife data, both in the planted areas and in the HCV-

areas. To enable everyone to participate, there are hardly any rules that observers must adhere

to. For each sighting, location (identity of production block or forest site), date and species

must be noted, as well as the number of individuals observed. Apart from this, there is no

prescribed, standardized field method and most of the records are casual sightings.

To make these data usable for the management of plantations, the collected data need

to be converted into relevant information, such as local differences in occurrence of species

or in species diversity, which may then be related to environmental factors or management

practices. Unfortunately, retrieving reliable information from casual sightings is challenging.

Data as collected here are referred to in the scientific literature as unstructured or

opportunistic data. (Van Strien *et al.* 2013; Kamp *et al.* 2016). Such data are collected by

volunteer observers in many countries around the world and are also known as citizen science

data (Silvertown 2009).

Because the field method is unstandardized, it is difficult to determine whether the

difference in occurrence between two locations is real or is due to one location being more

intensively studied than the other. For unstructured data, it is therefore mandatory to adjust

for variation in field effort. This is not an easy task, especially if there is no information at all

available about the field effort applied, as in the current study. It is extremely difficult to

derive inferences on abundance of species from unstructured data (though see Johnston *et al.*

2025), but it is often feasible to estimate occupancy, *i.e.*, the proportion of spatial units

occupied by the species. Analyses of unstructured data are particularly successful when

occupancy models are used (Kéry *et al.* 2010; Van Strien *et al.* 2013; Isaac *et al.* 2014;

MacKenzie *et al.* 2018). But not all applications have been fruitful (Kamp *et al.* 2016), and

much will depend on the dataset available.

Our ultimate goal is to apply citizen science data with occupancy models on a routine

basis to support nature management in large plantations in tropical regions (Maharani *et al.*

2025). This is an ambitious goal and as far as we know we are the first to scientifically

explore this. Here we report on the first steps towards that goal. The aim of this paper is to

develop custom occupancy models for species living in an oil palm plantation and to test

whether several complications in the data might distort the results.

Material and methods

Area and data

Defining the production blocks and forest sites in the KAL as our sampling sites, we

distinguish 463 sites in the KAL-area, 21 of which are completely covered with forest. The

latter are not only the large HCV areas mentioned earlier, but also smaller forest islands

within the estate which are not in use for palm oil production (Fig. 1). The other sites (from

now on referred to as non-natural sites) are dominated by oil palms and infrastructure, but

may also contain ponds, waterways and small patches of forest regrowth. The surface area of

the non-natural sites is 30 ha on average but varies between sites (Fig. 1). Most forest sites

are considerably larger, especially the HCV-sites, which unfortunately could not be split into

smaller subsites because sightings in the HCV-sites were not precisely localized.

More than 400 observers provided data. Observers were allowed to record any species

group they wanted. But because most records cover five species groups only - namely birds,

mammals, reptiles, higher plants (*i.e.*, only *Magnoliopsida*) and insects (mainly butterflies

and dragonflies), - we focused on these groups, abandoning data on other groups. This is our

standard dataset, in which records are available from 387 sites for the 2020-2024 period. For

about 200 sites, annual records are available (Table 1). On average, sites were visited 6-8

times per year (see Nvisits per site in Table 1), often by different observers who typically

reported only one or a few species (rarely > 10) per visit (see List length in Table 1). Some

sites which were never surveyed; these are mainly situated in recent plantings at the western

and eastern border of the estate. Records of the same species on the same date and site

collected by different observers were deduplicated because these may refer to the same

sighting as observers are frequently in the field together.

Occupancy models

Occupancy models aim to estimate occupancy of a species while considering the detection

probability (MacKenzie *et al*. 2018). This means that a different detection probability of a

species due to differences in *e.g.* field effort, observer experience or species abundance, does

not translate into a different occupancy estimate of the species (Kéry *et al*. 2010). This can be

particular useful for unstructured data because these models may still be able to properly

estimate occupancy even when no standardized field method has been used and no

information about field effort is available (Kéry *et al.* 2010; Van Strien *et al.* 2013; Isaac *et*

al. 2014). To be able to separate occupancy from detection, occupancy models consist of two

hierarchically coupled Generalized Linear Models (GLMs), one to describe the true state of

sites (presence or absence) and one to describe the detection in sites, given that the species

does occur (MacKenzie *et al*. 2018). Both submodels may be made a function of covariates,

which help to meet model assumptions that both occupancy and detection must be either

constant across sites and visits or otherwise differences should be modelled (MacKenzie *et al.*

2018). Covariates also offer opportunities to examine their effects on occupancy and

detection.

The occupancy submodel estimates the annual proportion of occupied sites in the

statistical population represented by the sampled sites. We estimated annual occupancy using

a multi-season model for single species (Doser *et al.* 2022b). Our most comprehensive

submodel is specified as follows:

$z_{it} \sim \text{Bernoulli}(\psi_{it})$

[1]

$\text{logit}(\psi_{it})$ = intercept + year + habitat of site + distance to large forest + site size   [2]

where z_{it} is the estimated occupancy (0 or 1) and ψ_{it} represents the occupancy probability of

the species in site i and year t. Occupancy is modelled as a function of an intercept, year,

habitat of the site, distance of the site to large forest and site size. Habitat of the site can be

forest or non-forest; forest is taken when the site is a forest site or a non-natural site with a

forest patch. Distance to large forest represents the distance of the center of a site to the

nearest large forest areas; these are either forests around the estate or the HCV-areas within

the estate. Site size is included to adjust for variation in surface area of the sites. Our main

interest is in the annual occupancy estimates which we assessed for each species by summing

the estimated z_i values over sites and year (finite sample occupancy; MacKenzie *et al.* 2018).

The detection submodel estimates detection per visit and the most comprehensive

model is specified as:

$y_{ijt} \sim \text{Bernoulli}(p_{ijt} \times z_{it})$

[3]

$\text{logit}(\text{detection})$ = intercept + list length + habitat of observation + observer

[4]

in which the observations y_{ijt} indicate that the species was detected ($y_{ijt} = 1$) or not ($y_{ijt} = 0$) at

location i during visit j in year t. The observations are considered as the product of occupancy

z_{it} and the probability p_{ijt} of detecting the species in location i during visit j in year t.

(MacKenzie *et al.* 2018). Detection is modelled as a function of an intercept, list length,

observer and habitat of observation. There are no year effects in this model because data were

too sparse to estimate reliable detection estimates which vary between the years. Length of

species lists per visit was used as covariate because we expected lower detections in shorter

lists. We did not apply list length categories (as in Van Strien *et al*, 2013) but used list length

as a linear detection predictor. Habitat of the observation can be forest or non-forest; forest is

taken when the observation was in a forested part of a site; a species may be more difficult to

spot there. Observer identity was modelled as a random effect to take into account the

variation in detection between observers (Schmidt *et al.* 2023). Estimating detection p is only

possible if repeated visits are available for at least some sites (MacKenzie *et al.* 2018). The

replicated visits need to be done in a period of closure, meaning that the state of all locations

(occupied or not occupied) has not changed during the period between the visits. In contrast

to studies using European data (*e.g.,* Van Strien *et al.* 2013), we here consider an entire

calendar year as the closure period, thereby assuming that the study species reside in the area

all year round. This does not necessarily mean that a species is present in a site during the

entire year, but rather that a species may use the site year-round (MacKenzie *et al.* 2018). Our

preliminary analyses showed no effect of Julian date on detection, so we did not include

Julian date as a covariate in the model.

Occupancy models require detection and non-detection records while our dataset only

contains presence records (detections) of five species groups. We created a non-detection

record for all species of these five groups not being observed during a field visit (Van Strien

et al. (2013). We ran the models in a Bayesian framework using the R-package *spOccupancy*

(Doser *et al.* 2022) in R v. 4.3.3 (R Core Team, 2024). All quantitative covariates (distance to

large forest, site size and list length) were standardized to have mean 0 and standard deviation

1 (Doser *et al.* 2022). *spOccupancy* allows to account for spatial autocorrelation of

occupancy sites, which may be useful for our study area where sites are adjacent to each

other. Unfortunately, the large inaccuracy in the locations of observations within the large

HCV-sites made it impossible to apply a spatially explicit model. With the covariate distance-

to-large-forest, however, we included a variable in the model describing spatial gradients in

the study area.

More than 300 different species of the five species groups were reported in 2020-

2024, but for the majority of them too few presence records have been collected to allow

statistical analysis. Models were only run for species with at least five presence records each

year and more than 150 records in total. These were 23 species: 13 birds, 7 mammals and 3

reptiles. To find the model which best fitted the data, we ran 18 different models per species.

In these models, one or several covariates were omitted from the model described by [2] and

[4] (see Table S1 for an overview of the 18 models). The model with the lowest value of the

Widely Applicable Information Criterion (WAIC) was considered the best model (Doser *et*

al. 2022). For these top models we performed posterior predictive checks to compute

Bayesian *p*-values as a measure of model fit. More specific, following the recommendation of

Doser & Kéry (2022), we used both the Freeman-Tukey statistic and the Chi-Square statistic,

and grouped the data across sites as well as across replicates. Ideally, each Bayesian *p*-value

is around 0.5.

We adopted the default priors of *spOccupancy* and ran the models with three parallel

Markov chains of 60,000 iterations each, discarding the first 50,000 as burn-in and a thinning

rate of 10. A parameter was considered significant when the 95% Bayesian credible interval

(CRI) of the posterior sample of a parameter did not include 0. The standard deviation of the

sample from the posterior distribution of parameter was interpreted as standard error of that

parameter.

Alternative datasets

We created several alternative datasets to study the effect of two complications in the data

and applied the same 18 models as for the standard dataset. Firstly, observers did not make

complete checklists of species groups, nor did they use a fixed list of species to consider.

Consequently, there is no unique way to generate non-detection records. If an observer only

noticed, say, plant species, and ignored any sighting of the other four species groups, non-

detections generated for other species groups are not justified. To examine if this affects

occupancy estimates, we created three alternative datasets differing in the way non-detections

were created: (1) we filtered data from the three most often reported groups (birds, mammals

and reptiles) and discarded records from higher plants and insects. This implies that we

generated non-detections for our 23 study species only from sightings of birds, mammals and

reptiles and no longer from plants and insects, (2) in addition to using only data from these

three species groups, we included only observers with records of the same species group as

the study species. So, if the study species were a mammal, only sightings of observers

reporting mammals were used to generate non-detections and the same goes for birds and

reptiles; (3) in addition to using data from three species groups, we included only observers

who had recorded all three species groups, thereby further reducing the number of observers

(Table 2). The three extra datasets are called (1) Nondet3grp, (2) Nondet3grp+obs1grp and

(3) Nondet3grp+obs3grp and occupancy results were compared with those of the standard

dataset. All filtering actions reduced the number of non-detections, and to a lesser extent also

the number of detections (Table 2).

Secondly, unstructured data as our dataset not only lack a standardized field method

but also have no sampling design to properly select study sites. In our case, forest sites and

non-natural sites surrounding forest sites have been oversampled, so the measurements might

not be representatives for the entire estate (Boyd *et al.* 2023). On the other hand, data came

from almost the entire area, which does not suggest obvious spatial bias. There is, however,

an imbalance in sampling which we are concerned about: 108 sites (28% of all 387 sites)

have only been surveyed in one year, most frequent in 2024. If the differences in occupancy

between 2020 and 2024 would depend on the sites that were surveyed only once, then we

have no convincing evidence of a change. To check this, we created two more datasets: one

in which all sites surveyed in one year only were deleted (Remove_sites1year) and one in

which sites visited only in 2024 were deleted (Remove_sites2024), and compared annual

occupancies. Obviously, these two datasets contain fewer sites than the standard dataset

(Table 2).

Results

Standard dataset

Almost all models applied to the standard dataset converged according to the Gelman-Rubin

Rhat statistic (Rhat < 1.1). Only nine out of 414 models (18 different models * 23 species)

did not converge in all parameters, most frequently not in case of *Spilornis cheela,* a raptor

bird species. The top model according to the WAIC-value varied between species (Table 3).

For several species, the most comprehensive model (model 1 in table 3) fitted best, for

example in case of *Hylobates albibarbis* (Gibbon) and *Pongo pygmaeus* (Orangutan). For

other species simpler models performed better, *e.g.*, for *Liopeltis tricolor*, a snake species.

The top model for the latter species contained only effects of site size, species list length and

observer and no ecological variables at all. The Bayesian *p*-values produced by three out of

the four tests for the top models were mostly between 0.2-0.75, suggesting a reasonable fit.

But for half of the species *p*-values < 0.2 were obtained according to the Freeman-Tukey test

when data were grouped across sites (Table 3).

Detection probability varied between species, with *Varanus salvator* (a large monitor

lizard) having the highest rate of 0.26 (Table 3). This means that *Varanus salvator* has been

reported during one-quarter of the visits to occupied sites. Here, a visit stands for a single

visit of an average observer collecting a species list of mean length outside forest habitat. For

most species detection is low, frequently even below 0.1 (Table 3). Detection increased with

longer species lists (Table 3; see example in Fig 2A). In line with our expectation, many

species appeared to be less visible in forest habitat, such as *Centropus sinensis*, a cuckoo

species (Table 3), although this may also be because these species spend less time in forest

habitat. In contrast some others were better detectable in forest habitat or spend more time in

forest habitat, *e.g.*, *Macaca nemestrina* (a monkey species). Furthermore, observer effects

were relevant for all species, as we already suspected. Models without observer effects

consistently finished low in the model selection.

Mean probability of occupancy of *Varanus salvator* is 0.97 (Table 4), suggesting that

this species makes use of the entire study area. *Pongo pygmaeus*, for example, has a much

lower mean occupancy of 0.26. Several species benefitted from the availability of forest

habitat in the site including *Macaca nemestrina*, *Macaca fascicularis* and *Pongo pygmaeus*

(Table 4). Furthermore, the distance to the nearest large forest affected the occupancy

probability for about half of the species. Not surprisingly, *Hylobates albibarbis* had a

significantly higher occupancy in sites with forest habitat and situated in the vicinity of large

forest areas (Table 4; Fig. 2B), and the same applies to *Pongo pygmaeus*. Some other species,

however, achieved their highest occupancy rate further away from the large forest, *e.g.*,

Spilopelia chinensis, a dove species). For almost all species, occupancy was higher in larger

sites (Table 4). Fig. 3 shows examples of annual occupancy, for *Pongo pygmaeus* and

Amaurornis phoenicurus (a waterbird species).

Alternative datasets

The models converged somewhat less often in the alternative datasets than in the standard

dataset. To enable comparisons between datasets, we did not delete any of the species from

the results. Often but not always the same model was selected as top model in the alternative

dataset as in the standard set (Table S2). Mean detection in 2020-2024 derived from the three

datasets with alternative procedures to generate non-detections was significantly higher than

when based on the standard dataset (Fig. 4A; paired t-tests; P<0.05; n=23). This is not

unexpected because the three alternative datasets all have fewer non-detection records than

the standard data (Table 2). Mean occupancy estimates in 2020-2024, however, did not differ

between those derived from the standard dataset and those based on the three alternative

datasets (Fig. 4B; paired t-tests; P>0.05; n=23). Thus, the occupancy estimates do not appear

to depend on the exact way non-detections were generated.

The two datasets created to study removal of poorly surveyed sites produced similar

detection and occupancy estimates as found for the standard data (Fig. 4A & B; paired t-test;

P>0.05; n=23). Also, differences between 2020 and 2024 derived from these datasets were

strongly correlated with those based on the standard data (Pearson's r > 0.99; P <0.01; n=23).

Discussion

Many researchers who have to do with the collection and analysis of unstructured data have

pointed out the downsides of these data: bias when field effort is not taken into account,

spatial bias due to lack of sampling design, low detection when field efforts are limited and

uncertainty about non-detections when it is not sure which species are being considered (*e.g.,*

Altweg & Nichols 2019; Brown & Williams 2019). In some citizen science projects, these

shortcomings are reduced by discouraging the collection of casual records and instead

focusing on complete checklists, *i.e.*, lists of all species observed and identified by a

participant at a particular time and place (*e.g.,* eBird, see Kelling *et al.* 2019). This provides

more clarity about non-detections, and higher detection probabilities. If more information

about the observation process is provided, for example time spent or length of route during

the visit, there are more opportunities in statistical analyses to adjust for field effort (Johnston

et al. 2018; Van Strien *et al.* 2022). With a smartphone app such information may be

generated automatically (Altweg & Nichols 2019).

The collection of data in the KAL area is slowly moving in this direction. A subgroup

of observers has recently been selected to use a fixed list of species which should be recorded

when observed (Maharani *et al.* 2025). The hope is that this will lead to longer species lists.

This group will work with a smartphone app that can record the spatial coordinates of each

observation, which makes it possible to derive field efforts to some extent. The availability of

spatial coordinates makes it possible to localize observations on a small scale afterwards.

This will solve one of the obvious shortcomings of the current KAL data, namely the overly

large forest sites.

Still, it is not the intention to limit data collection to fixed lists only. On the contrary,

the idea remains to encourage as many workers as possible to participate in data collection, to

promote involvement in the protection of biodiversity. There may still be considerable

potential, because there are many observers who contributed only a few records so far. That

leaves us little choice but to deal with all shortcomings of the data. We have shown that the

occupancy estimates were unaffected by the way non-detection records were generated. The

fact that many records were collected by a relatively small group of dedicated observers can

partly explain this, as they collected records from all five groups. We also showed that

visiting sites only once did not influence the results. It is encouraging that the models yielded

meaningful relationships between occupancy and distance to large forest and forest habitat

preference. These relationships confirm existing knowledge, thereby enhancing confidence in

the usefulness of the data being collected in the KAL estate. With longer time series data, it

may be interesting to study whether these relationships are changing over time. An increase

in occurrence further away from large forest areas may indicate greater use of non-natural

sites and/or higher permeability of the plantation.

But problems remain, the biggest one being the short species lists in our data (Table

1). This leads to the generation of many non-detections (one for each species not observed)

which induces low detection rates per visit. Although there are quite a few replicated visits

per site (Table 1), these do not fully compensate for the low detection and the result is that

occupancy estimates for many species are far from precise (MacKenzie *et al.* 2018). Using

simulation data, Kery & Royle (2016; p. 588) showed that the precision of the occupancy

estimates becomes low when p is less than about 0.1-0.2. Most of our species have detection

rates < 0.2 and indeed, annual occupancy estimates are imprecise, with standard errors of

annual occupancy > 0.05 or even > 0.1 (Table 4). To improve this, more data are needed,

preferably in the form of longer species lists. Another problem is that model fit was not yet

sufficient for all species, which contributes to the uncertainty of inferences. The lack-of-fit

test revealed that spatial variation in occupancy and detection is not yet adequately modeled

for a number of species (Table 3; Doser & Kéry 2022). Model fit might be enhanced by

including more adequate covariates as well as spatial autocorrelation in the model. With more

annual data it also becomes more feasible to include year-dependent detection estimation. So

far, we assumed detection probability was equal in all five years. But it is better to consider

potential changes in detection, for example because of increasing average skill of observers

(Kéry *et al*. 2010).

In conclusion, although we have made progress in model development and solved

several data complications, more is needed to achieve our goal to use unstructured data for

plantation management purposes. With more data, more precise occupancy estimates may be

obtained for the 23 study species, and the number of study species may be further expanded

as well. Also, spatially finer applications will then become feasible.

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453
454 **Supporting information**

455 Table S1 and S2

457 Table 1. Annual field effort in the KAL standard dataset. Nsites is the number of sites with

458 observations, Nrecs is the total number of presence records, Nvisits per site is the mean number

459 of visits per site, List length is the mean number of all observed species per visit.

Year	Nsites	Nrecs	Nvisits per site	List length
2020	191	3047	8.3	1.9
2021	232	4055	7.1	2.4
2022	139	4462	7.4	4.3
2023	185	3348	7.5	2.4
2024	269	2567	6.0	1.6

Table 2. Properties of datasets per species obtained under different procedures (see text for

explanation). Nsites is the number of sites with observations of five or three species groups

(depending on the dataset). Nvisits per site is the mean number of visits per site, List length is

the mean number of all observed species per visit from 5 or 3 species groups. Nobservers is

the number of observers. Ndetect. and Nnon-detect. are the mean number of detection and

non-detection records of the 23 study species.

Dataset	Nsites	Nvisits /site/yr	List length	Nobservers	N detect.	Nnon-detect.
Standard data	387	7.2	2.4	372	534	6757
Nondet3grp	386	7.0	2.2	367	534	6499
Nondet3grp+obs1grp	382	7.1	2.3	255	534	6336
Nondet3grp+obs3grp	374	7.2	2.3	132	512	6135
Remove_sites1year	279	7.8	2.4	365	523	6570
Remove_sites2024	340	7.4	2.4	370	530	6681

Table 3. Detection parameter estimates under the top model per species. See Table S1 for the

meaning of model ID's. Bayesian *p*-values are according to the Freeman-Tukey statistic with

data grouped by sites (Doser & Kéry 2022). *p* is mean detection probability in 2020-2024 (±

se), *i.e.,* the backtransformed intercept as specified in formula [4]. Coefficients of list length,

habitat of observation and observer are on the logit scale. No entry indicates that the covariate

is not included in the model. Asterisks refer to significant differences from zero derived from

95% credible intervals.

Species	*Model ID*	*Bayesian p-value*	*p*	*List length*	*Habitat of observation*	*Observer*
Acridotheres javanicus	8	0.32	0.08 ± 0.01	0.69 *	-1.25 *	1.00 *
Alcedo meninting	1	0.07	0.02 ± 0.01	0.73 *	-0.4 *	3.33 *
Amaurornis phoenicurus	8	0.11	0.09 ± 0.01	0.67 *	-1.59 *	0.77 *
Anthracoceros malayanus	10	0.16	0.03 ± 0.01	0.48 *		1.23 *
Callosciurus notatus	7	0.61	0.04 ± 0.01	0.65 *		0.78 *
Callosciurus prevostii	3	0.23	0.02 ± 0.01	0.54 *	0.39 *	1.35 *
Centropus sinensis	8	0.34	0.17 ± 0.01	0.63 *	-0.63 *	0.37 *
Corvus enca	13	0.27	0.02 ± 0.01	0.46 *		2.14 *
Egretta garzetta	1	0.18	0.07 ± 0.01	0.49 *	-0.98 *	1.25 *
Elanus caeruleus	12	0.10	0.06 ± 0.01	0.6 *		1.24 *
Gracula religiosa	1	0.08	0.06 ± 0.01	0.46 *	-0.59 *	0.51 *
Halcyon smyrnensis	14	0.51	0.06 ± 0.01	0.69 *	-1.02 *	1.31 *
Hirundo tahitica	11	0.38	0.02 ± 0.01	0.41 *	-1.43 *	2.01 *
Hylobates albibarbis	1	0.06	0.04 ± 0.01	0.47 *	1.22 *	2.20 *
Liopeltis tricolor	15	0.31	0.01 ± 0.01	0.7 *		2.14 *
Macaca fascicularis	7	0.01	0.16 ± 0.02	0.59 *		1.56 *
Macaca nemestrina	1	0.02	0.07 ± 0.01	0.57 *	0.37 *	1.31 *
Malayopython reticulatus	2	0.37	0.05 ± 0.02	0.49 *	-1.37 *	3.10 *
Nannosciurus melanotis	1	0.03	0.05 ± 0.01	0.57 *	-0.39 *	1.72 *
Pongo pygmaeus	1	0.08	0.06 ± 0.02	0.55 *	0.99 *	2.93 *
Spilopelia chinensis	11	0.19	0.14 ± 0.01	0.59 *	-1.15 *	0.38 *
Spilornis cheela	13	0.28	0.01 ± 0.01	0.67 *		2.69 *
Varanus salvator	14	0.17	0.26 ± 0.02	0.86 *	-0.31 *	0.67 *

Table 4. Occupancy parameter estimates under the top model per species (see table 3 for model ID's). ψ is the mean finite sample annual occupancy, averaged over 2020-2024. SE is the standard error of annual occupancy, also averaged over 2020-2024. Coefficients of habitat of site, distance to forest and site size are on the logit scale. No entry indicates that the covariate is not included in the model. Asterisks refer to significant differences from zero derived from 95% credible intervals.

Species	ψ	SE	Habitat of site	Distance to forest	Site size
Acridotheres javanicus	0.65	0,09			1.83 *
Alcedo meninting	0.83	0,07	-1.21	0.45 *	1.34 *
Amaurornis phoenicurus	0.84	0,06			1.21
Anthracoceros malayanus	0.53	0,12	1.11	-0.61 *	
Callosciurus notatus	0.48	0,09	0.64	-0.66 *	1.55 *
Callosciurus prevostii	0.63	0,14	1.22		1.63 *
Centropus sinensis	0.84	0,05			1.71 *
Corvus enca	0.30	0,11	0.99		2.04 *
Egretta garzetta	0.69	0,08	-0.40	0.44 *	2.28 *
Elanus caeruleus	0.55	0,08		-0.64 *	1.42 *
Gracula religiosa	0.24	0,07	1.47 *	-0.38	2.14 *
Halcyon smyrnensis	0.57	0,09			
Hirundo tahitica	0.59	0,09		0.3	
Hylobates albibarbis	0.33	0,08	1.33 *	-1.22 *	1.53 *
Liopeltis tricolor	0.41	0,12			2.23 *
Macaca fascicularis	0.39	0,05	1.61 *	-0.58 *	1.69 *
Macaca nemestrina	0.47	0,09	1.10 *	-0.89 *	1.56 *
Malayopython reticulatus	0.38	0,10		-0.44 *	2.02 *
Nannosciurus melanotis	0.33	0,07	1.47 *	-0.31	2.05 *
Pongo pygmaeus	0.26	0,07	1.22 *	-0.59 *	2.08 *
Spilopelia chinensis	0.90	0,05		1.15 *	
Spilornis cheela	0.52	0,18	2.00 *		
Varanus salvator	0.97	0,02			1.83 *

Figure Legends

Fig. 1. Map of the KAL- estate in West Kalimantan, Indonesia.

Fig. 2. Relationship between (A) expected detection (± credible intervals) of *Varanus*

salvator and the number of species observed during a visit and (B) between expected

occupancy of *Hylobates albibarbis* and distance to large forest.

Fig. 3. Annual occupancy (± se) of (A) *Pongo pygmaeus* and (B) *Amaurornis phoenicurus.*

Fig. 4. (A) Mean detection ((± se; backtransformed intercept; see text) and (B) mean

occupancy (± se) in 2020-2024 of 23 species. Each bar represents a different dataset. Asterisk

indicates significant difference with standard dataset (paired t-test; P <0.05; n= 23).

Table S1. Overview of models. Model 1 is the most comprehensive model described in the
main text. The others are models in which one or more covariates have been omitted. No
entry indicates that the covariate is not included in the model.

Model ID	Habitat of site	Distance to forest	Site size	List length	Observer	Habitat of observation
1	x	x	x	x	x	x
2		x	x	x	x	x
3	x		x	x	x	x
4	x	x		x	x	x
5	x	x	x		x	x
6	x	x	x	x		x
7	x	x	x	x	x	
8			x	x	x	x
9	x			x	x	x
10	x	x		x	x	
11		x		x	x	x
12		x	x	x	x	
13	x		x	x	x	
14				x	x	x
15			x	x	x	
16	x			x	x	
17		x		x	x	
18				x	x	

Table S2. Top model per species per dataset according to WAIC. See table S1 for the meaning of model IDs.

Species	Standard	Nondet3grp	Nondet3grp+obs1grp	Nondet3grp+obs3grp	Remove_sites1yr	Remove_sites2024
Acridotheres javanicus	8	8	8	8	8	8
Alcedo meninting	1	1	1	1	1	1
Amaurornis phoenicurus	8	8	3	8	8	8
Anthracoceros malayanus	10	10	10	10	10	10
Callosciurus notatus	7	12	12	7	7	12
Callosciurus prevostii	3	8	8	3	8	8
Centropus sinensis	8	3	8	3	8	8
Corvus enca	13	13	13	13	13	13
Egretta garzetta	1	1	1	2	2	2
Elanus caeruleus	12	12	12	7	12	7
Gracula religiosa	1	1	1	13	3	3
Halcyon smyrnensis	14	14	11	11	14	14
Hirundo tahitica	11	2	11	2	14	11
Hylobates albibarbis	1	1	1	1	1	1
Liopeltis tricolor	15	15	15	15	13	15
Macaca fascicularis	7	7	7	7	7	7
Macaca nemestrina	1	1	1	1	1	1
Malayopython reticulatus	2	2	2	2	2	2
Nannosciurus melanotis	1	1	1	3	1	3
Pongo pygmaeus	1	1	1	1	1	1
Spilopelia chinensis	11	11	11	11	11	11
Spilornis cheela	13	13	7	13	7	12
Varanus salvator	14	11	11	8	8	2

Figure 1

Figure 2A

Figure 2B

Figure 3A

Figure 3B

Figure 4A

Figure 4B