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Authors: Higashide, Daishi, Kuriyama, Takeo, Takagi, Shun, Nakashima, Yoshihiro, Fukasawa, Keita, et al.

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Daishi Higashide, Takeo Kuriyama, Shun Takagi, Yoshihiro Nakashima, Keita Fukasawa, Gota Yajima, Minoru Kasada and Mayumi Yokoyama

D. Higashide (https://orcid.org/0000-0003-1186-1263) ✉ (dhigashide@gmail.com), T. Kuriyama, S. Takagi and M. Yokoyama, Inst. of Natural and Environmental Science, Univ. of Hyogo, Aogaki, Tamba, Hyogo, Japan. DH also at: Research Center for Wildlife Management, Gifu Univ., Gifu City, Gifu, Japan. – Y. Nakashima and G. Yajima, College of Bioresource Science, Nihon Univ., Fujisawa, Kanagawa, Japan. – K. Fukasawa, Biodiversity Division, National Inst. for Environmental Studies, Tsukuba, Ibaraki, Japan. – M. Kasada, Graduate School of Agriculture and Life Sciences, Univ. of Tokyo, Bunkyo-ku, Tokyo, Japan and Graduate School of Life Sciences, Tohoku Univ., Aramaki, Aoba-ku, Sendai, Miyagi, Japan.

Population growth in wild boars and feral pigs *Sus scrofa* has negative environmental and economic implications worldwide. Accordingly, it is necessary to monitor population trends for appropriate management. Despite the potential for bias, relative abundance indices based on signs of activity have the potential to be practical, low-cost monitoring tools for data collection at a local scale and over large areas. However, few studies have examined the effectiveness of specific signs as measures of relative wild boar abundance in comparison with reliable density estimates. In this study, we examined whether three activity signs (digging marks, rubbing marks and fecal pellet groups) could be used as relative abundance indices for wild boar. In particular, we conducted transect surveys for signs of activity as well as camera trap surveys from September 2017 to January 2018 at six sites in Hyogo Prefecture and eight sites in Chiba Prefecture, Japan. We modeled the relations between the number of activity signs and wild boar densities or abundances estimated from camera trap data in a hierarchical framework. Fecal pellet counts is a well-established method for estimating the abundance of herbivores, including wild boar; however, we found few fecal pellet groups in our study area, and the counts were not related to wild boar densities. Instead, we found that digging marks were strongly associated with estimates of wild boar density. Although fluctuations in the number of digging marks may be affected by factors other than boar density, including environmental conditions and seasonality, our results suggest that digging marks are an effective relative abundance index for evaluations of the spatial patterns of wild boar in Japan.

Keywords: camera trap, density, digging, feces, random encounter and staying time model, rooting, rubbing, *Sus scrofa*

Introduction

The wild boar *Sus scrofa* is one of the most widely distributed terrestrial mammals in the world, and its distribution has expanded both naturally and artificially by management and intentional introductions (Oliver and Leus 2008). Additionally, wild boar populations have increased over the past few decades in various parts of the world (e.g. Europe: Massei et al. 2015; United States: Snow et al. 2017). Wild boar populations, depending on the distribution and density, may have diverse ecosystem and economic impacts (Barrios-Garcia and Ballari 2012). For example, crop damage (Schley et al. 2008), the spread of diseases (Gortázar et al. 2007), and changes in the composition of plant and animal communities (Massei and Genov 2004) have been reported.

In Japan, wild boar populations have increased and the species range has expanded over the past few decades (MOE 2015). The Japanese government estimated that wildlife damage to crops in 2016 resulted in losses of 17.2 billion yen, of which 5.1 billion yen was caused by wild boars (MAFF 2018). In 2013, the Japanese government set a target of reducing populations of free-ranging wild boars and sika deer *Cervus nippon* in half by 2023 (MOE and MAFF 2013). To achieve this goal, each prefecture has conducted culling based on the Specified Wildlife Conservation and Management Plans for wild boar and sika deer. Furthermore, in September 2018, classical swine fever (CSF) reemerged in Japan after 26 years, affecting both domestic pigs *S. scrofa domesticus* and wild boars (Postel et al. 2019). The delivery of bait vaccines is being promoted as a control measure to limit the spread of CSF in wildlife (Isoda et al. 2020).

In most cases, the resources (funds, materials and labor) available for these measures are limited; thus, efficient strategies are needed to meet management goals. In particular, spatial culling quotas according to local densities are effective in wildlife management, including wild boar management (McMahon et al. 2010, Pepin et al. 2017). Therefore, reliable estimates of population abundance and trends are important for the adaptive management of wildlife (Nichols and Williams 2006).

Various methods have been proposed to estimate the absolute density or relative abundance of wild boars (Engeman et al. 2013, Enetwild Consortium et al. 2018). For example, nocturnal distance sampling with thermal imagers (Franzetti et al. 2012, Focardi et al. 2020) and capture–mark–recapture with ear tags (Hebeisen et al. 2008) or DNA (Ebert et al. 2012) are used to estimate the absolute density of wild boar. Recently, methods for the estimation of the absolute density of mammals from camera trap data without individual identification have been devised and used, such as the random encounter model (REM; Rowcliffe et al. 2008), spatially explicit N-mixture model (Chandler and Royle 2013), distance sampling (CTDS; Howe et al. 2017), and random encounter and staying time model (REST; Nakashima et al. 2018), and some of these have been applied to wild boar (Palencia et al. 2021). However, methods for estimating absolute density are often not suitable for monitoring over large spatial areas (e.g. prefectures, regions or states) or over long time periods because they are labor-intensive and expensive. In these cases, relative abundance indices (proxies) are widely used owing to relatively low costs and labor requirements (Schwarz and Seber 1999, Stephens et al. 2015). This approach assumes that the proxy is directly related to animal density and the relation is constant over space and/or time. An increasing dependence on proxies without the verification of prerequisites has been criticized (Pollock et al. 2002). However, some studies have shown that proxies are linearly associated with true abundances (Nimmo et al. 2015). Additionally, Iijima et al. (2013) suggested that evaluations of population dynamics based on multiple proxies and the number of captured animals are effective for estimating deer population sizes. In any case, relationships between proxies and population density should be verified to improve their use in wildlife management.

Hunting data are commonly used to evaluate relative abundance (Acevedo et al. 2007, Enetwild Consortium et al. 2018). However, these data have some limitations; for example, they can be collected only when/where hunting occurs and they may be skewed by hunter-related bias (Acevedo et al. 2007, Enetwild Consortium et al. 2018). Alternatively, relative abundance indices based on signs of mammalian activity are effective monitoring tools. Feces (pellets, dung and scat) are typically used to estimate the relative abundance of wild boar (Vicente et al. 2004, Acevedo et al. 2007, Plhal et al. 2014, Ferretti et al. 2016), and Abaigar et al. (1994) used digging (rooting) and tracks. Ideally, indices of relative abundance should have a linear relationship with the true abundance and this relationship should not change spatially or temporally (Enetwild Consortium et al. 2018). However, few studies have examined the effectiveness of signs of activity as measures of relative wild boar abundance by comparisons with reliable estimates of density (Anderson and Stone 1994).

In this study, we examined the effectiveness of various signs of activity as relative abundance indices to evaluate spatial differences in local densities of wild boars. Among signs of activity derived from wild boars (Allwin et al. 2015), we focused on digging marks, rubbing marks and fecal pellet groups, which are likely to be present in forested, warm and temperate areas. We conducted transect surveys and camera trap surveys simultaneously at 14 sites with different wild boar densities in two prefectures in Japan. We evaluated the effectiveness of the three signs as relative abundance indices of wild boars by determining relationships with local densities and abundances estimated from camera trap data.

Material and methods

Study area

The field study was conducted at six sites (H1–H6) in Hyogo Prefecture and at eight sites (C1–C8) in Chiba prefecture, Japan (Fig. 1). The Hyogo prefectural government employed a rectangular grid system (2′30″ in latitude, 3′45″ in longitude, with cells of about 4.6 × 5.5 km) established by the Ministry of the Environment of Japan for the spatial unit to evaluate the wildlife population status. The Chiba prefectural government divided 13 municipalities into 71 units for wildlife management. Therefore, we adopted these management units for the selection of study sites. Site elevations ranged between 10 and 950 m a.s.l. in Hyogo and between 40 and 320 m a.s.l. in Chiba. The mean annual temperatures during the last 10 years (2009–2018) at Toyooka (Hyogo; 3.4 m a.s.l.), Himeji (Hyogo; 38.2 m a.s.l.) and Katsuura (Chiba; 11.9 m a.s.l.) meteorological stations (Fig. 1) were 14.8, 15.6 and 16.2°C, respectively, and the mean annual precipitation estimates were 2167, 1459 and 2068 mm, respectively (JMA 2019). The mean annual maximum snow depth is 492 mm at the Toyooka meteorological station, and the other two stations do not measure snow-related parameters owing to negligible snowfall (JMA 2019).

About 67% of Hyogo Prefecture is forested area (MAFF 2019) mainly composed of secondary deciduous broad-leaved forests dominated by Konara oak *Quercus serrata* and Chinese cork oak *Q. variabilis*, secondary evergreen coniferous forests dominated by Japanese red pine *Pinus densiflora*, and artificial evergreen coniferous forests of Japanese cedar *Cryptomeria japonica* or Hinoki cypress *Chamaecyparis obtusa*. Only 30% of Chiba Prefecture is covered with forest (MAFF 2019). These areas are composed mainly of secondary deciduous broad-leaved forests dominated by Konara oak and evergreen coniferous forests of Japanese cedar, Hinoki cypress and Japanese red pine. Also, secondary evergreen broad-leaved forests dominated by Itajii *Castanopsis sieboldii* are seen in the southeastern area. The forest conditions at each site are shown in the Supporting information.

Between 1960 and 2000, about 4000–6000 wild boars year^{-1} were harvested or culled in Hyogo Prefecture; recently, these hunting bags have increased, reaching 18 000 wild boars year^{-1} in 2010 (Yokoyama 2014). Agricultural damage caused by wild boars has become a serious issue

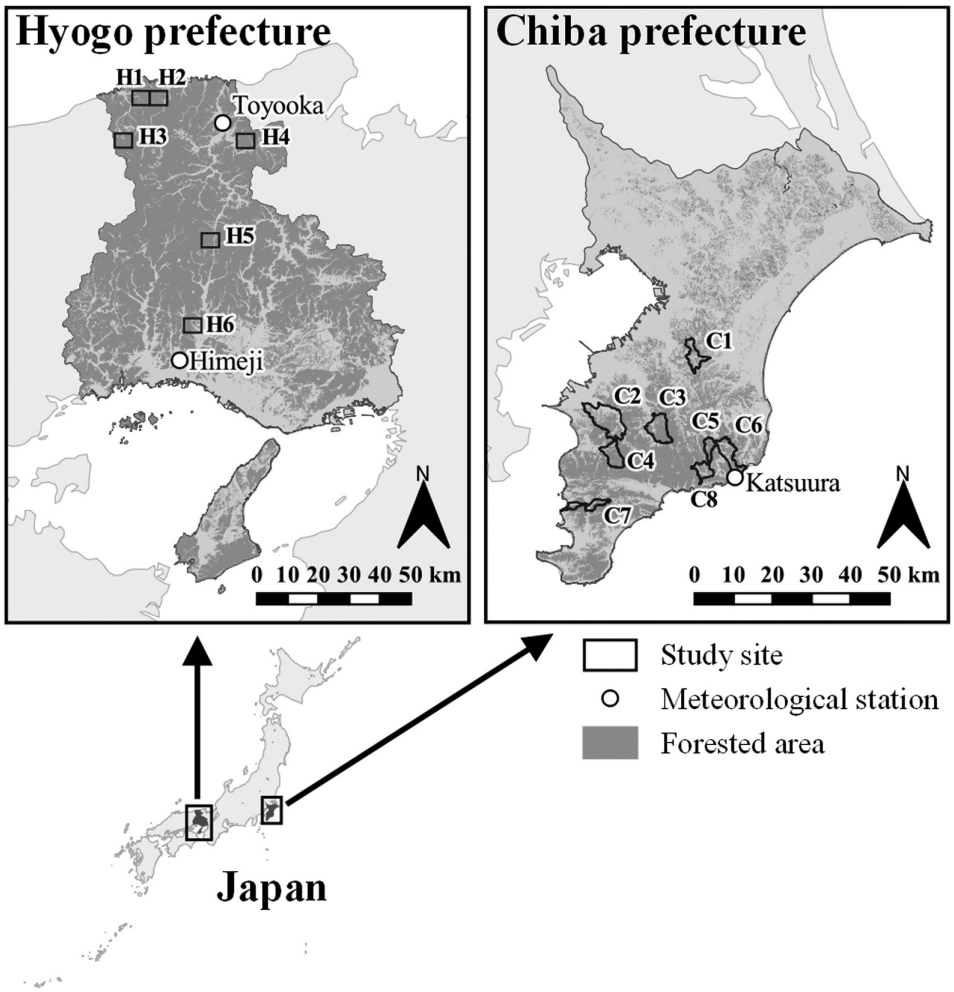

Figure 1. Study sites (black circles) for signs of activity on transects and camera trap surveys conducted in Hyogo and Chiba Prefectures with locations of meteorological stations (white squares). Forested area (dark gray shaded area) is drawn based on data provided by the Geographical Survey Institute of Japan.

throughout Hyogo Prefecture (Kuriyama et al. 2018). Wild boars in Chiba Prefecture were believed to be extinct in the mid-1970s. The current population likely originated from artificially introduced boars in the mid-1980s with subsequent expansion, which caused agricultural damage in the southern part of the prefecture (Asada 2011). The annual counts of harvested or culled wild boar were less than 1000 until 2000 in Chiba Prefecture, but these hunting bags have recently increased, reaching 22 000 wild boars in 2015 (Chiba Prefecture 2017).

Selection of the study period

The farrowing season of wild boar typically lasts from April to July in Japan (Tsuji et al. 2013). Furthermore, wild boar have larger litter sizes compared with other similarly sized ungulates (Carranza 1996) and adult females have high fertility rates (Bieber and Ruf 2005, Tsuji et al. 2013). Therefore, the wild boar population is expected to increase steadily and drastically during this period.

Wild boar populations decrease through harvesting or culling. The hunting season is from 15 November to 15 March in Hyogo and from 15 November to 15 February in Chiba. However, in recent years, culling has been carried out year-round to protect crops and has accounted for the majority of captures (MOE 2019). It is therefore difficult to select a study period that avoids the risk of human-derived mortality in Japan.

The rate of disappearance of fecal pellet groups, often used as a relative abundance index for ungulates, changes seasonally due to changes in temperature, rain and dung beetles (Massei et al. 1998). Although data for wild boar are lacking, pellet groups of sika deer disappear rapidly in the summer (during June–August) under the Japanese climate (Koike et al. 2013). We selected autumn to winter as the study period, when variation in the wild boar density is expected to be low and fecal pellets are likely to remain over long periods. We conducted a survey for signs of activity along a transect once at each site from October to December 2017 and a camera trap survey for one or two months, including this date (Supporting information).

Signs of activity along the transect

Prior to the field survey, we established one transect of >5 km within each site using Quantum GIS (ver. 2.18.19, <www.qgis.org/>). Transects were set along the forested mountain ridge to minimize variation in topographical conditions

among transects (sites) and to ensure that it was possible to walk along the route, avoiding steep terrain. Transects were separated by at least 3 km. Based on the reported average monthly home range size of wild boar of 50–400 ha (Caley 1997, Massei et al. 1997, Kay et al. 2017, Koh et al. 2018), individuals were not likely to traverse multiple transects during the study period.

We trekked once along the transect at each site, counted signs of wild boar activity (digging marks, rubbing marks and fecal pellet groups) within 1 m on both sides of the transect (total width, 2 m), and recorded counts in sections of about 100 m. Digging (rooting) marks were pits formed on the ground by the foraging behavior of wild boar, and a pit with distinct boundaries (mounds) was counted as an independent mark (Supporting information). Signs formed only on the surface of the ground, such as disturbances of fallen leaves, may also be derived from wild boar but were excluded owing to uncertainty. When it was difficult to distinguish the independence of digging marks, they were recorded as a single large-scale mark. However, because large-scale digging marks accounted for only about 3.1% of the total digging marks and were likely derived from the foraging behavior of the same individual (or herd), we used both marks for analyses without distinction. Rubbing marks formed by wild boars scratching their bodies were identified by mud attached to the trunk or by the wear of bark (Supporting information). We counted the trees with these features. We defined one fecal pellet group as a pile of feces believed to be produced from one defecation from a single wild boar. To determine whether adjacent groups were independent, the level of freshness (drying or weathering) and size of pellets were evaluated. These signs of wild boar activity are relatively easy to distinguish from those of other mammals.

Camera trap survey

We placed infrared-triggered cameras at 30 locations during a one-month period at six sites (H1–H6) in Hyogo Prefecture as well as at 20 locations for about one month at one site (C1) or 10 locations for about two months (with a location change after one month) at seven sites (C2–C8) in Chiba Prefecture. We estimated the densities of wild boar from camera data by the REST model (Nakashima et al. 2018). The estimated densities by the REST model are relatively unbiased even when survey effort is low; however, the precision is improved by increasing survey effort (the number of locations and survey duration). However, increasing the survey period by 20 days or more has little effect on precision (Nakashima et al. 2018). Therefore, we set the survey period to one month at each location. Each camera was randomly located within an area of 20 m from the transect route or the nearby forested ridgeline to unify the topographical conditions of the transect survey.

Three infrared-triggered camera models were used, the Bushnell Trophy Cam HD or Bushnell Trophy Cam Aggressor No Glow in Hyogo Prefecture and Browning Strike Force HD Pro in Chiba Prefecture. Cameras were set to video mode (HD: 30 s, AG: 10 s, SF: 20 s) with the minimum wait time (≤1 s) to prevent missed shooting. We defined the equilateral–triangular focal areas for each of the three camera models considering its field of view and detection area and analyzed only the records obtained in the areas (Supporting information). Although the focal areas differed among camera models, it is clear from the definition of the REST model described later that there is no effect on the expected values for densities. To clearly record the stay of wild boar in the focal area, cameras were mounted on the tree trunk about 20–30 cm above the ground and marking stakes were installed as landmarks at each apex of the triangular focal area. Then, we adjusted the direction and angle of the camera in reference to the position of the marking stakes while checking the field of view on a monitor (built into SF) or with a tablet device connected via USB (HD and AG). After the adjustment, we removed the marking stakes to avoid effects on the behavior of wild boars.

We played all videos captured by cameras and recorded the number of wild boars entering the focal area, the length of staying time and the research period for each camera. The research period was the total number of effective camera trap days, excluding the days of our field survey and periods when the camera did not work properly due to battery depletion, accidental animal attacks on the cameras and so on. When the same individual stayed in the focal area continuously across multiple videos, we collectively regarded the stays as one observation record.

Density and abundance estimation from camera trap data

Among various methods, we used the REST model (Nakashima et al. 2018) and Poisson–Poisson N-mixture model (PP model; Kéry and Royle 2015) to estimate densities or abundances of wild boar at each site without individual identification from camera trap data.

The REST model requires some assumptions, including the certain detection of animals entering the focal area (Nakashima et al. 2018); however, it is an efficient and realistic method for estimating the density of ground-dwelling mammals lacking individually recognizable markings (Palencia et al. 2021). In the model, the relationship between animal density D and camera trap data is described by the following equation:

$$D = E(Y) \times E(T) / (sHa) \quad (1)$$

where s is the focal area of the camera trap defined prior to the survey, H is the research period, $E(Y)$ is the expected number of animal encounters and $E(T)$ is the expected staying time per encounter. Nakashima et al. (2018) pointed out the necessity of estimating the proportion of time that animals are active (a) to correct the total research period H because inactive animals are inevitably less detectable by cameras. Thus, we estimated a of the wild boars in each prefecture using the activity package in R described by Rowcliffe et al. (2014).

Prior to population density estimation, we chose probability distributions of observed staying time and the number of observed animal encounters using model selection criteria. The observed staying time (T) for each encounter was regarded as a non-negative, continuous random variable following an arbitrary temporal probability distribution, such

as the exponential, gamma, Weibull and log-normal distributions. Similarly, the number of observed animal encounters (Y) during the sampling period (H) can be regarded as a non-negative, discrete random variable following an arbitrary probability distribution, such as Poisson, negative binomial, zero-inflated Poisson and zero-inflated negative binomial distributions. We estimated parameters for probability distributions of T and Y for each site using Bayesian methods. However, we estimated T for each site by treating inter-site variation as a random effect with mean zero and variance σ^2 because it was not possible to estimate the parameter independently for some sites with low wild boar densities and few observed passes. The posterior distribution was estimated using the Markov chain Monte Carlo (MCMC) method by simulating posterior samples of parameters and their variances. A gamma distribution with shape (0.001) and rate (0.001) parameters was used as the prior distribution for staying time T, dispersion parameter for the number of animal encounters Y and boar density D. We selected the gamma distribution for T (Supporting information) and zero-inflated negative binomial distribution for Y (Supporting information) based on the WAIC (Watanabe–Akaike information criterion, Watanabe 2010).

The N-mixture model is widely used to estimate animal abundance (when the home range includes the survey location) based on spatially and temporally replicated counts (Kéry and Royle 2015). Its derivative the PP model can effectively explain the structure of camera trap data because it can accommodate multiple counts for the same individual within a single sampling occasion by assuming that the number of detections per individual follows a Poisson distribution (Kéry and Royle 2015, Nakashima 2020). The number of animals for each site i in location j, N_{ij} is assumed to follow a Poisson distribution:

$$N_{ij} \sim \text{Poisson}\left(\lambda_i\right) \tag{2}$$

where λ_i is the expected number of animals per sampling location at site i. The observation process is described by the following equation:

$$y_{ijt} \sim \text{Poisson}\left(N_{ij} \times \mu_i\right) \tag{3}$$

where y_{ijt} is the number of individuals detected at site i location j during t sampling events (day), and μ_i is the expected number of times in which an individual is detected at each location at site i during a sampling event. We estimated the parameters λ_i and μ_i for each site using MCMC simulations. Uniform distributions from 0 to 100 and from 0 to 1 were used as the prior values for λ_i and μ_i, respectively.

Relationships between signs of activity and wild boar densities

We modeled the relations between the observed number of activity signs AS_{ij} (digging marks, rubbing marks and fecal pellet groups) found on transect i section j and wild boar densities or abundances D_i at site i in a hierarchical framework as follows:

$$\log\left(\mu_{ij}\right) = \alpha + \beta \times \log\left(D_i\right) + \log\left(TL_{ij}\right)$$

$$p_{ij} = r / \left(r + \mu_{ij}\right)$$

$$AS_{ij} \sim \text{Negative binomial}\left(p_{ij}, r\right) \tag{4}$$

where p_{ij} is the probability parameter and r is the size parameter for the negative binomial distribution. We treated D_i as a latent variable associated with the REST and PP models. In the model, the length of transect i section j, TL_{ij} (i.e. observation effort), is used as an offset term. We estimated the coefficients α and β using MCMC simulations. The prior distributions of α and β were uniform distributions from -100 to 100 and that of r was the uniform distribution from 0 to 100.

MCMC simulations were performed using JAGS (ver. 4.3.0, <www.mcmc-jags.sourceforge.net>, accessed 11 October 2017) called from R (ver. 3.3.2, <www.r-project.org>, accessed 3 November 2016) with the runjags package (Denwood 2016). We ran three MCMC chains in parallel for 20 000 iterations, following a burn-in period of 20 000 iterations for each chain, with thinning to every 20th sample. The medians, 50% and 95% credible limits, and variances of wild boar density, abundance and coefficient estimates were calculated as the posterior summary. Model convergence was examined using the potential scale reduction factor (PSRF; Gelman and Rubin 1992) and by verifying no divergent transitions. Convergence is approximately reached if PSRF is close to one.

Then, we evaluated the model by comparing the median of the posterior distribution of signs of activity (as expected values) and observed values. We used the following three indices (Moriasi et al. 2007) for model evaluation: 1) coefficient of determination, which describes the degree of collinearity between observed and expected values; 2) Nash–Sutcliffe efficiency (NSE), which describes the relative magnitude of the residual variance compared with the explained variance; and 3) percent bias (PBIAS), which estimates the model's tendency to overpredict (PBIAS > 0) or underpredict values (PBIAS < 0).

Results

We found, on average, 29.3 (range, 1.2–66.5) digging marks km^{-1}, 9.6 (0.0–51.0) rubbing marks km^{-1} and 0.3 (0.0–1.2) fecal pellet groups km^{-1} along the transects (Table 1). We obtained 523 and 2388 video files of wild boar and 225 and 606 independent staying records within the focal area during 6042 and 4985 effective camera trap days for Hyogo and Chiba Prefectures, respectively. Wild boars showed crepuscular and nocturnal activity patterns in both prefectures (Supporting information), and the proportions of time spent active were 0.35 (95% CI, 0.27–0.44) and 0.46 (0.38–0.52) in Hyogo and Chiba, respectively. The medians of the posterior distributions of boar density determined by the REST

Table 1. Counts of signs of wild boar activity and the length of transects at each site.

Pref.	Site	Transect length (km)	Number of activity signs of wild boar km^{-1} (N)					
			Digging marks		Rubbing marks		Fecal pellet groups	
Hyogo	H1	6.24	10.6	(66)	2.7	(17)	0.0	(0)
	H2	7.44	32.7	(243)	14.4	(107)	0.7	(5)
	H3	6.05	1.2	(7)	1.5	(9)	0.0	(0)
	H4	5.76	13.9	(80)	0.3	(2)	0.0	(0)
	H5	6.17	14.6	(90)	0.0	(0)	0.0	(0)
	H6	7.99	13.9	(111)	7.6	(61)	0.6	(5)
Subtotal		39.64	15.1	(597)	4.9	(196)	0.3	(10)
Chiba	C1	5.20	23.7	(123)	51.0	(265)	0.0	(0)
	C2	5.61	66.5	(373)	24.1	(135)	0.2	(1)
	C3	5.57	11.3	(63)	7.5	(42)	0.0	(0)
	C4	5.25	64.0	(336)	11.2	(59)	0.4	(2)
	C5	5.53	23.1	(128)	11.9	(66)	0.2	(1)
	C6	5.62	35.2	(198)	1.8	(10)	1.2	(7)
	C7	5.30	62.5	(331)	6.2	(33)	0.6	(3)
	C8	6.41	49.1	(315)	0.3	(2)	0.0	(0)
Subtotal		44.49	42.0	(1867)	13.8	(612)	0.3	(14)
Total		84.13	29.3	(2464)	9.6	(808)	0.3	(24)

model varied from 0.7 to 114.3 wild boars km^{-2} among sites and the abundance determined by the PP model varied from 0.02 to 0.70 among sites (Table 2). All MCMC simulations converged (PSRF close to one).

For the relations between signs of activity and wild boar densities, the median values (95% CI) of parameters α and β estimated by MCMC simulations were 1.70 (0.77–2.37) and 0.59 (0.37–0.89) for digging marks (Fig. 2a) and −1.04 (−2.53 to 0.47) and −0.11 (−0.61 to 0.52) for fecal pellet groups (Fig. 2c). However, the MCMC sampling distribution for the relationship between rubbing marks and wild boar densities did not converge well. The expected values of digging marks from MCMC simulations were positively correlated with the observed values ($R^2 = 0.82$, $p < 0.001$), and NSE was high (0.82) and PBIAS was close to zero (2.3) (Table 3). The expected values of fecal pellet groups from MCMC simulations were not correlated with the observed values (Table 3).

Similarly, α and β estimated from the relationship with the abundance determined by the PP model were 4.77 (4.23–5.48) and 0.97 (0.62–1.42) for digging marks (Fig. 3a), 5.02 (4.26–6.09) and 2.09 (1.56–2.85) for rubbing marks (Fig. 3b), and −0.35 (−2.15 to 2.14) and 0.60 (−0.47 to 1.99) for fecal pellet groups (Fig. 3c). The expected values of digging marks from MCMC simulations were positively correlated with the observed values ($R^2 = 0.79$, $p < 0.001$), and NSE was high (0.78) and PBIAS was close to zero (3.5) (Table 4). The expected values of rubbing marks and fecal pellet groups from MCMC simulations were weakly or not correlated with the observed values (Table 4).

Discussion

Of the three signs of wild boar activity, we found that only digging marks were strongly associated with density estimates obtained using the REST model (Fig. 2a) and with abundance estimates obtained by the PP model (Fig. 3a). Furthermore, the model showed very good performance based on assessment indices (Moriasi et al. 2007). Based on these results, the number of digging marks reflected the wild

Table 2. Estimated wild boar densities obtained from the REST model, abundances obtained from PP model and camera-trapping details for each study site.

Pref.	Site	No. of locations	Camera model[a]	Effective camera trap days	Estimated densities by REST model (km^{-2})			Estimated abundances by PP model		
					2.5%	50%	97.5%	2.5%	50%	97.5%
Hyogo	H1	30	HD	859	0.8	2.7	10.5	0.06	0.09	0.14
	H2	30	HD	1039	5.6	11.4	24.4	0.14	0.20	0.28
	H3	30	HD	1029	3.6	11.6	50.0	0.07	0.10	0.15
	H4	30	AG	843	0.1	0.7	5.4	0.00	0.02	0.05
	H5	30	AG	1173	0.9	3.1	12.1	0.06	0.12	0.29
	H6	30	HD	1099	1.2	2.6	6.7	0.08	0.11	0.16
Chiba	C1	20	SF	522	10.3	26.7	83.2	0.20	0.28	0.39
	C2	10 × 2	SF	710	19.3	37.5	82.1	0.38	0.48	0.62
	C3	10 × 2	SF	696	4.0	10.7	30.9	0.15	0.21	0.29
	C4	10 × 2	SF	475	12.1	29.2	75.1	0.54	0.70	0.91
	C5	10 × 2	SF	667	18.0	41.1	105.0	0.19	0.26	0.35
	C6	10 × 2	SF	615	0.6	2.3	10.2	0.13	0.19	0.27
	C7	10 × 2	SF	715	52.3	114.3	278.2	0.37	0.47	0.61
	C8	10 × 2	SF	585	18.3	47.3	153.6	0.18	0.25	0.34

[a]HD, Bushnell Trophy Cam HD; AG, Bushnell Trophy Cam HD Aggressor No Glow; SF, Browning Strike Force HD Pro.

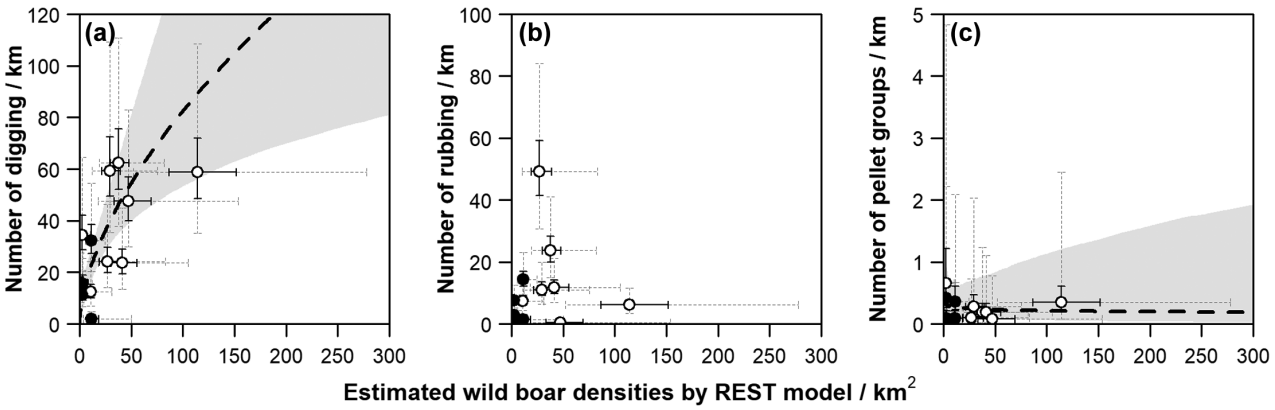

Figure 2. Relationship between wild boar densities (50% credible intervals, gray dashes; 95%, black bars) estimated by the REST model from camera trap data and counts per kilometer for digging marks (a), rubbing marks (b) and fecal pellet groups (c) at 14 sites in Hyogo (black dots) and Chiba (white dots) Prefectures. Predictions by the hierarchal model are shown as median values (black dashes) and 95% credible intervals (gray shaded areas).

boar density and abundance in our study area and is reliable, to some extent, as a relative abundance index to examine spatial patterns, consistent with a previous report by Anderson and Stone (1994). However, the median β value was 0.59 in the regression against the wild boar density by the REST model (that is, the number of digging marks is saturated at high densities), whereas it was 0.97 in the regression against the abundance by the PP model (that is, close to linear). Therefore, it should be noted that the relation with wild boar density may vary. Our results conflict with those of previous studies suggesting that there is no relationship between digging marks and wild boar density and digging marks are therefore not a suitable predication index (Hone et al. 1988, Massei et al. 2018). These conflicting results may be related to a difference in wild boar densities, which were 0.89 wild boars km^{-2} (Hone et al. 1988) and 0.71–6.99 wild boars km^{-2} (Massei et al. 2018) in previous studies, compared with 0.7–114.3 wild boars km^{-2} at our study sites. According to Welander (2000), digging is affected by various factors, including year, season, habitat type, soil category and availability of natural food resources above and below ground. Accordingly, factors other than wild boar density can result in substantial variation in the number of digging marks. Therefore, as in this study, if densities differ on the order of dozens of wild boars km^{-2} or more, it may be possible to roughly evaluate abundance using the number of digging marks; however, this may not be applicable when the variation in density is low. Additionally, given that the rooting frequency is related to the production of hard masts (Bruinderink and Hazebroek 1996), it should be noted that the relationship between the wild boar density and the number of digging marks is affected by annual fluctuations and spatial synchronization.

Table 3. Model evaluation indices for MCMC simulations of the relationships between signs of activity and wild boar densities by the REST model.

Signs	R^2	NSE	PBIAS (%)
Digging	0.82***	0.82	2.3
Rubbing	NA	NA	NA
Feces	−0.03n.s.	−0.05	24.7

R^2, coefficient of determination; NSE, Nash–Sutcliffe efficiency; PBIAS, percent bias; ***$p < 0.001$; n.s., $p > 0.05$.

Rubbing behaviors in wild boars function to scratch the skin and remove mud, hair and ectoparasites (Allwin et al. 2015). Our prediction that the number of rubbing marks reflects the density of wild boars was not supported by our results. There are several potential explanations for this observation. First, rubbing in wild boars is often associated with wallowing behavior (Allwin et al. 2015); however, the distribution of wallows is spatially nonuniform. In addition, other than marks left by wild boars covered in mud, signs of rubbing are difficult to detect. Second, rubbing marks detected as bark wear form more easily for some tree species than others, and once formed, remain for a long time. Finally, although we counted trees with rubbing marks in this study, tree species and tree density may differ among sites. Because it is difficult to consider all of these factors, we conclude that rubbing marks are not a reliable relative abundance index for wild boars.

Fecal counts are a standard and effective indicator of herbivore abundance (e.g. rabbit *Oryctolagus cuniculus*, Wood 1988; kangaroo Macropodidae, Vernes 1999; red deer *Cervus elaphus*, Forsyth et al. 2007). They are also used for estimating the relative abundance of wild boars (Acevedo et al. 2007, Plhal et al. 2014) and are related to observed density (Hone 2012). Although the survey period was determined to maximize fecal pellet groups remaining under the Japanese climate, few fecal pellet groups were found, and these counts were not related to wild boar densities. Previous studies have reported averages of 4.5–16.3 fecal pellet groups/200 m^2 in the Czech Republic (Plhal et al. 2014) and 0.9 fecal pellets m^{-2} (18 pellets/200 m^2) in Australia (Hone and Martin 1998); we found, on average, only about 0.03 fecal pellet groups/200 m^2 for 14 sites. Although differences in boar densities can lead to differences in numbers of fecal pellet groups, it is unlikely that about 100 times more wild boars inhabited these areas than our study area. Hone and Martin (1998) reported that the higher the temperature and precipitation, the faster the disappearance of fecal pellets of wild boars. Therefore, the differences among studies might be explained in part by the higher temperatures and precipitation in our study area than in the previous study

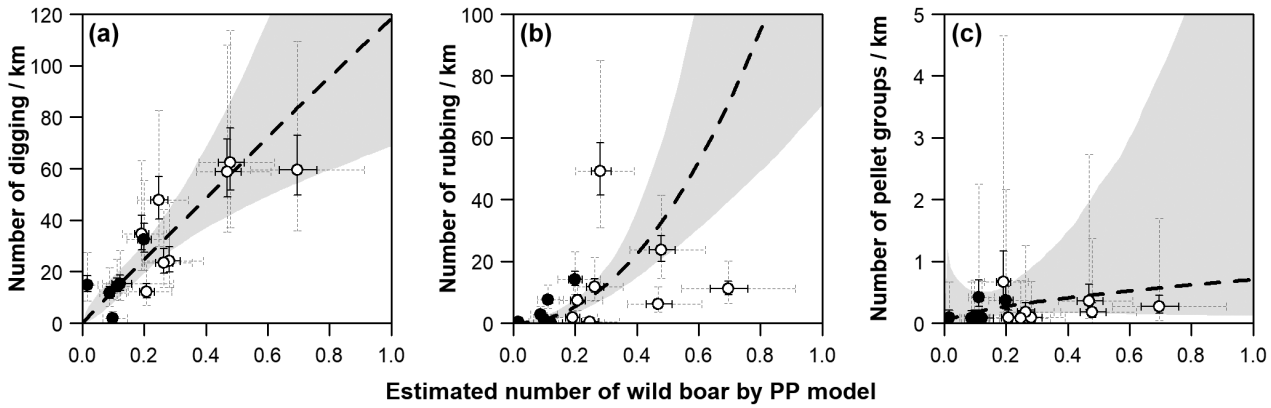

Figure 3. Relationship between wild boar abundances (50% credible intervals, gray dashes; 95%, black bars) estimated by the PP model from camera trap data and counts per kilometer for digging marks (a), rubbing marks (b) and fecal pellet groups (c) at 14 sites in Hyogo (black dots) and Chiba (white dots) Prefectures. Predictions by the hierarchal model are shown as median values (black dashes) and 95% credible intervals (gray shaded areas).

areas (Supporting information). Additionally, dense understory vegetation obstructs visibility and prevents the detection of pellets (Zabek et al. 2016). However, the effectiveness of pellet counts as a relative abundance index for sika deer has been confirmed in Japan, including our study area, and the method is used nationwide (Hamasaki et al. 2007). Therefore, the low pellet detection in our study area may be explained by properties specific to wild boar as well as environmental conditions. Wild boars defecate less frequently than other ungulates and have site preferences for defecation (Ebert et al. 2009, Plhal et al. 2014). In addition, various factors, including dung beetles, digging behavior of wild boars, moisture and composition of feces, might affect the rate of feces disappearance (Massei et al. 1998). Kosugi and Sakamoto (1994) reported that dung beetles (*Onthophagus ater* and *O. lenzii*) strongly favor feces of wild boar over those of sika deer and Japanese hare *Lepus brachyurus* in Japan. These characteristics of wild boars and their feces may explain the scarcity of fecal pellet groups on forested mountain ridges, at our study sites, and/or in temperate Japan.

Populations of wild boars and feral pigs are increasing worldwide and have significant impacts on the environment and economy. In Japan, human–wild boar conflicts, including the appearance of wild boar in urban landscapes and the spread of classical swine fever, are increasing, and prefecture-level administrations require information about population trends to address these issues. However, large-scale surveys for estimating absolute density are generally very expensive. In such cases, signs of activity are alternative indexes to understand spatial abundance. Although fecal counts are the most frequently used relative abundance index for wild boar, our results indicate that it may not be an effective parameter in Japan. Although temporal (year and/or season) fluctuations in the relationship between population density and activity signs should be noted, our results support the effectiveness of digging marks as a relative abundance index of wild boar. Understanding differences in spatial density by extensive surveys using this relative abundance index will guide the proper allocation of effort and resources for effective population management.

Table 4. Model evaluation indices for MCMC simulations of the relationships between signs of activity and wild boar abundances by the PP model.

Signs	R^2	NSE	PBIAS (%)
Digging	0.79***	0.78	3.5
Rubbing	0.31*	0.27	7.9
Feces	−0.03n.s.	−0.39	33.6

R^2, coefficient of determination; NSE, Nash–Sutcliffe efficiency; PBIAS, percent bias; ***$p < 0.001$; *$p < 0.05$; n.s., $p > 0.05$.

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Author contributions

All authors contributed to the sample collection, data analysis or the writing and review of the manuscript.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.5hqbzkh6h> (Higashide et al. 2021).

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Supplementary information (available online as Appendix wlb-00869 at <www.wildlifebiology.org/appendix/wlb-00869>).