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# Feasibility assessment of active and passive acoustic monitoring of sika deer populations

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**Abstract:**

Regardless of whether populations of sika deer (*Cervus nippon*) are native or introduced, their distribution continues to expand, presenting new ecological threats in several regions of the world, especially Japan. Consequently, there is growing demand for precautionary measures against such expansion, which is primarily associated with males during the initial stage of invasion. Therefore, the present study introduces two novel approaches—passive acoustic monitoring (PAM) and active acoustic monitoring (AAM)—to detect males with high sensitivity, using their howls during the rut. This study verifies the feasibility of these approaches by comparing them with existing methods based on spotlights and camera traps at five sites that support different deer densities. To validate PAM, we set unattended sound recorders to evaluate the time and variation in howl frequency at different sites. In addition, we measured the detection range of the howl. To verify AAM, we assessed whether sika deer males are vocally responsive to audio playbacks, and if so, the extent to which the frequency of the howl-back against different sound sources could explain male abundance. Both the PAM and AAM successfully detected males, even at sites with extremely low deer density where detection using existing methods failed. PAM had a detection zone of around 6 ha in defoliated forests, which was >200-times greater than that of camera traps. The frequency of howl-back immediately after playbacks was higher than that of spontaneous howls; thus, AAM proved effective at explaining male abundance when using playbacks of real howls. In conclusion, our findings suggested that bioacoustic approaches could enhance the monitoring of low-density deer populations that might be in the initial stage of deer invasion or at the stage where the target density has been reached following population control.

**Key words:**

bioacoustic monitoring; camera trap; *Cervus nippon*; howl; low-density population; spotlight count

## Introduction

The overpopulation of cervids (family Cervidae) causes many problems, including damage induced by feeding on agricultural and forestry products, as well as native biodiversity. Such problems are well documented in Europe and North America (Gill, 1992; Fuller and Gill, 2001; Rooney, 2001; Côté et al., 2004), as well as in various areas of far-east Asia and Russia that support the native ranges of sika deer (*Cervus nippon*) (Aramilev, 2009; Takatsuki, 2009). Sika deer were artificially introduced to North America, Europe, the British Isles, and New Zealand during the 19th and 20th centuries. However, the serious threats associated with this species have since become apparent in these regions (Gill, 1992; Fuller and Gill, 2001; Bartoš, 2009; Takatsuki, 2009).

With growing demand to address the serious threats posed by sika deer, arguments for implementing appropriate adaptive management of their populations have intensified with respect to the expected management goals, population monitoring methods, and practical techniques for population regulation (Kaji et al., 2010; Nugent et al., 2011; Baiwy et al., 2013; Ijima et al., 2015). The ideal target density of sika deer is regarded as <20% of the carrying capacity in a given location, which is the threshold used to avoid the appearance of browsing lines of deer (Kaji et al., 2010). In response, most local governments in Japan have set the official target density at 5 deer/km$^2$ (Uno et al., 2007). Various techniques exist to monitor when deer populations exceed the target density, including block counts (Maruyama and Furubayashi, 1983), fecal pellet counts (Marques et al., 2001), aerial-photographic counts (Kaji et al., 2004), and the camera trap method (Dougherty and Bowman, 2012). To facilitate monitoring procedures, indices of the relative density or population, along with adaptive management practices, have been devised in recent years (Kaji et al., 2010). For example, the spotlight index is useful for evaluating population trends, because of its small error estimates and consistent trends (Uno et al., 2006; Ueno et al., 2010). Despite efforts to develop estimates of the absolute or relative abundance of deer, only a few feasible and affordable options are available to monitor population trends within an acceptable error range in regions with low deer density. Under these circumstances, even alternative population indices are difficult to use because of zero-inflated data on the presence of this species (Welsh et al., 1996).

Techniques for population monitoring that can be applied to low densities of deer are required during the initial stage of invasion, when precautionary responses are urgently needed, or once the target density of deer has been reached (i.e., the ex-post evaluation stage). In general, the male-to-female ratio is remarkably high at the periphery of deer ranges, or in areas where intense culling has been implemented (Asada, 2013). This type of population dynamic is called the lag phase in the discipline of population ecology. Reproductive success is low during the lag phase owing to the high cost of finding a mate, i.e., the Allee effect is suppressed (Crooks and Soulé, 1999). Lag-phase management has been developed to manage introduced species and involves preventing animals from shifting from the lag phase to the increasing phase in population dynamics (Lewis and Kareiva, 1993; Crooks and Soulé, 1999; Taylor and Hastings, 2005). Thus, this type of management could be applied to deer (Asada, 2013). However, to implement lag-phase management effectively, highly sensitive techniques are required to assess population trends in deer, especially males.

Here, we introduced a novel approach to evaluate the abundance of sika deer males using loud calls emitted by them during the rut (for details on variations in their vocalizations, see Section 2.3.1.) as a population index. Previously, bioacoustic methods have been utilized to monitor the population trends of fishes and marine mammals, which are difficult to observe, mark, or recapture (Marques et al., 2013). Such methods have generated widespread attention because they offer the potential of greater detection ranges, both underwater and in dense forests (Hobson et al., 2002; Blumstein et al., 2011; Depraetere et al., 2012; Aide et al., 2013; Marques et al., 2013; Kalan et al., 2015). Bioacoustic methods used to assess the abundance of animals fall into two broad categories: (1) passive acoustic monitoring (PAM), which relies on the detection of sounds spontaneously emitted by a target animal, and (2) active acoustic monitoring (AAM), which relies on the return echo of a transmitted acoustic signal being reflected off the target and, thus, detected (Marques et al., 2013). In a broader sense, AAM includes a type of sound playback survey, which has been developed for sound-producing animals who respond to acoustic stimuli, such as birds (Legare et al., 1999; Watson et al., 1999; Conway et al., 2005) and primates (Peck et al., 2011; Gestich et al., 2016). Behavioral studies have shown that the adult males of most cervids emit loud calls during the rut (De Vos et al., 1967; Kiley, 1972). Furthermore, some cervid species are vocally responsive, producing calls that can be elicited by audio playbacks. For example, red deer stags (*Cervus elaphus*) roared in response to a common roar reproduced by a loudspeaker, with a probability of 92% (Garcia et al., 2014), whereas roe deer bucks (*Capreolus capreolus*) counterbarked in response to a sound source at a rate of approximately 35% (Reby et al., 1999).

Therefore, the present study aimed to define the potential and limits of PAM and AAM for sika deer males occupying sites with different population densities. We compared these acoustic approaches with the existing approaches of spotlight and camera-trap surveys. In particular, we aimed to answer specific questions when using PAM and AAM under field conditions. For PAM, we verified: (1) feasibility— by determining how the density of males and the time of day influenced the frequency of loud calls in an area of interest, (2) efficiency—by identifying the detection range of loud calls using a sound recorder, and (3) sampling optimization—by determining the minimum sampling effort required to obtain evidence of the presence/absence of males in an area. For AAM, we ascertained: (1) feasibility—by determining whether sika deer can be regarded as a vocally responsive species, (2) sampling optimization— by determining the optimal sound source required to provoke loud calls by males; (3) practicality— by determining to what extent the frequency of loud calls elicited by audio playbacks could explain male abundance.

## 2. Methods

### 2.1. Study area

Since the mid 1980s, the range of sika deer in Japan has extended to the northeastern mainland, which is covered with cool-temperate forests and is subject to heavy snowfall (Takatsuki, 2009). Within this area, we established three study sites—Konsei, Kotoku, and Senjyu—in the Nikko Region, some parts of which have become typical breeding ranges of the deer in recent years, and two sites—Komado_N and Komado_S—in the Aizu Region, where deer ranges have formed more recently (Fig. 1). Two other ungulate species also occur in these two regions: Japanese serows (*Capricornis crispus*) and boars (*Sus scrofa*). The gray wolf (*Canis lupus*), the only predator, became extinct in the previous century. There was little difference in forest composition among the two study regions. Both regions contained patches of broadleaf forests, mainly composed of beech (*Fagus crenata*), oak (*Quercus crispula*), and elm (*Ulmus davidiana*), and conifer plantations, including larch (*Larix kaempferi*) and cedar (*Cryptomeria japonica*). In contrast, the understory vegetation varied widely with deer density, in order of decreasing density. For instance, only low-growing herbaceous plants were present in Senjyu, whereas sparse bushy trees were present in Kotoku and Konsei and dense shrubs were present in Komado_N and Komado_S. The visibility in the forests decreased considerably in the same order. The mean ambient temperature and total precipitation during the main survey periods were 9.3°C and 45.0 mm in the Nikko Region (October 2015) and 12.1°C and 26.5 mm in the Aizu Region (October 2016), respectively.

**2.2 Spotlight and camera-trap surveys**

To verify the effectiveness of the bioacoustic methods, it was necessary to acquire preliminary valid population estimates at each site. We thus conducted spotlight counts of deer on fixed survey routes along forest roads at the three sites in the Nikko Region during October 2015, and at the two sites in the Aizu Region during October 2016 (Fig. 1). Considering the continuity of forests, the route set at Komado_S was divided into three segments. Eight surveys were conducted in Senjyu, Konsei, and Komado_N, and seven surveys were conducted in Kotoku and Komado_S. The counts began 2 h after sunset or 2 h before sunrise and we used a vehicle driven at 10–20 km/h on each route. Two observers used a hand-held spotlight (Q-Beam LED, Brinkmann, TX, U.S.) to search each side of the route. When male deer were found, the vehicle was swiftly stopped perpendicular to the direction of the animal to measure the distance to it with a laser range finder (Laser 1000AS, Nikon, Japan). We then recorded their age based on the antler morphology (Miura, 1984a). To estimate the absolute abundance at each site, we analyzed the available results using the distance sampling method with the software Distance 6.2 (Thomas et al., 2010). To model the detection function, we tested all possible functions (uniform, half-normal, and hazard-rate), and we selected the best model based on the Akaike information criterion (AIC).

We also measured the relative abundance index (RAI), as an index of species abundance, through the camera-trap surveys at all sites, excluding Konsei and Kotoku. Here, we defined RAI as the number of photographs of sika deer males per survey effort. In Senjyu, we set nine cameras at >200-m intervals along suspected deer trails from October 1 to 31, 2015. Eight and twelve cameras were set at >100-m intervals on animal trails in Komado_N and Komado_S, respectively, from September 10 to October 11, 2016. Different camera models were used at different sites—D444 (Moultrie, AL, U.S.) was used in Senjyu, and both HC500 (Reconyx, WI, U.S.) and Model#119734C (Bushnell, KS, U.S.) were used evenly in the remaining sites. However, all models were low-glow infrared cameras and the camera settings were standardized: a 1-min capture delay between consecutive actuations based on the method described by Dougherty and Bowman (2012). We used photographs of males taken during the night (i.e., the exact period from sunset to sunrise) to match the measurement time of the spotlight surveys and calculated the mean and 95% confidence interval (CI) of the RAI at each site. Each CI was estimated by 10,000 bootstrap resamples on a normal interval estimation using the package simpleboot in R 3.2.5 (R Development Core Team, 2016).

## 2.3. Bioacoustic methods

### 2.3.1. Vocalization features of sika deer

The rut of sika deer extends from late September to early March, peaking in October (Miura, 1984a). During the rut, juveniles and older males greatly increase their range of call types and calling frequency (Minami and Kawamichi, 1992). Previous acoustic analyses showed that the call types emitted by males fall into 10 categories. Two of these call types are typical loud calls emitted by males during the rut: (1) the moan, which is high-pitched, then drops to a lower pitch, and is usually only produced singly, and (2) the howl, which is a high-pitched whistling call that is usually repeated two to four times (Miura, 1984b; Minami and Kawamichi, 1992). The moan is used to retain the tight grouping of females in the harem, whereas the howl is emitted to advertise the territory, whether females are present or not (Minami and Kawamichi, 1992). Hence, only the howl was used in the present study, because only a few females might have been present in sites where the density of deer was low.

**2.3.2. PAM**

We placed four, two, and three unattended sound recorders (Song Meter SM2+, Wildlife Acoustics, MA, U.S.), respectively, at the sites of Senjyu, Komado_N, and Komado_S, at >1-km intervals, to avoid duplicate recordings. We mounted all recorders on trees at a 1.5-m height and equipped them with two omnidirectional microphones (flat frequency response between 20 Hz and 20 kHz) pointing horizontally. The gain of the microphone preamplifier was set to the default value of + 48 dB. As the howls made by sika males were below 8 kHz (Minami and Kawamichi, 1992; Long et al., 1998), we set a sampling rate of 16 kHz in stereo. The audio files were saved in the lossless compressed format (.wav).

Contiguous recordings were made in Senjyu from October 9 to 14, 2015, and in Komado_N and Komado_S from October 7 to 11, 2016, without any interval. The total recording times for each recorder were 112 h in Senjyu and 86 h both in Komado_N and

Komado_S. To quantify the frequency of each howl, we reviewed the respective recordings using the bioacoustic analysis software Song Scope 4.1.3A (Wildlife Acoustics, MA, U.S.). Aural identification of the howl was fairly easy, based on visual scans of spectrograms, because no similar sounds occur in nature. We then counted the mean howl frequency in three ways (i.e., per hour, per day, and per peak period) and compared them among sites. Finally, we estimated the minimum sampling effort required to determine the occurrence of males, or the minimum time expected to record the howl at least once, at sites with different densities of deer, based on the lower limit of the bootstrapped 95% CI of the howl frequency (the same setting as described in Section 2.2).

### 2.3.3 Detection range

To measure the detection range of the PAM, we evaluated the attenuation of howls under field conditions. For this purpose, we recorded howls using a portable recorder (LS-14, Olympus, Japan) with a directional microphone (AT9944, Audio-Technica, Japan) in the ".wav" format, by directly following sika males in Senjyu in October 2014. When recording, we also measured the sound pressure level (SPL) with a sound level meter (SD-2200, Fuso, Japan), as well as the distance to deer using the range finder (described above) to calculate the theoretical SPL within 1 m of an audio source ($L_1$), using the following formula: $L_1 = 20\log_{10}(r) + L_2$, where $r$ is the distance to the deer and $L_2$ is the SPL at $r$. We successfully recorded howls from 10 different males, and the mean theoretical SPL was estimated as 96.4 ± 8.5 (standard deviation [SD]) db ($N$ = 10).

We played the recorded howl at the theoretical SPL with a loudspeaker (PDX-B11, Yamaha, Japan) and recaptured the playbacks from 10 to 150-m apart at 10-m intervals using the Song

Meter (the same setting as described in Section 2.3.2). This experiment was conducted under the most common forest cover in the cool-temperate climate, i.e., defoliated forests of beech (38°45′21″31N, 139° 45′10″72E), in November 2014. The ambient temperature and background noise were 16.0°C and 41.1 db, respectively. We defined the detection range as the distance at which the sound patterns of howls could be automatically detected in audio files using the sound recognizer of Song Scope (Agranat, 2009). This sound recognizer uses a complex digital signal processing algorithm based on hidden Markov models. The algorithm considers the spectral and temporal features of individual syllables and how syllables are organized into more complex songs (Kogan and Margoliash, 1998).

#### 2.3.4. AAM

As observed for red deer (Garcia et al., 2014) and roe deer (Reby et al., 1999), sika deer become stimulated and aroused by playbacks of deer calls (Minami, 1993). We assessed the potential of the howl-back of sika deer males against multiple sound sources (Table 1). We assigned the average howl sound, which was recorded through the former experiment (see Section 2.3.3), as the sound source played with the loudspeakers. Because deer calls specialized for sika deer were not available, we here used several commercial products aimed at attracting cervids inhabiting North America, which are comparable in size to sika deer. We set test points at >500-m intervals along the same routes used for the spotlight survey, i.e., 10 points for every route in the Nikko Region, and 12 and 13 points for Komado_N and Komado_S, respectively (Fig. 1). We played the respective sound sources at >1-min intervals in a random order according to each point at dawn (04:00–07:00) and dusk (16:00–19:00). Consistent with spontaneous howls (Miura, 1984b), we played each instrument for 4 s in sets of four at all test points for each experiment.

Based on the available data on the latency to roar back by red deer (Garcia et al., 2014), we counted the frequency of howl-backs for 10 s after playback. Eight, six, and five experiments, respectively, were conducted in Senjyu, Kotoku, and Konsei in October 2015, whereas seven and five experiments, respectively, were conducted in Komado_N and Komado_S in October 2016. We then compared the howl-back frequency among the sound sources using the Kruskal-Wallis test ($\alpha = 0.05$).

Considering the pseudo-responses caused by spontaneous howls during the experiments, we calculated the bootstrapping 95% CI (the same setting as described in Section 2.2) of the probability of spontaneous howls during the time of each experiment, using the same recording data for the PAM. Finally, to validate the extent to which the howl-back frequency could explain male abundance, we built generalized linear mixed models (GLMMs) using the frequencies caused by each sound source as the response variables. When building the models, we used a Poisson distribution with a logarithmic link function with background noise (db). The encounter rate of males was used as the explanatory variable, whereas study site was used as a random factor. Because the density of males in open sites might vary with time, we could not use male density itself, as estimated by the spotlight survey. Therefore, we used an alternative index, the encounter rate, which is defined as the abundance of males at the time of each playback experiment, within the effective strip width estimated by the distance sampling method used in this study. We selected the best-fitting models for each sound source according to the AIC. Modeling was performed using R 3.2.5 with the glmmML package.

## 3. Results

### 3.1. Spotlight and camera-trap surveys

The spotlight survey could not be used to estimate the population density at the sites in the Aizu Region, because no males were found on the routes (Table 2). The mean density of males was extremely high in Senjyu (12.92 individuals/km$^2$) and was >5 times higher than the density observed in Kotoku and Konsei. Similar results were confirmed by the camera-trap surveys, whereas the RAI was 0.37 individuals/camera-night (CN) in Senjyu, with zero and one male being captured in Komado_N and Komado_S, respectively.

**3.2. PAM**

Unlike the spotlight and camera-trap surveys, PAM detected the presence of males in both regions (Fig. 2). The howl frequency peaked at a similar time in all three regions (i.e., Sennjyu, Komado_N, and Komado_S), with bimodal peaks occurring at dawn and dusk, except for an additional peak in the evening (21:00) at Komado_S. The SEs of howl frequency in the Aizu Region were relatively high, due to the extremely low male density.

The attenuation of howl sounds inside the forests became pronounced, as shown by visual scans of the spectrograms and auditory-based identification when the distance from the loudspeaker exceeded 100 m (Fig. 3). The sound recognizer produced by Song Scope showed that howls could be correctly detected up to a distance of 140 m.

To estimate the minimum sampling effort required for PAM, we compiled the mean howl frequency per day and per peak period (Table 3). The lowest howl frequency occurred in Komado_N (i.e., most recently formed range), with the lower 95% CI of 0.30 per day and 0.08 per period. This result meant that >3.33 recorders × days and >12.50 recorders × periods represented the minimum sampling effort required to confirm the presence/absence of males in the initial stage of invasion.

### 3.3. AAM

We repeatedly confirmed that howls followed audio playbacks at every site (Fig. 4). The probability of spontaneous howls occurring during each experiment was 0.97% (95% CI, 0.80–1.15), 0.04% (0.01–0.07), and 0.09% (0.05–0.13) in Senjyu, Komado_N, and Komado_S, respectively. These upper 95% CIs demonstrated that most howls confirmed after playback represented true responses. The howl-back rates did not vary widely with the different sound sources (Kruskal-Wallis test: $P > 0.05$ for all sites). The current distance sampling method estimated the effective strip width of each route as 37.9, 24.5, and 32.0 m in Senjyu, Konsei, and Kotoku, respectively; however, this value was not obtained for the sites in the Aizu Region, where no males were found (Table 2). Based on these widths, we calculated the encounter rates for each playback experiment, and used these rates to build models, excluding the dataset from the Aizu Region. The best-fitting models, when using the respective sound sources, demonstrated that the howl-back rate against the playback of recorded howls efficiently explained male abundance, as shown by the highest δAIC, with nearly 50% deviance being explained (Table 4).

## 4. Discussion

Both native and introduced (exotic) sika deer are considered to have the potential to expand their distribution (Fuller and Gill, 2001; Bartoš, 2009; Ohashi et al., 2014); thus, a wide variety of issues are expected to be encountered in the future. Hence, precautionary measures against such issues are required; yet, the management of cervids, including sika deer, tends to be implemented after problems become obvious (Fuller and Gill, 2001; Côté et al., 2004; Takatsuki, 2009). Existing techniques to monitor populations within the framework of initial management efforts to regulate overabundant cervids have proven beneficial, especially spotlight surveys (Whipple et al., 1994; Uno et al., 2006; Garel et al., 2010). The reliability of the spotlight survey based on distance sampling is dependent on vegetation cover, because the effective strip width narrows with decreasing visibility in the forests (Whipple et al., 1994). Thus, spotlight surveys are not effective when used in study sites with low deer density where the browsing line of deer has not yet appeared, as demonstrated in the present study (Table 2).

With recent developments in statistical techniques, the camera trap survey could provide a population index, such as the RAI, and the absolute abundance of deer (Dougherty and Bowman, 2012; Ikeda et al., 2013). Yet, camera traps have a technical disadvantage due to a limited detection zone in which they can detect the heat signature and motion of a target. For instance, the detection zone varies widely with current camera traps, ranging between 15.8 and 324.1 $m^2$ (Meek et al., 2012). In the present study, the maximum detection zone was observed using the HC500 (Reconyx). Our results showed that limited detection zones are detrimental for detecting rarely encountered (or widely dispersed) animals (Table 2).

Like the camera trap survey, PAM is a hands-off approach used to assess population abundance. Although the detection zone of PAM needs to be verified under more diverse landscape and climatic conditions, its detection zone was estimated as 61,544 $m^2$ ($= 140^2 \times \pi$) in defoliated forests, which was nearly 200-times wider than that of the HC500 camera. Aside from detectability, PAM might have more advantages that overcome two major sampling errors associated with placement and observers in camera-trap surveys. Because camera-trap surveys completely depend on visual information, the selection of a camera location to optimize capture probability tends to result in non-random, biased placement (Foster and Harmsen, 2012). In comparison, audio information is less sensitive to the local environment, such as the position of standing trees or the presence/absence of animal tracks in front of the recorder. Consequently, placement bias is minimal for PAM. Moreover, PAM readily analyzes large amounts of data through automated data collection and sound discrimination of a subject species (Marques et al., 2013). Consequently, inter-observer bias does not exist for PAM (i.e., it is automated), but it often arises when photographs from camera-trap surveys are checked manually (Foster and Harmsen, 2012). Thus, the greatest benefit of the PAM may be its user-friendliness, especially for wildlife managers without substantial experience.

The diel rhythms of sika deer males emitting howls were not influenced by animal density, with bimodal peaks being commonly observed around sunrise and sunset (Fig. 2). Thus, we recommend that the recording period should be narrowed to occur only during these bimodal peaks, which would help to prolong the monitoring period by economizing the battery life and storage capacity of the recorder, as well as saving time processing the sound discriminations. The evaluations in the present study demonstrated that PAM is highly beneficial for population assessments during the initial stage of deer invasion, and during the ex-post stage (following population control), because it confirmed the presence/absence of males at a given site. Unfortunately, because the existing methods (i.e., the spotlight and camera-trap surveys) detected few males in the present study sites with extremely low deer density, we could not obtain comparative data to validate the detailed relationships between howl frequency and male density. To expand the application of PAM to quantitative population assessments, further experiments are required in enclosures containing sika deer males of known abundance.

The experiments performed by the present study using AAM verified that sika deer are sound-producing cervids that respond to acoustic stimuli, similar to red deer (Garcia et al.,

2014) and roe deer (Reby et al., 1999). Even though sika deer males responded to most sound sources (Fig. 4), inter-individual variation in howl-back rates might increase when exposed to unfamiliar artificial sounds, such as deer whistles. This issue might be supported by the fact that the howl-back frequency against familiar sounds (i.e., recorded real howls) was not always the highest, but most efficiently reflected male abundance at that time. Thus, AAM using a playback of a real howls might represent a feasible way of assessing population abundance, even when the density of deer is low. However, the season when AAM is used should be noted because the frequency of spontaneous howls varies over time during a rut (Minami and Kawamichi, 1992; Yen et al., 2013). For instance, it would be best to avoid using AAM during all months except October, which is the peak month of the rut (Miura, 1984a).

In some cases, the sounds emitted by animals have a distinctive pattern, which can be used to identify individuals (Fox, 2008; Marques et al., 2013). Fortunately, a recent study demonstrated that the howl emitted by sika deer males is a typical sound used to discriminate individuals (Yen et al., 2013). This phenomenon facilitates using PAM and AAM within the framework of capture-recapture sampling techniques (Thompson, 2012), which might improve the accuracy of estimates. Thus, a bioacoustic approach could become integral for the efficient monitoring of sika deer populations, as well as other sound-producing cervids that respond to acoustic stimuli.

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## Figure Captions

Fig. 1. Study area located in eastern Japan. Black solid lines and white dots in (A) and (B) show the routes used for the spotlight survey and the test points used for active acoustic monitoring (AAM), respectively. The total route length was 9.9 km in Konsei, 6.2 km in Kotoku, 5.2 km in Senjyu, 12.7 km in Komado_N, and 14.9 km in Komado_S (L1 = 7.5, L2 = 2.0, L3 = 5.4).

Fig. 2. Hourly variation in the frequency of howls emitted by male sika deer, confirmed using Song Meters set in the Nikko and the Aizu Regions in October 2015 and 2016, respectively. Values in parentheses and white bars represent *N* and SE, respectively. Sunrise and sunset occurred approximately at 5:40 a.m. and 5:10 p.m., respectively, in each area.

Fig. 3. Sound spectrograms of the playbacks of howls emitted by male sika deer, which were recorded at different distances. The signal becomes stronger from green to red within the spectrograms.

Fig. 4. Comparison of the howl-back rate among study sites, conducted in the Nikko Region (Senjyu, Kotoku, Konsei) in October 2015 and in the Aizu Region (Komado_N, Komado_S) in October 2016. Bars represent SE. *N* is the number of experiments conducted at each site. Abbreviations of sound sources are shown in Table 1.

Table 1. Audio features of the sound sources used for active acoustic monitoring (AAM) of sika deer populations.

| Classification | Abbreviation | Manufacturer | Product name | Max. SPL (db)[a] | Formant (kHz)[b] | | Sounds used | |
|---|---|---|---|---|---|---|---|---|
| | | | | | F1 | F2 | Nikko | Aizu |
| Loudspeaker[c] | Real | Harman, CT, U.S. | JBL Xtreme | 100.4 | 1.5 | 3.0 | ✓ | |
| Loudspeaker[c] | Real | TOA, Japan | ER-2830W | 120.7 | 1.5 | 3.0 | | ✓ |
| Electronic sound[d] | Bleat | Primos, MS, U.S. | Speakeasy deer | 91.4 | 0.5 | 1.0 | ✓ | |
| Whistle | Ranger | Carlton's Calls, IA, U.S. | Long ranger | 92.7 | 2.0 | 2.5 | ✓ | |
| Whistle | Wheeze | Primos, MS, U.S. | Grunt wheeze | 103.2 | 1.0 | 2.5 | ✓ | ✓ |
| Whistle | Grunter | Primos, MS, U.S. | Hardwood grunter | 93.8 | 0.5 | 1.0 | ✓ | ✓ |

[a]Measured using the sound level meter within 1 m of each source.

[b]First and second formant (F1 and F2), which are the major components of sound used to determine vowels, were identified using the Song Scope 4.1.3A.

[c]Recorded howl was played through the loudspeakers.

[d]Only the bleat sound was selected from the instrument.

Table 2. Absolute and relative abundance of male sika deer[a] in the Nikko and Aizu Regions of eastern Japan, estimated by spotlight and camera-trap surveys.

| | Spotlight survey | | | | | Camera-trap survey | | | |
|---|---|---|---|---|---|---|---|---|---|
| | # observed on routes | Mean density | 95%CI | | | RAI | 95%CI | | Camera night |
| Sites (regions) | (ind./km) | (ind./km$^2$) | Lower | Upper | *N* | (ind./CN) | Lower | Upper | (CN) |
| Senjyu (Nikko) | 1.05 | 12.92 | 9.21 | 18.13 | 8 | 0.37 | 0.28 | 0.47 | 279 |
| Konsei (Nikko) | 0.08 | 1.47 | 0.57 | 3.77 | 8 | n.d. | | | |
| Kotoku (Nikko) | 0.12 | 2.17 | 0.63 | 7.42 | 7 | n.d. | | | |
| Komado_N (Aizu) | 0.00 | n.a. | | | 8 | 0.00 | 0.00 | 0.00 | 248 |
| Komado_S (Aizu) | 0.00 | n.a. | | | 7 | 0.00 | 0.00 | 0.01 | 372 |

[a]Fawns and yearlings were excluded because they could not howl.

Table 3. Mean frequency of howls by male sika deer per day (01:00 –24:00) and per peak period—during both dawn (04:00–07:00) and dusk (16:00–19:00)—, recorded with Song Meters.

| | Day | | | | Peak period | | | |
|---|---|---|---|---|---|---|---|---|
| | | 95% CI | | | | 95% CI | | |
| Sites (Regions) | # howls/day | Lower | Upper | *N* | # howls/period | Lower | Upper | *N* |
| Senjyu (Nikko) | 47.80 | 36.54 | 59.21 | 20 | 20.70 | 15.87 | 25.47 | 20 |
| Komado_N (Aizu) | 1.38 | 0.30 | 2.46 | 8 | 0.75 | 0.08 | 1.42 | 8 |
| Komado_S (Aizu) | 4.64 | 2.17 | 7.16 | 11 | 2.00 | 0.93 | 3.07 | 11 |

Table 4. Mean ± SE coefficients of explanatory variables in the best-fitting generalized linear mixed models used to estimate the frequency of howl-backs by male sika deer against each sound source in the Nikko regions, Japan.

| Response variable[a] | Intercept | Encounter rate | Background noise | AIC | δAIC[c] | %DE[d] |
|---|---|---|---|---|---|---|
| Real | 2.96 ± 1.42[b] | 2.97 ± 0.86[b] | −0.08 ± 0.04 | 21.81 | 9.60 | 49.63 |
| Ranger | −0.69 ± 0.78 | 0.69 ± 1.38 | | 29.26 | −1.75 | 1.06 |
| Bleat | −0.13 ± 0.33 | 0.59 ± 0.90 | | 34.37 | −1.60 | 1.39 |
| Wheeze | 3.34 ± 1.32[b] | 1.25 ± 1.01 | −0.07 ± 0.04[b] | 48.50 | 0.65 | 10.30 |
| Grunter | 0.00 ± 0.50 | 1.43 ± 0.90 | | 51.85 | 0.27 | 4.72 |

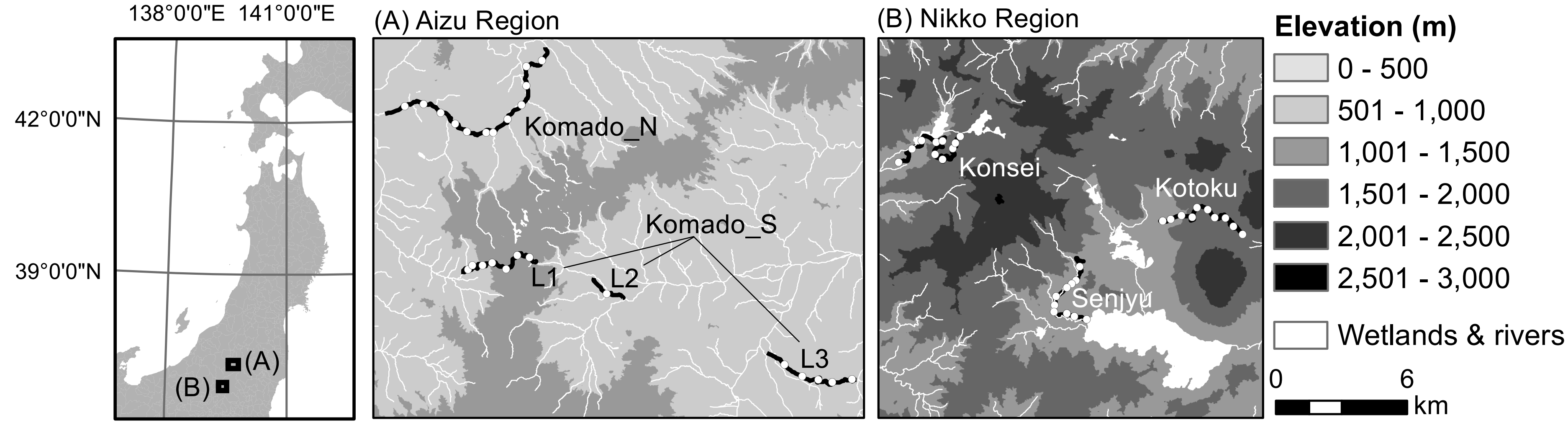
[a]Full terms of the abbreviations are provided in Table 1.

[b]$Pr(z) < 0.05$

[c]δAIC indicates the difference from the AIC value in the null model.

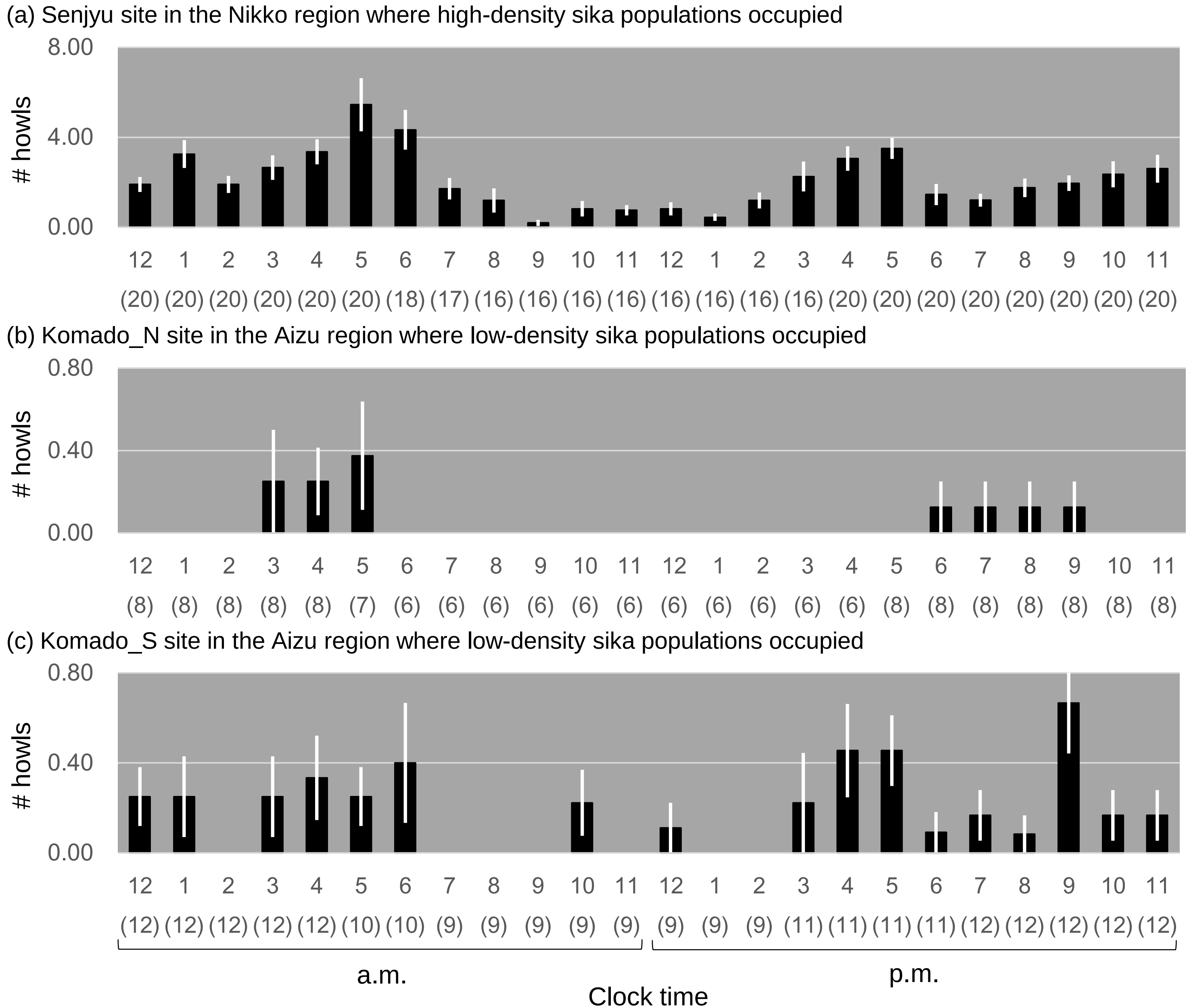
[d]DE indicates deviance explained; %DE = (1-Deviance/Null deviance) × 100

Fig. 1



138°0'0"E
141°0'0"E
42°0'0"N
39°0'0"N
(A)
(B)
(A) Aizu Region
Komado_N
Komado_S
L1
L2
L3
(B) Nikko Region
Konsei
Kotoku
Senjyu
Elevation (m)
0 - 500
501 - 1,000
1,001 - 1,500
1,501 - 2,000
2,001 - 2,500
2,501 - 3,000
Wetlands & rivers
0
6
km

Fig. 2



(a) Senjyu site in the Nikko region where high-density sika populations occupied
8.00
4.00
0.00
# howls
12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11
(20) (20) (20) (20) (20) (20) (18) (17) (16) (16) (16) (16) (16) (16) (16) (16) (20) (20) (20) (20) (20) (20) (20) (20)
(b) Komado_N site in the Aizu region where low-density sika populations occupied
0.80
0.40
0.00
# howls
12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11
(8) (8) (8) (8) (8) (7) (6) (6) (6) (6) (6) (6) (6) (6) (6) (6) (6) (8) (8) (8) (8) (8) (8) (8)
(c) Komado_S site in the Aizu region where low-density sika populations occupied
0.80
0.40
0.00
# howls
12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11
(12) (12) (12) (12) (12) (10) (10) (9) (9) (9) (9) (9) (9) (9) (9) (11) (11) (11) (11) (12) (12) (12) (12) (12)
a.m.
p.m.
Clock time

Fig. 3

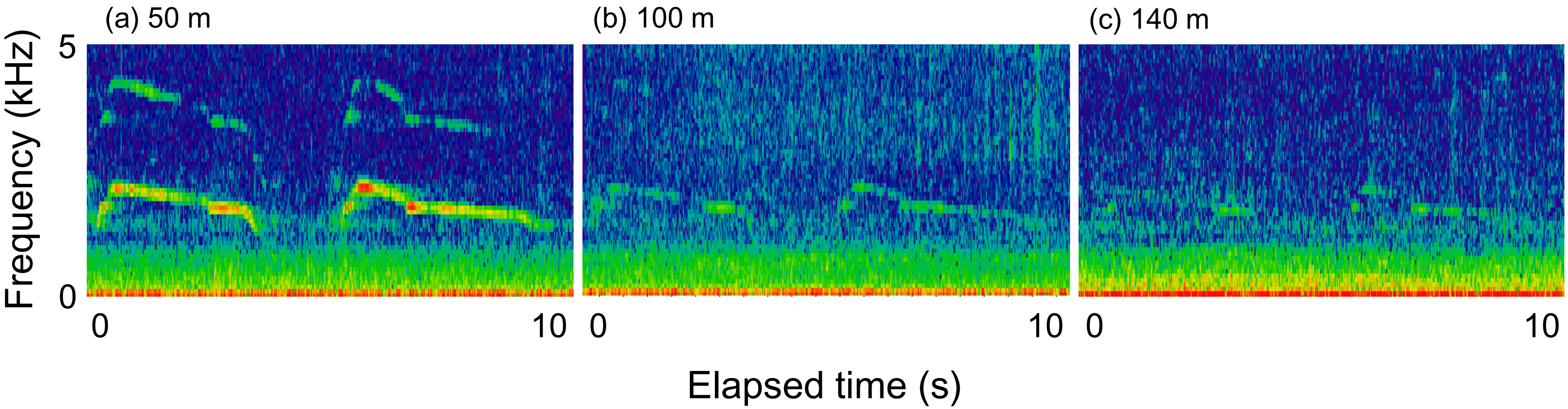
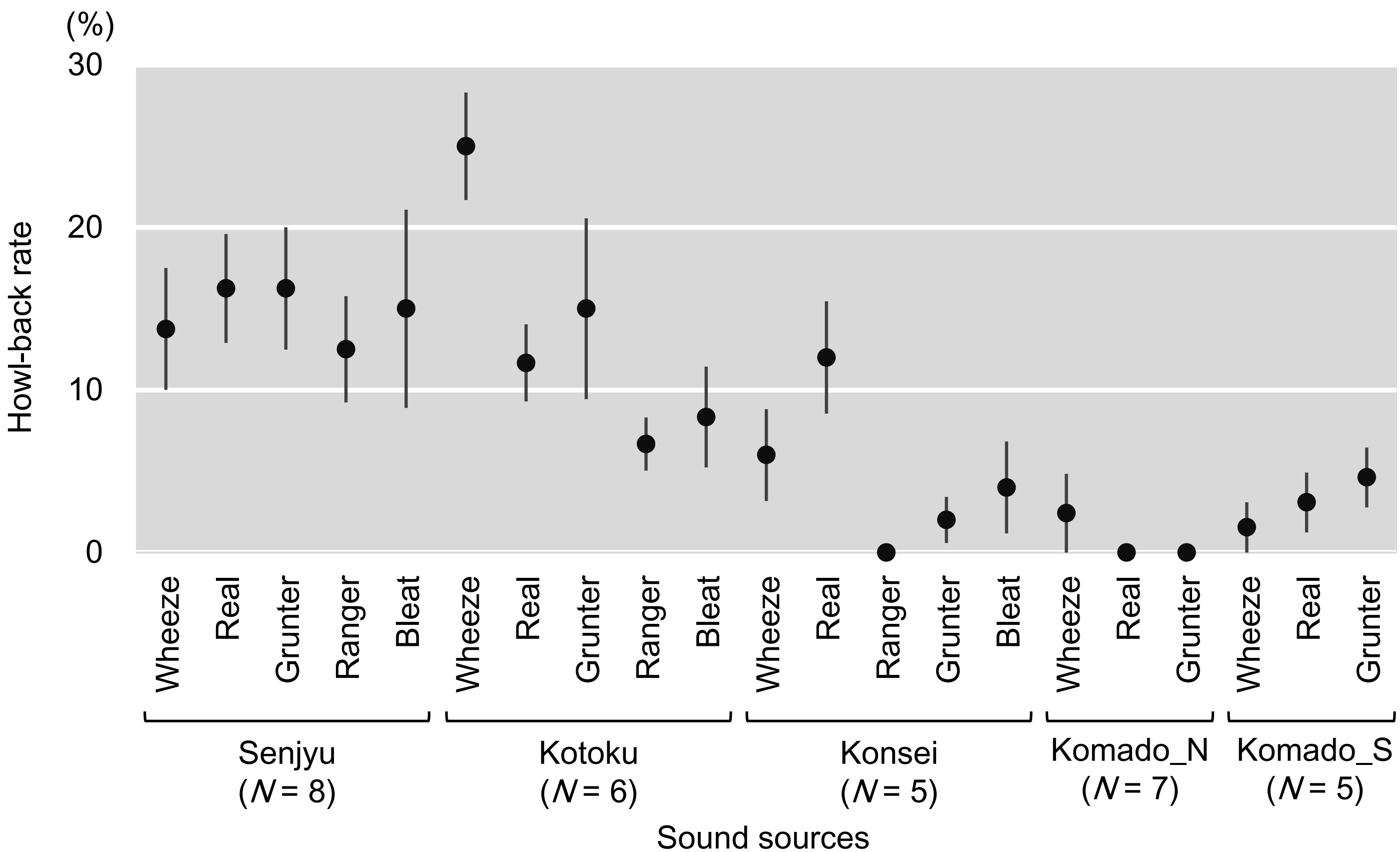


Fig. 4


(%)
30
20
10
0
Howl-back rate
Wheeze
Real
Grunter
Ranger
Bleat
Wheeze
Real
Grunter
Ranger
Bleat
Wheeze
Real
Ranger
Grunter
Bleat
Wheeze
Real
Grunter
Wheeze
Real
Grunter
Senjyu
(N = 8)
Kotoku
(N = 6)
Konsei
(N = 5)
Komado_N
(N = 7)
Komado_S
(N = 5)
Sound sources