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ORIGINAL ARTICLE

Effects of land use and climate on the distribution of the Jungle Nightjar *Caprimulgus indicus* in Hokkaido, northern Japan

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Abstract Although the relative importance of land use and climate to large-scale bird distributions has received great attention, it is difficult to separate the effects of land use and climate, and there are few studies on bird abundance distributions on a large scale. Here, we examined the effects of land use and climate on the abundance of the nocturnal Jungle Nightjar *Caprimulgus indicus* in Hokkaido, northern Japan. We chose 125 sampling sites with low correlations ($|r| < 0.58$) between land use and climate, and combined a playback method with a hierarchical model (N-mixture model). We thereby accounted for the possibility that we could not detect all individuals during the field survey. Results show that Jungle Nightjar abundance was greater at sites within a 4-km radius of moderate forest cover (~75%) and with high average temperatures during the breeding season. Moreover, the effects of land-use were greater than those of climate. Mapping predictions of Jungle Nightjar abundance indicated that suitable areas are distributed in southern and central Hokkaido and around the margins of montane zones. Factoring in the covariation of land use and climate, land use may be the most important driver of the distribution of the Jungle Nightjar in Hokkaido.

Key words Abundance, Forest cover, Playback, N-mixture models, Topography

Changes in land-use and climate are two key threats to contemporary biodiversity worldwide (Thomas et al. 2004; Foley et al. 2005; Bellard et al. 2012; Garcia et al. 2014; Haddad et al. 2015; Newbold et al. 2015), and their relative importance to large-scale bird distributions is a topic of active examination and discussion (Jetz et al. 2007; Barbet-Massin et al. 2012; Beale et al. 2013). Thus far, it has been suggested that land use has a substantial effect on bird distributions at small scales (i.e., landscape or regional; Ferraz et al. 2007; Quesnelle et al. 2013), and a lesser effect than climate and topography at larger scales (i.e. national or continental; Davies et

al. 2007; Barbet-Massin et al. 2012). However, several studies have indicated that the effects of land use may be underestimated due to strong correlations among land use, climate, and topography (Yamaura et al. 2011; Reino et al. 2013).

These apparently small effects may be due to the traditional use of species presence/absence data. Most studies conducted at large scales have considered the presence/absence or species richness of a given species based solely on binary presence/absence data (Thuiller et al. 2004; Davies et al. 2007; Barbet-Massin et al. 2012) because these are easier to obtain than abundance data (Gaston et al. 2000). On the one hand, abundance can vary widely with land-use changes due to the positive relationship between abundance and habitat area (Fischer & Lindenmayer 2007). On the other hand, presence/absence cannot

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change when at least one individual is present. Therefore, the effects of land use may increase when we consider abundance data rather than the presence/absence paradigm used in most previous studies of large-scale bird distributions (Howard et al. 2014). Indeed, abundance is a fundamental metric in basic and applied ecology (Sagarin et al. 2006; Gaston & Fuller 2008), and thus should be used when examining the relative effects of land use and climate on bird distributions at large scales (Howard et al. 2015; Inger et al. 2015).

Our objective was to examine the relative effects of land use, climate, and topography on the large-scale distribution of the Jungle Nightjar *Caprimulgus indicus* in Hokkaido, northern Japan, using abundance data. The Jungle Nightjar breeds in open habitats surrounded by forests (Kiyosu 1965; Fujimaki 1973), and appears in various habitats types (e.g. grasslands, meadows, farmlands, deciduous broadleaf forests, pine forests and plantation forests) (Kiyosu 1965; Dement'ev & Gladkov 1966; Fujimaki 1973; Cleere & Nurney 1998). Therefore, both open habitats and forests should be important for the Jungle Nightjar. The Japanese population of the species has declined dramatically in recent decades (Amano & Yamaura 2007), possibly as a consequence of the effects of land-use change, i.e. a reduction in open habitats combined with forest maturation (Yamaura et al. 2009).

Climatic factors such as temperature are also likely to affect the large-scale distribution of the Jungle Nightjar. In a related species, the European Nightjar *C. europaeus*, Morris et al. (1994) suggested that colder springs and summers could depress insect prey abundance, which would negatively affect their breeding. One of the main prey sources of the European Nightjar is a moth species (Cleere & Nurney 1998), and previous studies have shown that Lepidopteran species are more diverse and abundant in warmer regions in Britain (Turner et al. 1987; Roy et al. 2001). The Jungle Nightjar shares similar ecological traits with the European Nightjar, including body size, migratory behaviour, habitat, and prey (Kiyosu 1965; Dement'ev & Gladkov 1966; Fujimaki 1973; Cleere & Nurney 1998); thus, we expect that temperature affects the abundance of insect prey (e.g. moth species) and thereby the abundance of the Jungle Nightjar in Hokkaido.

Japan's northern island of Hokkaido (a single prefecture of approximately 83,424 km²) is a suitable region in which to address this problem because only

approximately 150 years have passed since modern land development began there (Hokkaido 1970), and large areas of lowland forests still remain. This situation allows us to select sampling sites to avoid correlations among land uses, climatic factors, and topography. In Hokkaido, approximately 70% of the land is covered by forests, 27% of which consist of plantations (Forestry Agency 2015). In Japan, many forest plantations are maturing due to the decline of forestry, and plantations under 10 years old now account for approximately 2% of the total (Forestry Agency 2015). In Hokkaido, forests planted in 2013 (i.e. new plantations) cover 92 km², which is a small proportion compared with the current total area of plantation in the prefecture (55,430 km²) (Forestry Agency 2015). Approximately 15% of Hokkaido consists of open, cultivated areas, including: rice fields (2,234 km²), vegetable crops (4,142 km²), and meadows and pastures (5,075 km²) (Ministry of Agriculture, Forestry and Fisheries 2015). We investigated the broad-scale abundance distribution of the nocturnal Jungle Nightjar using a combination of replicated point counts and a playback method, accounting for imperfect detection. Finally, we mapped the predicted abundance to understand the potential importance of land use to the large-scale distribution of this species.

There have been very few studies of Jungle Nightjar habitat selection, and their territory size and home range remain unknown. In contrast, the European Nightjar has been well studied, and its territory size and home range are clearly documented (Alexander & Cresswell 1990; Bowden & Green 1994; Conway et al. 2007; Sharps et al. 2015). While open habitat is essential for European Nightjar breeding, the size of open habitats required for territorial establishment is variable (Wichmann 2004; Cross et al. 2005; Verstraeten et al. 2011). Furthermore, Sharps et al. (2015) showed that open habitat is essential not only for nesting, but also for foraging, suggesting that open habitats may also be important to the Jungle Nightjar at both the territory- and home-range scales. We designed the field survey and analyses assuming that the territory size and home range of the Jungle Nightjar were similar to those of the European Nightjar.

MATERIALS AND METHODS

1) Study area and site selection

Hokkaido has a wide range of environmental gradients in climatic, topographic, and land-use conditions,

including annual mean temperature and precipitation, as well as elevation and forest cover. We selected 25 study regions across the island and established five sampling sites in each region (Fig. 1). Specifically, we established a total of 125 sampling sites with low correlations among explanatory variables ($|r| < 0.58$). Dormann et al. (2013) suggested that using explanatory variables with $|r| < 0.7$ is an appropriate countermeasure to the problem of collinearity. Therefore, we used all explanatory variables (see details in the “explanatory variables” section and Appendices 1, 3). In the case of the European Nightjar, song-post distances between adjacent territories are estimated to be approximately 300 m (Bowden & Green 1994; Conway et al. 2007). As we recorded male Jungle Nightjars responding within a 250-m radius of the centre of each sampling site, we spaced sampling sites over 800 m apart to prevent double-counting individuals. Although one sampling site was only 725 m away from the nearest neighbouring site, we included it in the analysis because we detected no Jungle Nightjars at the site.

2) Explanatory variables

We selected environmental factors that potentially affect Jungle Nightjar distribution: forest cover within 250 m and within 4 km of each sampling site as the land-use factor, temperature during the breeding season as the climatic factor, and elevation as the topographic factor. Details are shown below.

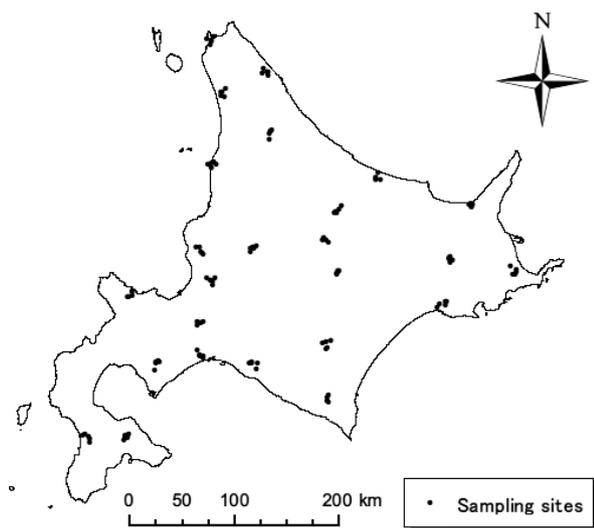


Fig. 1. Distribution of sampling sites, where we examined Jungle Nightjar abundance, in Hokkaido, northern Japan. Five adjacent dots represent sampling sites in one study region.

Land use

We selected the presence of forest cover, including all types of forests (e.g. natural deciduous broadleaf forests and coniferous plantations), as the land-use variable of interest. Although more detailed land-use types, such as old-growth natural forests or recently harvested areas of forestry plantations, may explain the distribution of the Jungle Nightjar more precisely, we were not able to obtain more detailed land-use data at the scale of this study. To assess scale-dependent effects of forest cover, we considered the forest cover at both the territory- and home range-scales. The territory of the European Nightjar falls within approximately 200 m of the nest (Bowden & Green 1994; Conway et al. 2007). The maximum home range size of the European Nightjar has been reported in several studies (Alexander & Cresswell 1990; Sharps et al. 2015). Alexander & Cresswell (1990) reported a mean maximum distance travelled per night of 3.1 km (maximum: 5.8 km), while Sharps et al. (2015) reported 747 m (maximum: 2.6 km). Sharps et al. (2015) considered that a complex forest landscape can lead to European Nightjars occupying small home ranges when foraging and nesting habitats exist in the vicinity. Because our sampling sites were embedded in varied landscapes with different proportions of land-use, we measured forest cover within 250 m and within 4 km of each sampling site (hereafter 250-m and 4-km forest cover, respectively) using ArcGIS 10.0 (ESRI, CA, USA). First, we made two circle buffers with radii of 250 m and 4 km centred on each sampling site. Then, we overlaid these circles on the High Resolution Land-Use and Land-Cover Map (2006–2011) provided by the Japan Aerospace Exploration Agency (JAXA), and measured forest cover within these circles. We corrected the 250-m forest cover using visual observations at each sampling site.

Climate

We selected average temperature during the breeding season (i.e., from June to August) as a representative climatic variable (see detail in Appendix 4). Although other climatic factors, such as precipitation, might also be candidate variables, we only selected the average temperature in order to reduce the number of explanatory variables. We calculated the average temperature during the breeding season at each sampling site using ArcGIS 10.0 (ESRI, CA, USA) and Mesh Climate Value 2000, which is a contiguous nationwide grid consisting of 1-km² squares with

30-year (1971–2000) mean monthly temperatures, provided by the Meteorological Agency of Japan.

Topography

We selected elevation as the topographic variable. Elevation is an essential environmental factor determining large-scale bird distributions (Davies et al. 2007). Furthermore, Kiyosu (1965) reported that Jungle Nightjar abundance was greater in areas at elevations of 400–1,500 m in Japan's main island, Honshu. While elevation and temperature are generally negatively correlated, and it is difficult to separate the effect of these factors, we solved this problem by selecting sampling sites with low correlation between elevation and temperature ($|r| < 0.58$). We determined the elevation at each sampling site using ArcGIS 10.0 (ESRI, CA, USA) and the 50-m digital elevation model (DEM) provided by the Geospatial Information Authority of Japan.

3) Field sampling

We used a playback survey to investigate Jungle Nightjar abundance (see Bibby et al. 2000). Playback surveys, in which the song of the focal species is broadcast and responses are noted (Fuller et al. 2012), have been used for the European Nightjar (Bartolommei et al. 2013) and the Blackish Nightjar *C. nigrescens* (Sberze et al. 2010), but not previously for the Jungle Nightjar. However, our preliminary surveys indicated that Jungle Nightjars could be called back throughout their breeding season (Yuichi Yamaura & Masayuki Senzaki personal observations). Thus, we conducted playback surveys from mid-June to early August 2014 on both clear and cloudy nights. The distances to which sounds travel are affected by wind strength and direction; therefore, we conducted surveys when wind speeds were < 5 m/s. We completed the surveys at night between 1930 and 0330, when Jungle Nightjars were most active. We visited each sampling site twice at intervals of at least 18 days. A survey lasted 10 minutes and consisted of five minutes of playback and five minutes of waiting. We played back the male territorial song using a speaker (PDX-B11: Yamaha, Hamamatsu, Japan) connected to a player (iPhone 5s: Apple, California, USA). The amplitude of the playback was set to be approximately 40 dB at 250 m from the speaker. We recorded the number of individuals responding simultaneously within a 250-m radius of each site for the duration of each survey (i.e. 10 minutes).

4) Statistical analysis

We used an N-mixture model to analyse abundance following Royle (2004). The model separates ecological processes from detection processes, and infers abundance and the effects of explanatory variables on these state variables (see details in Appendix 5).

The response variable was the number of individuals detected during each playback survey. For the analysis, we considered six explanatory variables in the ecological process model: 250-m and 4-km forest cover, their respective squared terms, the average temperature, and elevation. The squared terms of each forest cover, which represent single-peak (unimodal) effects of forest cover, were included because forest edge length is largest under moderate forest cover (Fahrig 2003), and it is possible that the Jungle Nightjar prefers areas with moderate forest cover. In the detection process model, we used observation date (1 = the first survey date, i.e., 16 June) as a single explanatory variable. All variables in the ecological process model were standardised in the analyses. We constructed models for all possible combinations of the explanatory variables and ranked them by Akaike's information criterion (AIC) (Burnham & Anderson 2002). When several models resulted in ΔAIC results < 2 , we performed model averaging and examined the relative importance of each explanatory variable (Burnham & Anderson 2002). We interpreted the effects of each variable in averaged models at the 5% significance level. We conducted these analyses using *unmarked* v. 0.10–6 (Fiske & Chandler 2011) under R v. 3.1.1 (R Development Core Team 2014).

It is possible that observation clock time also affects detection probability. Therefore, we examined the effects of observation clock time in the detection model of the N-mixture model using the data for which observation clock time was available (we did not record the survey time at all of the sites). We added observation clock time, which takes a value between -4.5 and 3.5 (i.e. -4.5 , 0 , and 3.5 indicate 1930, 2400, and 0330, respectively), and its squared term as explanatory variables. Other variables were the same as in the above analysis. However, the effect of observation clock time was not significant (Appendix 6), so we did not consider the effects of observation clock time in this study.

In this study, we established five sampling sites in each study region. Therefore, we tested whether there was an effect of spatial autocorrelation among sites using a Generalised Linear Mixed Model (GLMM) with log-link function and Poisson error. The maxi-

mum number of individuals detected at each site was treated as the response variable, the six environmental factors used in the hierarchical models described above were also treated as explanatory variables, and study region was treated as a single random variable. The random variable was assumed to follow a normal distribution with a mean of zero and a standard deviation of s . Results showed that the size of the effect of the random variable was smaller than effects of the explanatory variables (Appendix 8), and did not differ greatly from the results of the N-mixture models (e.g. Appendix 7–8). Therefore, we did not consider spatial autocorrelation in the N-mixture model.

5) Mapping the abundance distribution of the Jungle Nightjar

To predict the abundance distribution of the Jungle Nightjar in Hokkaido, we used the most parsimonious model among the N-mixture models with $\Delta AIC < 2$ (hereafter “the prediction model”). The prediction model had three explanatory variables (i.e. the average temperature, 4-km forest cover and its squared term). We divided Hokkaido into 500×500 -m grids and stored the values of each explanatory variable in each grid. Then, we calculated the expected number of territorial male nightjars in each grid (grid λ_i) by extrapolating from the prediction model. In this calculation, the expected number of territorial male

nightjars in each grid was adjusted by the grid size (A_i ; at most 250,000 m²) because the survey area at each site (i.e., 196,250 m² based on a 250-m radius circle) differed from the grid size, $\text{grid}\lambda_i = \lambda_i \times A_i / 250^2 \pi$. By assuming that urban areas and bodies of water are unsuitable for nightjar breeding (Cleere & Nurney 1998) in this abundance estimation, in each grid, we excluded areas classified as urban or water in the High Resolution Land-Use and Land-Cover Map (2006–2011) provided by JAXA. We used ArcGIS 10.0 for these mapping procedures.

RESULTS

We detected Jungle Nightjars at 23 of 125 sites. A maximum of three individuals were detected at any one site, and two individuals were detected at four sites (Fig. 2). A total of 19 individuals was detected during the first survey cycle and 25 during the second. The number of individuals detected in the first and second survey cycles differed at 12 sites.

In all, six N-mixture models had $\Delta AIC < 2$. In the N-mixture averaged model, 4-km forest cover and its squared term tied for the highest relative importance value (1.00), followed by the average temperature (0.84). The squared term of 4-km forest cover was also significant, and 4-km forest cover and the average temperature were marginally significant (Table

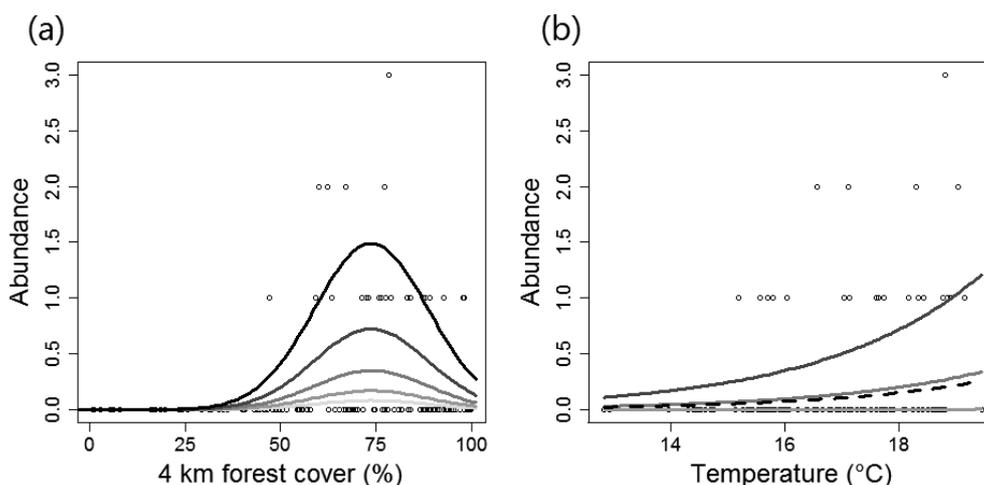


Fig. 2. Relationship between (a) abundance and 4-km forest cover, (b) abundance and average temperature during the breeding season. Lines were derived from the prediction model; dots represent the maximum number of individuals detected at each sampling site. (a) Five lines of different colours indicate the differences in average temperature during the breeding season, in descending order of darkness: 20°C, 18°C, 16°C, 14°C, and 12°C. (b) Five lines of different colours indicate the differences in 4-km forest cover in descending order of darkness: 100%, 75%, 50%, 25%, and 0%. The line of lightest colour (4-km forest cover=0%) is completely overlapped by the line of second lightest colour (4-km forest cover=25%).

Table 1. Results of model averaging for the N-mixture models. The abbreviations used are: SE: standard error; z : Wald statistic; $\text{Pr}(>|z|)$: p-value derived from z ; RIV: relative importance of variables; 4-km forest/250-m forest: forest cover within 4-km and 250-m of each sampling site; Temperature: average temperature during breeding season.

	Variables	Coefficient	SE	z	$\text{Pr}(> z)$	RIV	N containing models
Abundance	Intercept	-0.95	0.35	2.727	0.006		
	250-m forest	0.026	0.21	0.121	0.90	0.1	1
	(250-m forest) ²	-0.21	0.25	0.839	0.40	0.15	1
	4-km forest	1.26	0.67	1.892	0.058	1	6
	(4-km forest) ²	-1.77	0.76	2.322	0.020	1	6
	Temperature	0.50	0.26	1.915	0.056	0.84	5
	Elevation	-0.54	0.44	1.252	0.21	0.33	2
Detection probability	Intercept	0.56	0.45	1.242	0.21		
	Observation date	0.016	0.021	0.759	0.45	0.14	1

RIV takes a value between zero and one, and high RIV indicates that the variable is important.

Number of containing models indicates the number of models containing the variable among models with $\Delta\text{AIC} < 2$.

1). In other words, Jungle Nightjar abundance was greatest at sites with moderate forest cover (approximately 75%) within a 4-km radius and with high average temperatures during the breeding season (Fig. 2). The probability of detecting an individual was not affected by observation date (Table 1).

The most parsimonious model among the N-mixture models with $\Delta\text{AIC} < 2$ (i.e. the prediction model), was the model with the minimum AIC. In the prediction model, 4-km forest cover, its squared term, and the average temperature were also included, and the detection probability was estimated as approximately 0.65 (Appendices 5, 7). The mapping of expected abundance predicted abundant Jungle Nightjars in southern and central Hokkaido, which contains many grid cells with above-average temperature (Fig. 3; Appendix 2). Additionally, most suitable areas with moderate forest cover were predicted to fall between mountains and lowlands (Fig. 3; Appendix 2). We estimated the total number of territorial male Jungle Nightjars in Hokkaido to be 89,545.

DISCUSSION

The accuracy of the N-mixture model increases with increasing detection probability, especially with a detection probability of >0.1 (Yamaura 2013; Kéry & Royle 2016). We estimated the detection probability of the Jungle Nightjar to be approximately 0.65, indicating that our abundance estimates are likely to be reliable. However, we may have over-estimated Jungle Nightjar abundance in Hokkaido, partly because we were not able to consider detailed

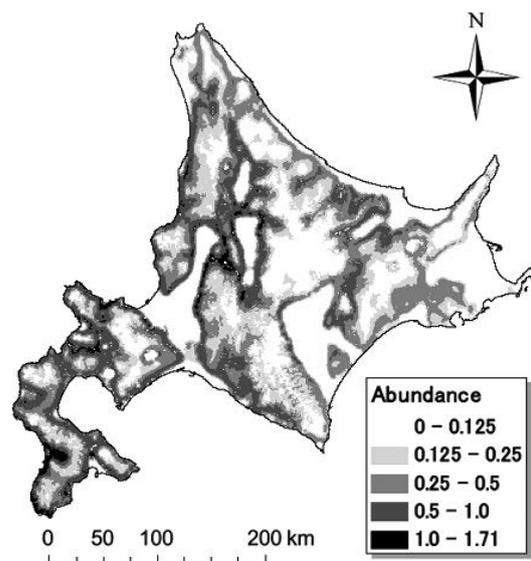


Fig. 3. Prediction abundance distribution of the Jungle Nightjar in Hokkaido. Abundance is the expected number of territorial male nightjars in each 500×500 -m grid.

land-use types. Future studies are required to solve this problem. To date, it has been challenging to accurately estimate abundance distributions of nocturnal bird species such as the Jungle Nightjar at large scales due to low detection probabilities. Our results suggest that combining the playback method with an N-mixture model might help in estimating the abundance distributions of other nocturnal bird species at large scales.

Jungle Nightjar abundance was non-linearly related to 4-km forest cover. In Japan, most prey sources of the Jungle Nightjar are forest insects (Yamashina

1941). Similarly, in the forested landscape of the UK, moth abundance is greater in old forests than in open habitats. However, the European Nightjar prefers open habitats for foraging (Sharps et al. 2015). Sierra et al. (2001) suggested that open habitats are suitable for finding flying prey insects near the ground, and for catching prey in the air. In terms of prey abundance and availability, it is likely that the Jungle Nightjar captures prey that spills over from forests into open habitats. Therefore, open habitats surrounded by forests are likely suitable for Jungle Nightjar foraging. This seems to explain why we found many Jungle Nightjars in areas with moderate forest cover (approximately 75%) within a 4-km radius.

We found no effect of 250-m forest cover. The size of open habitat at the territorial scale may not be very important. Furthermore, while territorial European Nightjars forage mainly within their territories during the incubation period, they forage within their entire home ranges during the breeding season (Alexander & Cresswell 1990; Cross et al. 2005). Thus, environmental factors within the home range seem to be more important than those within the territory for the Jungle Nightjar. However, our study may underestimate the effects of forest cover at the territorial scale. Assuming the territory of the Jungle Nightjar falls within approximately 250 m of the nest, the area of a territory could overlap slightly with a 250-m radius circle from a sampling site if the Jungle Nightjar placed the nest far from the sampling site.

As expected, Jungle Nightjar abundance was positively related to average temperature during the breeding season. This may reflect the fact that Lepidopteran species, a main prey source, are more abundant in warmer regions. Indeed, McGeachie (1989) reported that moth activity also increases with temperature in Britain, and Beck et al. (2011) showed that moth species are more abundant in warmer regions in Ecuador. Therefore, our results suggest that climate can also be an important driver of large-scale bird distributions using Jungle Nightjar abundance as a model case.

Although it has been suggested that both land-use and climate changes may have played roles in the decline of the European Nightjar in the late 20th century (Morris et al. 1994; Conway et al. 2007; Langston et al. 2007), the relative importance of these factors has long been unclear. Our results showed a greater importance of land use than climate for the abundance of the Jungle Nightjar (Table 1; Fig. 2). We

avoided confounding land use and climate, which can mask the specific effects of land use (Yamaura et al. 2011; Reino et al. 2013), by selecting sampling sites with low correlations between land use and climate. Our results suggest that both land use and climate affect large-scale bird distributions.

Mapping revealed that most suitable habitats with moderate forest cover were located between mountains and arable lands (Fig. 3; Appendix 2). In Japan generally, these areas have been maintained by land use practices closely related to human activities such as rice fields, vegetable crops, and grasslands (Fukamachi et al. 2001). In recent decades, however, such areas have been disappearing due to the decline of agriculture (Fukamachi et al. 2001). In Hokkaido, areas suitable for the Jungle Nightjar may increase due to increasing temperatures associated with global warming (Core Writing Team et al. 2014). Under this scenario, future land-use changes might pose a greater threat to the Jungle Nightjar than climate change. In this context, forest management may contribute to Jungle Nightjar conservation even in forested landscapes, as it has been shown that early-successional young forests created by harvesting provide important open habitats for the European Nightjar (Morris et al. 1994; Langston et al. 2007). Sharps et al. (2015) suggested that, within large plantation forest landscapes, a heterogeneous forest mosaic is important for the European Nightjar. In Japan, many plantations are maturing due to the decline of forestry (Forestry Agency 2015). If Japanese forestry recovers, the population and distribution of the Jungle Nightjar in Hokkaido may follow suit, although future studies are needed to test this hypothesis.

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