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ENVIRONMENTAL FACTORS AFFECTING THE REPRODUCTIVE RATE OF URBAN NORTHERN GOSHAWKS

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ABSTRACT.—Urbanization has increased with human population growth and the responses from raptor species are gaining more attention from both researchers and the public. Northern Goshawks (*Accipiter gentilis*) now breed in urban areas in Japan and Europe; however, there are few studies examining the factors that influence their reproductive rate in urban areas. We investigated the reproductive rate (number of fledglings per nest) of the Northern Goshawk population in an urbanized area of Japan from 2014 to 2016, and used a binomial mixture model to examine the relationship between the number of fledglings per nest and environmental factors such as nesting and foraging environments, anthropogenic disturbance, predation risk, and intraspecific competition. The goshawk nesting success rate from 2014 to 2016 was 71.6%, with an average reproductive rate of 1.7 fledglings per occupied nest. The percentage of canopy cover of nesting stands had a significant positive effect on fledgling numbers, and the number of adjacent occupied nests had a significant negative effect on fledgling numbers. The positive effects of canopy coverage may be explained by the protection offered by canopy against direct sunlight, wind, and rain. The negative effect of the adjacent occupied nests may result from an increase in the amount of time and energy goshawks spent in territory defense, and a decrease in available foraging habitat due to intraspecific competition.

KEY WORDS: *Northern Goshawk*; Accipiter gentilis; *breeding success*; *canopy coverage*; *density effect*; *interference competition*; *reproductive rate*; *urban*.

FACTORES AMBIENTALES QUE AFECTAN LA TASA REPRODUCTIVA DE *ACCIPITER GENTILIS* EN ÁREAS URBANAS

RESUMEN.—La urbanización ha aumentado con el crecimiento poblacional humano. Consecuentemente, se observa una mayor atención, por parte del público en general y de los investigadores, a la forma en la que las aves rapaces responden a este fenómeno. *Accipiter gentilis* se reproduce actualmente en áreas urbanas de Japón y Europa; sin embargo, son escasos los estudios que examinan los factores que influyen sus tasas reproductivas en áreas urbanas. Entre los años 2014 y 2016 investigamos la tasa reproductiva (número de volantones por nido) de una población de *A. gentilis* en un área urbanizada de Japón. Utilizamos un modelo mixto binomial para examinar la relación entre el número de volantones por nido y factores ambientales tales como los sitios de anidación y alimentación, las molestias antropogénicas, el riesgo de depredación y la competencia intraespecífica. El éxito reproductor de *A. gentilis* desde 2014 a 2016 fue 71.6%, con una tasa reproductiva promedio de 1.7 volantones por nido ocupado. El porcentaje de cobertura del dosel en los sitios de anidación tuvo un efecto positivo significativo sobre el número de volantones, mientras que el número de nidos adyacentes ocupados tuvo un efecto negativo significativo sobre estos. Los efectos positivos

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de la cobertura del dosel pueden explicarse por la protección que esta ofrece frente a la luz directa del sol, al viento y a la lluvia. El efecto negativo de los nidos adyacentes ocupados podría ser resultado del aumento en la cantidad de tiempo y energía que los individuos de *A. gentilis* dedicaron para la defensa del territorio y de la disminución en la disponibilidad de hábitat de alimentación debido a la competencia intraespecífica.

[Traducción del equipo editorial]

Successful raptor reproduction requires both a nesting and foraging habitat (Newton 1979). A good nesting habitat reduces the risk of predation (Mainwaring et al. 2014, Anderson et al. 2015), and creates a suitable microclimate for breeding (Robertson 2009). The foraging environment is important for satisfying both parent and nestling food requirements (Reynolds et al. 2006). The reproductive rate of raptors is affected by other environmental factors such as climatic factors (Fairhurst and Bechard 2005), artificial disturbance (Krüger 2002), intraspecific (Bretagnolle 2008) and interspecific competition (Krüger 2002), and predation (Krüger 2004). Therefore, to elucidate factors affecting reproductive rates of raptors, it is necessary to estimate the correlation between reproductive rate and various environmental factors.

Increasing urbanization worldwide significantly affects many animal species (Ramalho and Hobbs 2012). Urbanization has increased with human population growth, and the responses from species are gaining more attention from researchers (Bateman and Fleming 2012). Urbanization can bring drastic changes to the behavior and life history of birds (Dominoni et al. 2013). Sometimes it has a deleterious effect, such as the extinction or extirpation of a species or a decrease in population density (Marzluff and Ewing 2001). Conversely, some species have expanded their range into urban areas, not just temporarily, but also to breed (Bird et al. 1996, Boal and Dykstra 2018). Avian responses to urbanization differ according to species and taxonomic group. Urbanization may provide suitable conditions for habitation by some raptors due to reductions in intra- and interspecific competition, and more abundant prey (Chace and Walsh 2006). For example, Eastern Screech-Owls (*Megascops asio*) breeding in urban areas have higher reproductive rates than those breeding in rural areas (Gehlback 1996). However, increased risk of disease, chemical contamination, collision with buildings and vehicles, and decreased foraging areas have also been reported (Hager 2009). For example, Eurasian Kestrels (*Falco tinnunculus*) breeding in urban areas have lower reproductive rates than a nearby rural population (Sumasgutner et al. 2014). The varied responses of different species to urbanization underscore the urgent need for more ecological studies of raptors in urban environments (Morrison et al. 2016).

The Northern Goshawk (*Accipiter gentilis*) is a medium-sized raptor that is widespread in the northern hemisphere. Typical goshawk breeding habitat includes remote forested areas that are not subject to human-induced disturbance (Kenward 2006). Earlier studies on the reproductive rate of the goshawk, mainly in Europe and the United States, have been summarized by Kenward (2006). However, goshawks have expanded their range to urban areas in Japan and Europe and have been breeding in urban environments there (Higuchi et al. 1996, Rutz et al. 2006b). Urban goshawks' feeding habits (Würfels 1994, 1995, Altenkamp 2002, Rutz 2003, 2004, Rutz et al. 2006a), home ranges and space use (Rutz 2006), foraging strategies (Rutz 2012b), breeding-site selection (Natsukawa et al. 2017), reproductive parameters (Solonen 2008, Rutz 2012a, 2012b), and colonization history (Rutz 2008) have been investigated, but studies on the determinants of their reproductive rate are limited. Here, we report the results of an investigation of the reproductive rate of a Northern Goshawk population in an urbanized area from 2014 to 2016, in which we examine the relationship between the number of fledglings and environmental factors such as nesting and foraging environments, anthropogenic disturbance, predation risk, and intraspecific competition.

METHODS

Study Area. We studied urban goshawks within 793 km^2 in the Kanagawa Prefecture, central Japan, which includes Kawasaki City, Yokohama City, Yamato City, Zama City, Ebina City, Ayase City, Fujisawa City, Chigasaki City, and Samukawa Town (Fig. 1; see Natsukawa et al. 2017 for coordinates). The landscape is generally flat, with rolling hills and a mean altitude of 159 masl. The climate is mild, with an average monthly temperature of 15.8°C (mean monthly temperature range: 5.9–26.7). Rainfall is

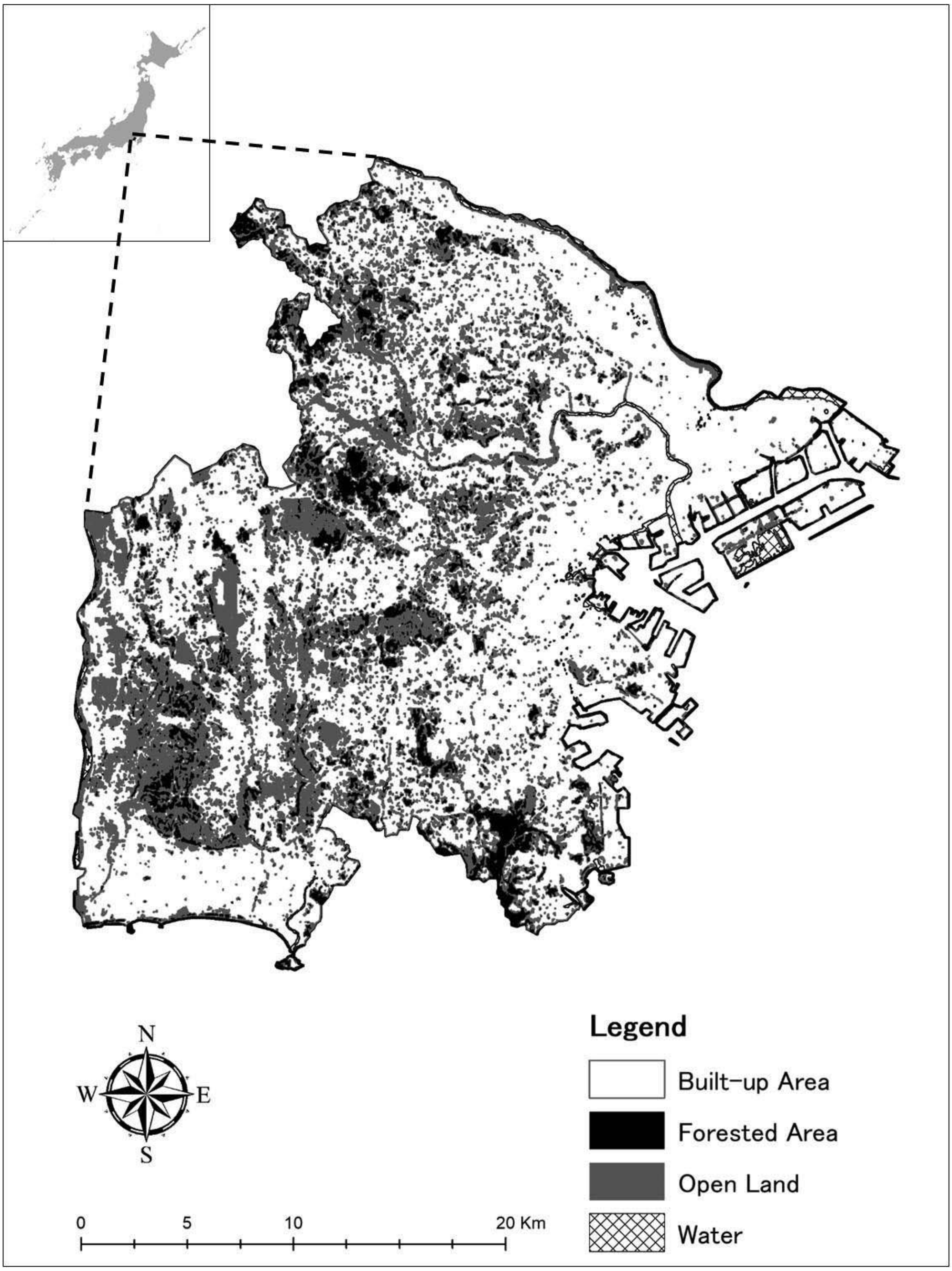

Figure 1. Eastern portion of Kanagawa Prefecture, Japan, study area for urban-breeding Northern Goshawks. Black shading indicates forested area (13.0%), grey indicates open land (11.8%), crosshatch indicates water (2.5%), and white indicates built-up areas (72.7%).

high in summer and autumn and lower in winter. Annual precipitation averages 1689 mm (maximum monthly average precipitation 234 mm, minimum monthly average precipitation 55 mm). Land-cover types in the study area included 13.0% forest, 11.8% open land (farmland, rice field, and grassland), 2.5% water, and 72.7% built area (paved road, residential area). Approximately 80% of this area was classified as Densely Inhabited Districts (DIDs). A DID refers to a block area (delineated by roads, rivers, etc., and ranging in size from 3000 to 5000 m^2) with a population density of $\geq$4000 people/km^2 or a similar-sized district of small neighboring sectors having a total population of $\geq$5000. DIDs are used for distinguishing between urban and rural areas in Japan.

Surveys of Breeding Goshawks. In 2014–2016, we investigated all forests in the study area on foot to find occupied nests of goshawks. We defined occupied nests as nests with the confirmed existence of a pair nest-building, copulating, egg-laying, or rearing young. Following Murase et al. (2015), we classified nests located within 400 m of a nest from the previous year as the same breeding site.

To determine the number of fledglings in an occupied nest, we visited each occupied nest 8 to 12 times, and we used binoculars (12×) and a spotting scope (25–50×) to observe the nests. Time per observation varied from 10 to 40 min, and distance from the observer to the nest tree varied from 60 to 148 m. We did not conduct these surveys on rainy days, as we anticipated that visibility would be compromised. We regarded nestlings that reached 80% of the average age of first flight as fledglings (Steenhof and Newton 2007), and we calculated reproductive rate as the number of fledglings per occupied nest. We defined breeding success as the proportion of occupied nests at which one or more nestlings fledged.

Measurements of Potential Covariates. *Local and landscape factors.* Following James and Shugart (1970), we measured canopy coverage within a radius of 11.3 m from the nest tree. We visually estimated the canopy coverage in 10% increments. We determined that a plot of 11.3-m radius was an appropriate size because our previous surveys of these forests showed that the vegetation structure (tree size, number of understory trees and shrubs, etc.) in the area up to this distance from the nests clearly differed from other places in the same forest (see Natsukawa et al. 2017).

We measured landscape-level factors using a land-cover map (resolution 10 m × 10 m) of the study area published by Japan Aerospace Exploration Agency (JAXA, http://www.eorc.jaxa.jp/ALOS/lulc/jlulc_jpn.htm), which reflected average land cover from 2006 to 2011. The land-cover map was subdivided into categories: forest, open land (farmland, rice fields, and grassland), water, vegetated built-up lands (total of block areas that have $\geq$30% small-scale vegetation of $\leq$900 m^2), and built-up lands (total of block areas that have $\leq$30% small-scale vegetation of $\leq$900 m^2).

We plotted a circle of radius 2 km, approximately the size of a goshawk home range in Japan (Kudo et al. 2005), around each nest and determined the percentage of land-cover types in each. Goshawks inhabiting the surveyed area tended to forage along forest edges (Natsukawa et al. 2017). Therefore, we measured the tangent length of forest and open area, and the tangent length of forest and vegetated built-up land. In addition, as an index to disturbance, we measured the distance from each nest to the nearest house. For these measurements, we used GIS software ArcMap 10.3.

Age of female breeders. Molted feathers of goshawks can be reliably used for sex identification, ageing, and individual identification without capture (Opdam and Müskens 1976). Three age classes (first-year, second-year, and third-year or older) can be distinguished by feather shape, coloration and patterning. We used this method to identify the age of female breeding birds. In addition, we also assessed the age of the breeding female bird by observing the belly feathers with binoculars or scope. Like molted feathers, this method can be used to classify ages into three categories (first-year, second-year, and third-year or older; Morioka et al. 1995).

Intra- and interspecific factors. To investigate the effect of intraspecific competition, we tallied the number of known occupied adjacent nests within a 2-km radius of each nest (Table 1). For three nests in 2014, four nests in 2015, and three nests in 2016 that were on the margin of the surveyed area, it was possible that there were adjacent occupied nests outside the study area. Therefore, we did not measure the potential covariates at these nests.

As an index to the number of potential predators of goshawk eggs or young, we counted the number of Large-billed Crows (*Corvus macrorhynchos*), Carrion Crows (*C. corone*), and Black Kites (*Milvus migrans*) within the study area by conducting a spot census near each nest stand (within 100 m) during

Table 1. Potential covariates of Northern Goshawk reproductive rate, measured for urban nests in Japan. Sample $n = 85$ nests (2014–2016).

ENVIRONMENTAL FACTORS	UNIT	MEAN (SD)	RANGE
Distance from nest tree to human residence	m	90.5 (57.1)	14.4–201.4
Canopy coverage[a]	%	80.1 (30.6)	20.0–100.0
Forest coverage[b]	%	14.9 (11.2)	1.5–50.3
Open (field, rice paddy and grass) coverage[b]	%	20.3 (13.0)	1.1–46.1
Vegetated built-up land coverage[b]	%	20.9 (12.6)	2.0–55.1
Built-up land coverage[b]	%	39.1 (18.8)	9.8–85.9
Tangent length between forest and open land[b]	km	5.8 (5.4)	0.0–30.5
Tangent length between forest and vegetated built-up land[b]	km	4.7 (3.3)	0.1–15.6
Area of forests with nests[b]	km^2	0.2 (0.2)	0.0–1.0
Number of adjacent occupied nests[b]	nest	0.7 (0.9)	0.0–3.0
Number of predators	bird	14.6 (9.8)	2.0–32.0
Average temperature during the incubation period (April)	°C	14.3 (1.5)	13.3–15.7
Average temperature during the nestling-rearing period (May–July)	°C	22.4 (4.2)	18.9–25.9
Total precipitation during the incubation period (April)	mm	144.2 (16.6)	88.0–154.5
Total precipitation during the nestling-rearing period (May–July)	mm	176.2 (38.2)	103.8–198.2

[a] Local-scale variable (11.3-m radius from the nest tree)

[b] Landscape-scale variable (2-km radius from the nest tree).

the time period from incubation (April) to early nestling-rearing (May). In the spot census, we counted the number of these species that were seen within 100 m of the fixed point within 30 min. We did not conduct the spot census surveys on rainy days, as we anticipated that visibility would be compromised.

Weather factors. Climate factors such as temperature and rainfall influence the reproductive rate of goshawks (e.g., Fairhurst and Bechard 2005). Therefore, we calculated average temperature and average total rainfall in the incubation period (April) and the nestling period (May–July) of each year from the meteorological data of the Japanese Meteorological Agency (http://www.data.jma.go.jp/obd/stats/etrn/index.php?prec_no=&block_no=&year=&month=&day=&view=). For the weather information, we used the observation data of the observatory nearest to each nest.

Statistical Analysis. To help explain the environmental factors affecting reproductive rate (here, the number of fledglings), we analyzed the data using a binomial mixture model (Royle 2004). In this model, it is possible to simultaneously estimate the number of individuals (the number of fledglings in this study) and the factors affecting the detection probability as a function of the covariates. Therefore, the model provides a powerful framework for correcting the observation error caused by false negatives (exist but not observed) and estimating unbiased true states (Kéry and Royle 2016). This model consists of two equations; a state model expressing the latent true state and an observation model expressing measured values including observation errors. We assumed that the state model follows a Poisson distribution and the observation model follows a binomial distribution. The covariates of the state model were local and landscape factors, age of adult birds, intra- and interspecific factors, and weather factors. The covariates of the observation model were the observation time per each survey and the distance from the survey site to the nest tree. All covariates used for analysis were normalized to 0 mean and 1 standard deviation. In this study, the regression coefficients were estimated by the maximum likelihood method and models of combinations of all covariates were created and ranked based on Akaike information criterion (AIC). Then, the model with the smallest AIC value was taken as the best-ranked model (Burnham and Anderson 2002). To avoid multicollinearity, we calculated correlation using a combination of all covariates, and did not use any model including a combination of covariates with $|r| > 0.7$. The effect of the covariates was considered significant when 0 was not included in the 95% confidence interval (Arnold 2010). We used statistical software R version 3.1.1 for all statistical analysis and the package "unmarked" (Fiske and Chandler 2011) to create the binomial mixture model. In this study, we used data obtained by pseudo-repeated sampling from the same breeding site and year. Therefore, we

Table 2. Determinants of breeding success analyzed using the binomial mixture model. Model with the smallest AIC is shown. The estimate is the intercept or regression coefficient. Lower is the 95% confidence interval lower limit value. Upper is the 95% confidence interval upper limit.

MODEL PARAMETER	ESTIMATE	LOWER	UPPER
State (Intercept)	−0.34	−1.19	0.52
State (Canopy coverage)	1.42	0.44	2.39
State (Number of neighbor nests)	−1.13	−1.66	−0.59
Detection (Intercept)	4.01	3.26	4.76

tested whether there was an effect of territory and year using a generalized linear mixed model with a log-link function and Poisson distribution. The maximum number of fledglings detected at each breeding site in each year was used as the response variable, the environmental factors used in the binomial mixture model were covariates, and territory and year were included as random variables. The random variables were assumed to follow a normal distribution with a mean of zero and a standard deviation of s or r. The results of this analysis indicated that the effects of the random variables were smaller than those of the covariates, and the results did not differ greatly from those of the binomial mixture models. Therefore, we did not consider pseudo-replication in the binomial mixture model.

RESULTS

Reproductive Rates. We located 31 occupied nests in 2014, 33 in 2015, and 31 in 2016, for a total of 95 from 2014–2016. All nests in the study were detected early in the breeding season and goshawks laid eggs in all occupied nests. Breeding success on the basis of occupied nests was 71.0% ($n=31$) in 2014, 72.7% ($n=33$) in 2015, 71.0% ($n=31$) in 2016, and 71.6% from 2014 to 2016 ($n=95$). The average number of fledglings per occupied nest was 1.7 ± 0.2 in 2014 (mean ± SE, $n=31$), 1.7 ± 0.2 in 2015 ($n=33$), 1.6 ± 0.3 in 2016 ($n=31$), and 1.7 ± 0.3 from 2014 to 2016 ($n = 95$). The minimum and maximum number of fledglings per nest in all years was 0 and 4, respectively.

Factors Affecting Reproductive Rate. The 10 nests on the margin of the surveyed area were excluded from the analysis as described above, so 85 nests were used for analysis (Table 1). Most (83 of 85) breeding females were $\geq$3 yr old; the remaining two birds were 2-yr-old females. As a result of model selection, in the best-ranked model, the state model included canopy coverage of the nest stand and the number of adjacent occupied nests within a 2-km radius, and there were no covariates included in the observation model (Table 2). Both covariates of the state model had statistically significant effects (Table 2). Greater canopy coverage had a large positive effect on the number of fledglings, while a greater number of adjacent occupied nests had a small negative effect (Fig. 2, Table 2). In contrast, no factors affecting the detection probability could be specified.

DISCUSSION

We found that canopy coverage of the nest stand and the number of the adjacent occupied nests were significantly related to reproductive rate (Fig. 2, Table 2). In addition, our analytical technique considered the false negative errors often found in ecological survey data by explicitly modeling the detection probability. Therefore, the results of this study should be less biased than those of studies applying traditional statistical methods that do not consider detection probability (Kéry et al. 2013).

The positive effect of canopy coverage of the nest stand may have been due to the protection it offers nestlings and adults from rainfall and increased temperature due to direct sunlight. Maximum temperature (Reynolds et al. 2017) and precipitation (Fairhurst and Bechard 2005) had negative effects on the reproductive rate of goshawks elsewhere. A closed canopy is thought to create a microclimate that is more favorable for breeding than an open canopy (e.g., McGrath et al. 2003). Peregrine Falcons (*F. peregrinus*; Anctil et al. 2014) and Cape Vultures (*Gyps coprotheres*; Pfeiffer et al. 2017) also have high reproductive rate in locations with physically protected nests. The early to middle portions of the goshawk nestling-rearing period (May–June) in the study area has the most rainfall, whereas the later part of the nestling-rearing period (the beginning of July) has the highest temperatures of the year, with strong direct sunlight. Nest locations that minimize the adverse effects of rain

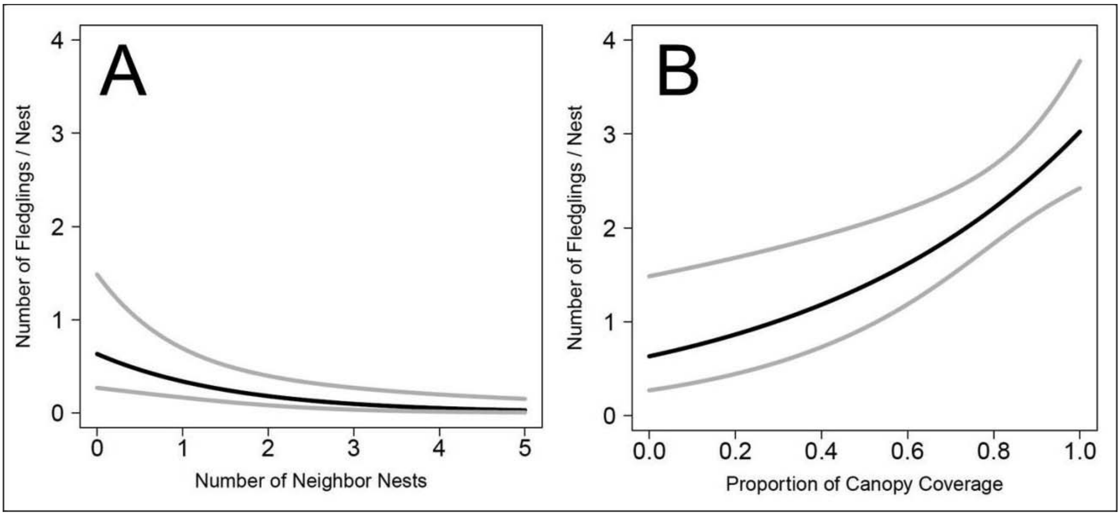

Figure 2. Relationships between the reproductive rate (number of fledglings per occupied nest) and covariates of the best-ranked binomial mixture model for Northern Goshawks in an urbanized area from 2014 to 2016 ($n = 85$ nests). (A) indicates the effect of the number of neighboring nests, and (B) shows the effect of canopy coverage. Black lines are fitted values. Grey lines represent 95% confidence intervals. Variable descriptions in Table 1.

and warm temperatures may enhance reproductive rate. In Japanese urban areas, because of the decline of forest management, canopy coverage is increasing, providing more suitable nesting habitats. Furthermore, trees that may hinder the flight of goshawks are also increasing in potential nest stands. Goshawks in urban areas prefer nest stands in forest environments that do not hinder flight, rather than areas of high canopy coverage (Natsukawa et al. 2017). In the current study, some goshawks used nesting environments where the canopy coverage was low, even though these areas were associated with lower reproductive rates.

The significant negative effect of the number of adjacent occupied nests on reproductive rate suggests density effects, such as a decrease in the number or size of foraging sites and an increase in the time-cost for territory defense due to an increase in individual interference (intraspecific competition). This latter is termed the interference competition hypothesis and is considered to be the main factor linked to the density effect (Both 1998). In fact, three pairs of goshawks that we observed extensively, stayed around their own nests until sunset after the retreat of an invading individual goshawk ($n = 8$ occurrences of this behavior among three nest sites). During those periods of vigilance, the nestlings were not fed at all (H. Natsukawa unpubl. data). Goshawk populations breeding in urban areas generally breed at a higher density than populations breeding in rural areas in Europe (Rutz et al. 2006b). Breeding goshawks are highly territorial and the nearest neighbor distance (NND) has little variability in areas where the environment is uniform (Rutz et al. 2006b). However, the forests in urbanized areas tend to be fragmented, and NND has greater variability. Goshawks inhabiting the study area select breeding sites where there is both forest and open space (Natsukawa et al. 2017), and NND can be as low as approximately 700 m in such sites. Urbanization of the study area is increasing, and forest and open areas each make up approximately 10% of the study area (see Methods). In urban areas where nesting and foraging sites are limited, density effects may occur because goshawk pairs are already breeding at a high density. The frequency of individual interference in raptors is closely related to NND (Newton 1979). Other raptors such as Ospreys (*Pandion haliaetus*; Bretagnolle et al. 2008) and White-tailed Eagles (*Haliaeetus albicilla*; Heuck et al. 2017) have decreased reproductive rates due to intraspecific interference competition.

In addition to direct interference as a cause of the density effect, the habitat heterogeneity hypothesis may also explain decreasing breeding success as density increases. This hypothesis posits that breeding density and breeding success are not directly related (Rodenhouse et al. 1997), but instead high-quality breeding sites are occupied first according to the ideal despotic distribution (Fretwell and Lucas 1969), with lower-quality breeding sites occupied later. As breeding density increases, the number of individuals breeding in low-quality breeding sites will increase, and thus overall reproductive rate will decrease. It has been suggested that the habitat heterogeneity theory explains, at least in part, the reproductive rate of goshawks (Krüger and Lindström 2001) and other raptors such as Eurasian Sparrowhawks (*A. nisus*; Newton 1991) and Spanish Imperial Eagles (*Aquila adalberti*; Ferrer and Donázar 1996). However, in our study, the number of fledglings produced in all nests located in areas with particularly high density (e.g., seven nests in the southwestern part of our study area with an average NND of about 1.2 km) was either one or zero per nest. This result, which differs from that of Krüger and Lindström (2001), suggests that interference competition, rather than habitat heterogeneity, influences the reproductive rate of goshawks.

Our study suggested that the high canopy coverage had a significant positive influence on the reproductive rate of goshawks and the density effect (likely due to interference competition) had a negative influence on the reproductive rate of goshawks. We were unable to investigate the relationship between food availability and reproductive rate, as has been studied elsewhere (e.g., Salafsky et al. 2005), due to a lack of prey data. We acknowledge that food availability is likely an important variable in the analysis of factors influencing reproductive rate, as it is in other raptor species (e.g., Terraube et al. 2012, Therrien et al. 2014), and we encourage other researchers to investigate this aspect of urban goshawk ecology. Studies on urban-breeding goshawks are much less common than studies of populations breeding in conventional habitats (Rutz et al. 2006b), and additional data are needed to strengthen the comparison among populations in different habitats (Rutz 2006).

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