Title	Predicting Off-Site Impacts on Breeding Success of the Marsh Harrier
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Citation	Journal of wildlife management, 81(6), 973-981 https://doi.org/10.1002/jwmg.21266
Issue Date	2017-08
Doc URL	http://hdl.handle.net/2115/71170
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6 RH: Senzaki et al. • Off-site Impacts on Raptors' Breeding Success

7 **Predicting Offsite Impacts on Breeding Success of the Marsh Harrier**

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14 **ABSTRACT** Construction of buildings, and other types of land uses by humans can
15 exert negative impacts on wildlife that live in the areas surrounding such developments
16 (i.e., off-site impacts). To reduce or lessen such impacts, it is important to determine the
17 biological metrics (e.g., abundance, breeding success) that are affected and at which
18 spatial scales. We monitored the eastern marsh harrier (*Circus spilonotus*) breeding in
19 wetland patches in northern Japan for 4 years and quantified its abundance (no. pairs) and
20 breeding success (no. juveniles) in natural environments compared to artificial land uses
21 in the surrounding areas. We developed a hierarchical model to simultaneously infer the
22 effects of foraging habitats and artificial land uses on the numbers of pairs and juveniles.

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We found that the amount of foraging habitat within 0.5 km of wetland patches positively influenced the number of pairs per patch and that the amount of artificial land use within 2.0 km from the patches negatively influenced the number of pairs per patch and the number of juveniles per pair. The number of juveniles per patch was therefore affected by these 2 features and was most susceptible to increased land use by humans within 2.0 km from the patches. Our results can be used to predict the magnitudes of off-site impacts on eastern marsh harriers before any additional development occurs. To effectively manage off-site impacts, we highlight the importance of considering species abundance and the biological processes mediating breeding success that are possibly affected by different land uses.

KEY WORDS abundance, hierarchical model, land-use change, off-site impacts, patch, reproductive success, spatial scale, wetland.

A primary cause of biodiversity loss worldwide is land use changes from a natural habitat to one dominated by human land use (i.e., on-site impacts; Jetz et al. 2007, Newbold et al. 2015). Mitigation measures and the future consequences of such losses have been intensively studied (Fitzherbert et al. 2008, Newbold et al. 2015). In recent years, however, other threats to biodiversity associated with off-site impacts have been recognized (Raiter et al. 2014, Hastie et al. 2015). Off-site impacts are negative in nature and occur at sites remote from the location of the disturbance (Raiter et al. 2014). Such impacts have rarely been evaluated prior to development because it is difficult to predict where and when such impacts occur. Therefore, a systematic framework for predicting off-site impacts is needed (Raiter et al. 2014).

Human development (e.g., construction of artificial land uses) in areas surrounding

patches of breeding habitats has been one of the most common negative off-site impacts on breeding wildlife. Principal concerns are reduction in foraging areas (Mahan and Yahner 1999) and an increase in artificial land use in areas surrounding breeding habitats (Cardador et al. 2011, Quesnelle et al. 2015). Such increases can exacerbate the extent of human disturbance and the numbers of collisions of wildlife with buildings surrounding their breeding habitat, which may decrease the number of individuals and their breeding performance in breeding habitats (Chace and Walsh 2006, Loss et al. 2015). Therefore, to evaluate the magnitudes of off-site impacts on biodiversity prior to development, it is necessary to know how breeding wildlife in their habitat patches respond to reductions in foraging area and increases in artificial land uses in regions surrounding the habitat patches (Palomino and Carrascal 2007).

For effective management of off-site impacts, it is important to measure the extent to which off-site impacts degrade certain biological processes and identify the spatial scales at which the off-site impacts are severe. Biological processes operate across multiple spatial scales (Wiens 1989, Chalfoun and Martin 2007, Mahon et al. 2016). For example, abundance may not be positively correlated with another important metric, actual reproductive success (Van Horne 1983, Vickery et al. 1992). Similarly, the most influential land-use spatial scale in terms of reproductive success may not be appropriate in terms of abundance, because successful reproduction requires higher levels of resources or larger extents of habitat to compensate for the additional costs that reproduction imposes on adult survival (Nur 1984, Korpimäki and Rita 1996). However, few studies have considered the multiple biological processes possibly affected by different land uses at different spatial scales, especially in human-disturbed landscapes

(Schlaepfer et al. 2002, Battin 2004, Bock and Jones 2004).

The objective of our study was to explore whether abundance and reproductive success responded differentially to off-site impacts at different spatial scales. We surveyed the numbers of pairs and juveniles of a model species, the eastern marsh harrier (*Circus spilonotus*), breeding in wetland patches in the Yufutsu plain of northern Japan, and quantified breeding responses to changes in the extents of foraging habitat and artificial land uses in the surrounding areas. We selected the eastern marsh harrier for 2 reasons: it is an endangered species in Japan, and thus a better understanding of the human impacts on this species is of prime importance (Japanese Ministry of the Environment 2012), and the species is a top predator in wetland ecosystems, and its presence or absence may alter predator-prey interactions that have ecosystem-wide consequences (Estes et al. 2011). Finally, to predict the expected off-site impacts on the harrier, we estimated the expected values of the number of pairs per patch and the number of juveniles per pair and per patch, in all wetland patches where harriers could potentially breed.

STUDY AREA

We conducted field surveys on the Yufutsu plain, central Hokkaido, northern Japan (211.6 km², 42° 37'N, 141° 43' E). This area was dominated by natural wetlands and forests until the early 1900s. Approximately 90% of the wetlands and 50% of the forests have been lost to agricultural land and urban areas (M. Senzaki, Hokkaido University, unpublished data), and the remaining wetlands are fragmented. We defined continuities of the common reed (*Phragmites australis*), bluejoint reedgrass (*Calamagrostis langsdorffii*), and sedges (*Carex* spp) as wetland patches. We treated these vegetation cover types,

surrounded by other landscape features (e.g., forests, grasslands, cultivated land, paddy [rice] fields, industrial sites) extending for >50 m, as separate wetland patches (Senzaki and Yamaura 2016). The study area contained 97 wetland patches, ranging in size from 1 ha to 101 ha. The study area had 20 solar power plants in 2015 covering 510 ha (M. Senzaki, unpublished data). More information on the study area is presented in Senzaki et al. (2015) and Senzaki and Yamaura (2016).

METHODS

Study Species and Patch Selection

The eastern marsh harrier is a medium-sized raptor species (length = 48–58 cm; Morioka et al. 1995). In our study area, the harriers arrive in late March and breed from early April to early August on a reed-bed in wetland patches. During the breeding period, they prey on small- or medium-sized birds and mammals outside of the breeding wetland patches (M. Senzaki, personal observation).

Based on our field observation of eastern marsh harriers, and on a previous study on the western marsh harrier (*Circus aeruginosus*; Cardador et al. 2009), the foraging area of breeding male eastern marsh harriers could extend to areas within an approximate 2-km radius of the nest. Therefore, to avoid spatial autocorrelation and pseudoreplication (Wiens 1989), we randomly selected 16 wetland patches (5.27–101 ha), the centroids of which were ≥ 4 km apart, as the study wetland patches. We used the centroids rather than the shortest distance between 2 given wetland patches, because harrier nests were observed in the interior of wetland patches.

Harrier Breeding Surveys

For harrier breeding surveys, we used the same monitoring procedure used in our

previous studies (Senzaki et al. 2015, Senzaki and Yamaura 2016). In summary, we conducted separate surveys of breeding attempts and subsequent breeding performance from April to mid-August, 2012–2015. In the breeding attempt surveys, we established observation points near each wetland patch and conducted 1–3 observational surveys between April and May of each year. Because we were not able to fully observe some wetland patches from a single observation point, we observed these patches from multiple observation points. During each observational period, we spent 2 hours observing harriers at each point. We determined whether each wetland patch had harrier pairs by observing any breeding behavior (i.e., nest-building, courtship feeding, feeding of chicks). We observed all wetlands 1–3 times on different dates (i.e., for 6 hr total if we did not detect harriers during the first or second observations). For the breeding performance surveys, we established additional observational points located approximately 200–300 m from the nests. We next conducted additional observations on 5 occasions between mid-July and mid-August. We did not visit each nest to directly count the number of chicks because nest visiting can cause nest predation by mammalian predators (M. Senzaki, personal observation). During each observation, we stayed at each observational point for 3 hours. We considered the maximum number of juveniles we could count simultaneously as the number of juveniles for each pair. All surveys were performed in accordance with the relevant guidelines and regulations of the Japanese Ministry of the Environment and were conducted in accordance with current Japanese laws.

Spatial Resolutions and Explanatory Variables

Breeding western marsh harriers, the ecology of which is similar to that of the eastern

marsh harrier, forage intensively during nesting in areas within an approximately 2-km radius from the nest (Cardador et al. 2009). Thus, we calculated the proportions of foraging habitat and artificial land use within 0.5, 1.0, 1.5, and 2.0 km from the centroids of each patch using the 1:25,000-scale actual vegetation map of the sixth Japanese National Survey of the Natural Environment conducted by the Japanese Ministry of the Environment with the aid of ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, CA, USA). We defined all vascular plant communities (except forests) and pastures as foraging habitats (Morioka et al. 1995). We defined paved roads, urban and residential areas, industrial areas, and solar power plants as artificial land uses. We treated all of the different types of artificial land use as a single variable because all are unsuitable for harriers and there were only small numbers of each individual type of human development.

The amount of each type of land use at larger spatial extents was correlated with the amount with the same land use at smaller spatial extents. Thus, in terms of the extents of the artificial land use and the foraging habitat, we calculated correlation coefficients at different spatial extents and selected the combination of spatial scales showing the lowest correlation ($r = 0.36$ and 0.51 for the artificial land use and foraging habitat, respectively; Figs. S1 and S2, available online in Supporting Information). Thus, we used variables derived from data acquired within 0.5 km and 2.0 km from the wetland patches in the following analyses.

To identify the final variables for inclusion in a hierarchical model dealing simultaneously with the numbers of pairs and juveniles, we constructed generalized linear mixed models (GLMMs) with Poisson errors for the numbers of pairs and juveniles

separately. The response variables were the number of pairs per patch and the number of juveniles per pair, respectively. We treated the aforementioned 4 variables as explanatory variables in each GLMM. Additionally, because larger wetland patches may harbor more pairs because of a positive area–abundance relationship (Yamaura et al. 2016), we treated log-transformed patch areas as an additional explanatory variable in the GLMM for the number of pairs. Because it is suggested that $|r| < 0.7$ is an appropriate countermeasure to the problem of collinearity (Dormann et al. 2013), we confirmed that the correlations were low between these variables and the log-transformed patch area ($r < 0.59$; Fig. 1). We used patch identity (ID) and the survey year as random variables in both GLMMs. These random variables can account for patch- and year-specific variance, respectively. In each GLMM analysis, we constructed models combining all possible explanatory variables and ranked them using Akaike’s Information Criterion for small sample situations (AIC_c). We used the variables included in the best model (i.e., the model with the lowest AIC_c) in the following hierarchical model. We conducted GLMM analyses using the lme4 (version 1.1-5) software (Bates et al. 2015) of R (version 3.0.2; R Core Team 2013).

Hierarchical Model and Estimation of Abundance and Reproduction

We developed the following hierarchical model enabling us to infer the effects of the explanatory variables selected in the GLMMs on the number of pairs per patch and the numbers of juveniles per pair and per patch. We assumed the number of observed pairs in patch i in year j (Np_{ij}) to be a Poisson random variable:

$$Np_{ij} \sim \text{Poisson}(\lambda_{ij}),$$

where $\bar{p}_{ij}$ is the expected number of pairs in patch i in year j , modeled as a function of the explanatory variables as:

$$\log(\bar{p}_{ij}) = \alpha_{int} + \alpha_k \times X_{ik} + \varepsilon_i + \varepsilon_j,$$

where α_{int} is the intercept term, α_k is a regression parameter of the explanatory variable k , and X_{ik} is the k th covariate at patch i ; ε_i and ε_j are normally distributed random site and year effects added to account for unexplained heterogeneities among sites and years.

The number of observed juveniles per patch i in year j (Nj_{ij}) was represented by a function of Np_{ij} and $\bar{p}_{ij}$, which is the expected number of juveniles per pair in patch i in year j . We assumed Nj_{ij} to be a Poisson random variable:

$$Nj_{ij} \sim \text{Poisson}(\bar{p}_{ij} \times Np_{ij}),$$

where $\bar{p}_{ij}$ is modeled as a function of explanatory variables as:

$$\log(\bar{p}_{ij}) = \beta_{int} + \beta_k \times X_{ki} + \delta_i + \delta_j,$$

where β_{int} is the intercept term, β_k is a regression parameter of the explanatory variables, and X_{ki} is the k th covariate at patch i ; δ_i and δ_j are the normally distributed random site and year effects. Using $\bar{p}_{ij} \times Np_{ij}$ to give the expected mean number of juveniles per patch, we set the Nj_{ij} values for patches without any pairs ($Np_{ij} = 0$) to zero (i.e., the structural zero). The Nj_{ij} values for patches with nonzero pairs ($Np_{ij} > 0$) could be ≥ 0 (the sampling zero) depending on the $\bar{p}_{ij}$ and Np_{ij} values. Similar ideas have been recently used to accommodate detection histories given the occurrence or abundance of a focal species at sampling sites (Kéry and Royle 2016, Yamaura et al. 2016). Based on such serial formulation, we could separately model the numbers of pairs and juveniles as functions of different land uses in a single hierarchical model.

We estimated the parameters of the above models using a hierarchical Bayesian modeling framework and Markov chain Monte Carlo (MCMC) techniques (Royle and Dorazio 2008). We assumed the priors of each explanatory variable followed normal distributions with means of 0 and variances of 10,000. Similarly, we assumed random site effects followed non-informative uniform priors defined by [0, 5]. We obtained the posterior distributions of all parameters by performing 3 chain runs of 100,000 simulations after a burn-in of 10,000, using JAGS version 3.3.0 (<http://mcmc-jags.sourceforge.net/>, accessed 15 Mar 2016); we employed R (version 3.0.2) software (R Core Team 2013) and the package R2JAGS (version 0.03-11; <http://cran.r-project.org/web/packages/R2jags/>, accessed 15 Mar 2016) to this end. We considered a model had converged if the $\hat{R}$ values (Gelman–Rubin statistic) of all parameters were <1.1 (Gelman and Hill 2006).

We calculated the expected number of pairs per patch (λp_{ij}) and the expected number of juveniles per pair (λj_{ij}) and per patch ($\lambda p_{ij} \times \lambda j_{ij}$) in wetland patches using estimates from the hierarchical model. We did not calculate such values for wetland patches of sizes <5.28 ha, which corresponded to the minimal patch area surveyed. Thus, we estimated these values for 48 wetland patches.

RESULTS

We identified 43 breeding pairs and 37 juveniles during the study period (Table 1). We observed ($\bar{x} \pm \text{SD}$) 0.67 $\pm$ 0.94 pairs per patch (range = 0–4, $n = 64$ [16 observed patches $\times$ 4 years]), 0.58 $\pm$ 1.48 juveniles per patch (range = 0–7, $n = 64$ [16 observed patches $\times$ 4 years]), and 0.86 $\pm$ 1.06 juveniles per pair (range = 0–3, $n = 43$; Table 1). The correlation coefficient between the number of pairs and juveniles per patch was 0.72 ($n = 64$ [16

observed patches $\times$ 4 years]).

Explanatory variables included in the best GLMMs were foraging habitat within 0.5 km and artificial land use within 2 km for pairs per patch and the artificial land use within 2 km for juveniles per pair (Table 2). For each best model, we calculated marginal and conditional R^2 values, which described the proportion of variance explained by the fixed factors only and by fixed and random factors, respectively (Nakagawa and Schielzeth 2013). The R^2 values (marginal [conditional]) were 0.46 (0.58) for pairs per patch and 0.21 (0.54) for juveniles per pair, indicating that our best models had good fit. In terms of juveniles per pair, although the AIC_c differences between the best model and other models were relatively small, the effects of explanatory variables other than the artificial land use within 2 km included in subsequent models were weak (Table 2). Thus, in the hierarchical model, we decided to use the foraging habitat within 0.5 km and artificial land use within 2 km as explanatory variables for pairs per patch and the artificial land use within 2 km as the explanatory variable for juveniles per pair. The ranges of foraging habitat within 0.5 km and artificial land use within 2 km were 21–87% and 2–37%, respectively ($n = 16$).

The hierarchical model showed that the number of pairs per patch was positively associated with the foraging habitat within 0.5 km and negatively associated with artificial land use within 2 km (Figs. 2a, d), although the effect of the artificial land use within 2 km was relatively weak because a small region of the 95% credible interval of the coefficient overlapped with zero (Table 3). The number of juveniles per pair was negatively associated with the artificial land use within 2 km (Fig. 2e, Table 3). Pairs per patch and juveniles per pair varied among sites and years; the fluctuations in the annual

251 numbers of juveniles per pair were especially large (Table 3). The number of juveniles
252 per patch was affected by the foraging habitat within 0.5 km via the positive effect of that
253 parameter on the number of pairs per patch and by the artificial land use within 2 km via
254 the negative effect of that parameter on pairs per patch and on juveniles per pair (Fig. 2).
255 Thus, juveniles per patch was more strongly affected by the artificial land use within 2
256 km than were the other 2 metrics (Figs. 2d–f).

257 We estimated the expected values of all 3 harrier parameters in 48 wetland
258 patches in our study area (Fig. 3). The expected number of pairs per patch in the current
259 wetland patches was 0.47 ± 0.58 ($n = 48$ patches). The expected number of juveniles per
260 pair was 0.46 ± 0.33 ($n = 48$ patches) and the expected number of juveniles per patch was
261 0.28 ± 0.53 ($n = 48$ patches) in the current wetland patches.

262 **DISCUSSION**

263 To effectively avoid or lessen off-site impacts and other anthropogenic impacts on
264 wildlife, it is important to evaluate the magnitude of such impacts on biological processes
265 at various spatial scales. We surveyed how breeding harriers responded to the amount of
266 foraging habitat and artificial land use in the surrounding areas. The number of harrier
267 pairs per patch was reduced when the area of foraging habitat within 0.5 km of the
268 wetland patch was reduced and when artificial land use increased within 2 km of that
269 wetland patch (Fig. 2a, d). The number of juveniles per pair fell as artificial land use
270 within 2 km increased (Fig. 2e). In terms of combinations of these relationships, we
271 found that the number of juveniles per patch was most susceptible to the artificial land
272 use within 2 km (Fig. 2f). Specifically, we showed that breeding pairs would disappear
273 from wetland patches where the foraging habitat within 0.5 km was below 40% (Fig. 2a)

and when the artificial land use within 2 km approached 40% (Fig. 2d). We also showed that, irrespective of foraging habitat within 0.5 km, breeding pairs would produce no juveniles in wetlands where the artificial land use within 2 km was over 20% (Figs. 2e, f). The number of juveniles per pair in this study (0.86 juveniles/pair) was lower than the figure reported in another region dominated by natural grasses (1.8–2.8 juveniles/pair between years; Fefelov 2001).

The vulnerability of the numbers of juveniles per patch to the artificial land use within 2 km is important. The results suggest the establishment of an ecological trap in wetland patches where the artificial land use within 2 km is >20%. In other words, despite the strong correlation between the number of harrier pairs and the number of juveniles per patch, it is possible that a management strategy focused on the number of harrier pairs may be insufficient to ensure the long-term harrier persistence, even if the number of pairs is successfully maintained in the short-term by maintaining a minimum level of foraging habitat within 0.5 km and controlling amount of artificial land use within 2 km.

Moreover, the most influential spatial scales differed among the metrics (i.e., pairs per patch or juveniles per pair) that were considered (Tables 2, 3). Therefore, our work highlights that conservation managers should evaluate multiple biological metrics affected by different factors at different spatial scales, and that management of juvenile harriers in our study region should focus on the artificial land use within 2 km. However, these conclusions are based only on ecological perspectives. The economic costs and long-term feasibility of management plans must also be evaluated in the future (Cardador et al. 2015). In practice, conservation plans are often constrained by limited time and

funding (Lambeck 1997, Roberge and Angelstam 2004). Moreover, our results do not mean that land use in the area beyond 2.0 km from harriers' nests is unimportant. Although we used a 2-km radius as the maximum spatial scale, there may be breeding eastern marsh harriers within the wider foraging area. In such cases, to avoid off-site impacts, management of foraging habitat and artificial land use beyond a distance of 2 km from nests may be required, although extending spatial scales for management may be more difficult because it would require restricting human activity in wider areas. Finally, although we included several types of artificial land uses in a single factor, each artificial land use type may have different impacts on harriers.

The impact of artificial land use within 2 km on the number of juveniles per pair can be explained by the negative impacts of human disturbance on juvenile survival, the hunting behavior of adult harriers, and adult harrier feeding rates when artificial land uses are present (Fernández et al. 1993, De la Torre et al. 2000, Rees et al. 2005, Arroyo and Razin 2006). Such impacts can occur throughout the entire foraging range and, hence, may also explain why the most influential spatial scale of artificial land use (i.e., 2 km) was larger than that of foraging habitat (i.e., 0.5 km). Similarly, high predation pressure upon intensification of human development may be, at least partially, responsible for the impact of artificial land use within 2 km on the number of juveniles per pair (Hethcoat et al. 2015). On the other hand, the strong effect of foraging habitat within 0.5 km on the number of pairs per patch may be explained by the fact that high prey availability in surrounding areas is of great importance when selecting breeding patches (Cornulier and Bretagnolle 2006). The large variance in the annual number of juveniles per pair may be explained by fluctuations in prey abundance, including the grey red-backed vole

(*Lethrionomys rufocanus*; Stenseth et al. 1996) or by differences in annual seasonal precipitation (Fisher et al. 2015). These results indicate that monitoring programs spanning several years are required to estimate the true impacts of environmental factors on wildlife (Magurran et al. 2010). In addition, the number of juveniles per pair had a weak relationship with foraging habitat within 0.5 km (Table 2). This is likely because harrier pairs might already select areas with greater proportions of foraging area.

Finally, we estimated the expected values of the 3 harrier parameters in 48 wetland patches in our study area (Fig. 3). These estimates can be used to predict the magnitudes of off-site impacts on harriers in each wetland patch before additional development begins or other land uses change.

MANAGEMENT IMPLICATIONS

The following management policies might be implemented to prevent predicted off-site impacts to eastern marsh harriers. To lessen impacts caused by a decrease in the foraging habitat within 0.5 km, offsets composed of suitable habitats, which compensate for habitat loss caused by development by generating ecologically equivalent gains elsewhere (Maron et al. 2012) may be appropriate. For example, changing non-foraging areas within 0.5 km of harrier breeding patches into foraging habitats may be effective, because grasslands converted from arable lands are important for foraging by the northern harrier *C. cyaneus* (Zuckerberg and Vickery 2006, Wilson et al. 2010). To lessen off-site impacts caused by an increase in the artificial land use within 2 km, it would be appropriate to avoid any additional development in areas within 2 km of harrier breeding patches (i.e., by separating development and conservation areas as much as possible). This option would be maximally effective when no development priority is evident near

wetland patches and where such patches are surrounded by undisturbed natural habitat (Benítez-López et al. 2010, Torres et al. 2016). Alternatively, because certain pairs still produced 2 juveniles under conditions of 20% artificial land use within 2 km (Fig. 2e), it is possible that site- or field-scale management focusing on the mechanisms underlying breeding failure, thus enhancing nest protection, might be effective (Santangeli et al. 2014).

ACKNOWLEDGMENTS

We thank Tomatoh Inc. for logistical support. MS was supported by Japan Society for the Promotion of Science (JSPS) KAKENHI grant no. 14J05368 and YY and FN by JSPS KAKENHI grants nos. 26292074 and 23248021, respectively.

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514 *Associate Editor: David Euler.*

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Figure captions

Figure 1

Correlation coefficients for the relations among proportion of foraging area (FA), proportion of artificial land use (AL), and patch areas at different spatial extents for patches of eastern marsh harrier habitat in northern Japan, 2012–2015. The terms 0.5_AL and 2.0_AL refer to the extent of artificial land use within buffered distances of 0.5 km and 2 km, respectively, from the estimated (gravity) center of survey patches. Similarly, the terms 0.5_FA and 2.0_FA refer to the extent of foraging habitat within buffered distances of 0.5 km and 2 km, respectively, from the estimated (gravity) center of survey patches. Histograms on the diagonal represent the frequency distribution of each variable.

Figure 2

The upper 3 boxes indicate the effects of the percentage of foraging area (FA) within 0.5 km of the wetland patches on the number of harrier pairs per patch (a), the number of juveniles per pair (b), and the number of juveniles per patch (c) for eastern marsh harriers, northern Japan, 2012–2015. The 5 lines in each box were derived using the hierarchical model; the various degrees of shading indicate differences in percentage of artificial land use within 2 km, in descending order of darkness (2%, 10%, 20%, 30%, and 37%). The bottom 3 boxes indicate the effects of the percentage of the artificial land use (AL) within 2 km of the wetland patches on the number of harrier pairs per patch (d), the number of juveniles per pair (e), and the number of juveniles per patch (f). All lines were derived using the hierarchical model, and the 5 different shadings employed in boxes (d) and (f) indicate differences in percentage of foraging area within 0.5 km in

descending order of darkness (87%, 80%, 60%, 40%, and 21%). The gray circles are actual values from field surveys.

Figure 3

The expected numbers of pairs per patch (a), the number of juveniles per pair (b), and the number of juveniles per patch (c) in terms of a combination of the percentage of foraging area (FA) within 0.5 km and the percentage of artificial land use (AL) within 2 km (solid lines) for eastern marsh harriers, northern Japan, 2012–2015. Only the number of juveniles per pair (b) varied depending on the value of a single factor (AL within 2 km). Gray circles indicate all potential breeding wetland patches in the study area ($n = 48$).

549 Table 1. Results of the eastern marsh harrier breeding survey, northern Japan, 2012–2015. In each year, we monitored 16 wetland
550 patches.

Metric	Year								Total	
	2012		2013		2014		2015			
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Pairs (no.)	11		10		12		10		43	
Juveniles (no.)	8		14		14		1		37	
Pairs/patch	0.69	0.87	0.63	0.98	0.75	1.13	0.63	0.89	0.67	0.94
Juveniles/patch	0.50	1.1	0.88	1.75	0.88	2.09	0.06	0.25	0.58	1.84
Juveniles/pair	0.73	0.90	1.40	1.26	1.17	1.11	0.10	0.32	0.86	1.06

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553 **Table 2.** Results of generalized linear mixed models of number of pairs per patch and number of juveniles per pair for eastern marsh
554 harriers in wetland patches, northern Japan, 2012–2015. We show all models with differences in corrected Akaike’s Information
555 Criterion (ΔAIC_c) < 2. Weight is the Akaike weight.

Response variable	Coefficient ($\pm$ SE)						ΔAIC_c	Akaike weight
	Intercept	Patch area	Foraging habitat within 0.5 km	Artificial land use within 0.5 km	Foraging habitat within 2 km	Artificial land use within 2 km		
Pairs/patch	–1.26 (0.39) **		1.14 (0.36) **			–0.70 (0.34) *	0.00	0.18
	–1.34 (0.45) **		1.26 (0.45) **				1.68	0.08
	–1.20 (0.36) ***	0.88 (0.25) ***			0.88 (0.37) *		1.76	0.08
	–1.36 (0.41) ***	0.71 (0.21) ***		–0.69 (0.44)	1.06 (0.48) *		1.93	0.07
	–1.29 (0.39) ***		1.09 (0.35) **		0.26 (0.36)	–0.67 (0.33) *	1.95	0.07
Juveniles/pair	–0.50 (0.49)					–0.67 (0.24) **	0.00	0.30
	–0.62 (0.50)				0.54 (0.46)	–0.87 (0.36) *	0.63	0.22
	–0.52 (0.50)		–0.20 (0.19)			–0.70 (0.24) **	1.49	0.14

556 *, **, and *** indicate significance levels $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.
557

Table 3. Estimated parameters for a hierarchical model seeking to explain adult and juvenile numbers of eastern marsh harriers in wetland patches where breeding occurred, northern Japan, 2012–2015. Successful convergence was evident based on $\hat{R}$ values (all < 1.1). “Site” and “Year” were treated as random effects.

Model parameters	Coefficient					$\hat{R}$
	$\bar{x}$	SD	95% credible intervals			
			Lower	Median	Upper	
Pairs/patch						
Intercept	−5.033	2.391	−10.764	−4.686	−1.281	1.001
Foraging habitat within 0.5 km	0.079	0.034	0.026	0.074	0.161	1.002
Artificial land use within 2 km	−0.099	0.068	−0.252	−0.094	0.023	1.003
Site	1.347	0.694	0.364	1.213	3.097	1.004
Year	0.312	0.429	0.008	0.187	1.453	1.008
Juveniles/pair						
Intercept	0.190	1.13	−2.235	0.19	2.493	1.003
Artificial land use within 2 km	−0.108	0.061	−0.238	−0.108	−0.008	1.004
Site	0.554	0.526	0.028	0.416	1.969	1.000
Year	1.669	1.028	0.348	1.405	4.304	1.001

563 Article Summary:

564 We quantified how eastern marsh harriers breeding in wetland patches responded to the amount of foraging habitat and artificial land
565 use in the surrounding areas. Our results showed that the number of juveniles per patch was most susceptible to the artificial land use
566 within 2 km of the wetland patches via direct impacts of artificial land use on the number of juveniles per pair and indirect impacts on
567 the number of pairs per patch.

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Figure 1

Figure 2

Figure 3