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Spatial Overlap between the Intermediate Egret *Egretta intermedia* and Its Aquatic Prey at Two Spatiotemporal Scales in a Rice Paddy Landscape

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Naoki Katayama, Tatsuya Amano, Go Fujita, and Hiroyoshi Higuchi (2012) Spatial overlap between the Intermediate Egret *Egretta intermedia* and its aquatic prey at two spatiotemporal scales in a rice paddy landscape. *Zoological Studies* **51**(7): 1105-1112. Quantification of patterns of spatial overlap between predators and prey at multiple spatiotemporal scales can be a useful approach to understanding hierarchical predator-prey interactions. To date, many empirical studies have focused on only fine spatial scales (less than a few hectares) except in pelagic marine systems. Furthermore, the temporal scale of predator-prey overlap has rarely been explored. This study investigated spatial overlaps between the Intermediate Egret *Egretta intermedia* and its aquatic prey at 2 scales in a rice paddy landscape in central Japan. At a broad spatial scale (more than several hectares), both the egrets and their prey tended to be more abundant in the area of rice fields using traditional irrigation practices than in the area of fields using modern practices, during the flooding periods from late May to late June. At a finer scale, there was a positive spatial correlation between abundances of egrets and their prey in each rice field only at the short temporal scale of a few days. These results suggest that hierarchical predator-prey interactions in rice paddy landscapes are caused by several processes operating at different spatiotemporal scales. http://zoolstud.sinica.edu.tw/Journals/51.7/1105.pdf

Key words: Agricultural intensification, Foraging ecology, Multi-scale patch selection, Predator-prey interaction, Spatial distribution.

Problems of pattern and scale are essential topics in recent studies of predator-prey interactions. In a heterogeneous landscape, prey may be patchily distributed at more than 1 spatial scale because of prey movement, patch depletion, or a variety of environmental factors operating at different scales (Kotliar and Wiens 1990, Wu and Loucks 1995). Generally, the temporal dynamics of patches are linked to spatial scales such that the spatial pattern of fine-scale patches changes faster than that of broad-scale patches (Wu and Loucks 1995, Fauchald et al. 2000). In this situation, predators need to track a changing spatial pattern of prey at several scales (Russell et al. 1992, Fauchald 1999). Consequently, spatial overlap between predator abundances and prey densities is expected at each spatial scale if the speed at which learning predators can track patches of prey abundances is faster than changes in prey distributions (Bernstein et al. 1988 1991). The duration of this overlap should be longer at broader spatial scales, reflecting the temporal scale of predator-prey interactions (Fauchald et al. 2000). Thus investigating the spatial overlap between predators and prey at more than 1 spatiotemporal scale can be useful in understanding hierarchical

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predator-prey interactions. However, many empirical studies to date only focused on fine spatial scales (less than a few hectares) except for some studies of pelagic marine systems (Mehlum et al. 1999, Fauchald et al. 2000). Furthermore, temporal scales of predator-prey overlap at both fine and broad spatial scales provide limited information (Fauchald et al. 2000, Benoit-Bird and Au 2003).

Rice paddy landscapes are suitable for exploring hierarchical predator-prey interactions, because tadpoles and small freshwater fish, important prey for top predators (e.g., egrets and herons), are patchily distributed at more than 1 scale. At a fine scale (less than a few hectares), high-density patches of aquatic prey are linked to field-scale agricultural practices, such as flooding and grass management, which are likely to change over a short time period, such as a few days to a week (Sato and Azuma 2004, Osawa et al. 2005, Kato et al. 2010, Katayama et al. 2011). At a broader scale (more than several hectares), high-density patches of prey are frequently linked to management systems, which are stable over a longer time period, such as weeks or months. For example, in Japan, modern drainage systems are often introduced to increase agricultural productivity at broad scales, but these usually reduce abundances of aquatic prey during periods of flooding in late spring and summer (Lane and Fujioka 1998, Donald 2004). The remaining areas of rice fields where the modern systems have not been introduced (i.e., areas of traditional fields) may be prey patches for top predators at broad scales.

In this study we investigated spatial overlaps between the Intermediate Egret *Egretta intermedia* and its aquatic prey (various tadpoles and fishes, including the dojo loach *Misgurnus anguillicaudatus*) at broad and fine spatial scales in flooded rice fields in central Japan. The egrets seemed to search for prey patches at both scales. At the broader scale, egrets frequently aggregated in areas of traditional fields during the breeding season from late spring to summer (Sato and Maruyama 1996, Lane and Fujioka 1998). Such areas can be predictable broad-scale patches of abundant prey for the egrets, and thus their spatial overlap can be observed for long periods, from weeks to months. At a finer scale, egrets searched for patches of abundant prey on the basis of foraging experiences within several hours (Amano and Katayama 2009). Consequently, their spatial overlap may be observed for a short time period, from hours to a few days, if the egrets can successfully track changes in prey distributions. Thus, this study addressed the following 2 questions: (1) Is there spatial overlap between the egrets and their prey at both broad and fine spatial scales?; and (2) If the overlap is observed at both scales, is the duration of the spatial overlap longer at the broad scale than at the fine scale?

MATERIALS AND METHODS

Study site and species

This study was conducted in a rice paddy landscape along the southern shore of Lake Kasumigaura in Ibaraki Prefecture, central Japan (36°02'N, 140°17'E; Fig. 1). The area is a flat lowland and consists mainly of rice fields, extending approximately 11 km from east to west and 0.5-2.0 km from north to south. The approximate size of a typical field is 0.6 ha (50 × 120 m), and there are approximately 890 fields at the study site.

There are 2 types of rice fields within the study site. In traditional fields, water is taken for irrigation from and drained into shallow earthen-sided ditches with permanent water bodies which are connected to nearby rivers. In modern fields, however, water is supplied via pipes and taps, and drained into deep concrete-walled ditches (Lane and Fujioka 1998). Earlier studies showed that the deep ditches prevent movements of frogs and fishes from the ditches into flooded rice fields for oviposition, and reduce their densities in modern fields (Lane and Fujioka 1998; see “Discussion” for more details). In the eastern part of the study site, there are both traditional and modern fields; in this study, we defined this area as the area of traditional fields (Fig. 1). In the western part, almost all rice fields are modern fields (the area of modern fields; Fig. 1). To investigate spatial overlap between egrets and their prey at both broad and fine scales, 24 evenly distributed fields were chosen within each of the areas of modern and traditional fields.

In Ibaraki Prefecture, there were approximately 20 breeding colonies of egrets and herons with 141-3470 individuals in each in 2000 (M. Fujioka unpubl. data). At the study site, there was a breeding colony located approximately 0.6 km from the closest point to the areas of observations (Fujioka et al. 2001; Fig. 1) that included several species: the Grey Heron *Ardea cinerea*, Great

Egret *A. alba*, Intermediate Egret, Little Egret *E. garzetta*, Cattle Egret *Bubulcus ibis*, and Black-crowned Night Heron *Nycticorax nycticorax*. Numbers of total individuals and of Intermediate Egrets in this colony in 2008 were 2941 and 1152, respectively (M. Mashiko unpubl. data).

During the breeding season between Apr. and July, these species fly to bodies of water, such as rivers, lakes, and rice fields, to feed and collect food for nestlings (Sato and Maruyama 1996). At our study site, a large proportion of Intermediate Egrets foraged in rice fields during the period of flooding in May and June in response to the appearance of abundant prey, such as various tadpoles and small freshwater fish, including the dojo loach (Tanigaki 2001, Amano and Katayama 2009).

Spatial distribution of prey species

The spatial distribution of aquatic prey was surveyed in the 48 rice fields in May and June 2008. Four 2-d surveys during daylight hours were conducted on 8-9 May, 20-21 May, 4-5 June, and 24-25 June. On the 1st day of each survey, 3 Mondori traps (Lane and Fujioka, 1998) made of 2.0-L plastic bottles were placed within arm's length of the edge of each rice field. The traps were baited with teabags containing commercial dried red worms (Pack de Akamushi; Gex Corp., Osaka, Japan) and fish food (Swimmy; Nippon Pet Food, Tokyo, Japan). Traps were collected on the 2nd day of the survey. All captured organisms of > 1 cm in length were identified to at least the genus level, counted, measured (total length), and released at their exact collection sites. The wet mass (g) was calculated for primary prey groups of egrets (Amano and Katayama 2009) i.e., tadpoles using the mean wet mass of a tadpole (0.43 g) and fish including the loach using allometric equations (Tanigaki 2001). For each prey group, the wet masses of prey in the 3 traps were averaged to give a mean for each rice field. The survey on each day was conducted just after the survey of egrets (see below) to avoid any effects on the behavior and distribution of egrets.

One potential problem with using traps is underestimating the density of fish in each field (only 59 individuals were collected; see "Results"). Thus, for the loach, assuming that the direct census method during the night, which measured more than 700 individuals in the 48 rice fields in 2009, could provide an accurate estimate of the true density (see Katayama et al. 2011 for more details), the densities collected by the traps and those directly counted by nighttime censuses in the 48 fields were compared using data in 2009. Results showed moderate but significant positive correlations between the 2 measurements (Pearson's correlation coefficient $r = 0.34$-0.52, $p < 0.05$ in each period). This suggests that although possessing measurement errors, survey

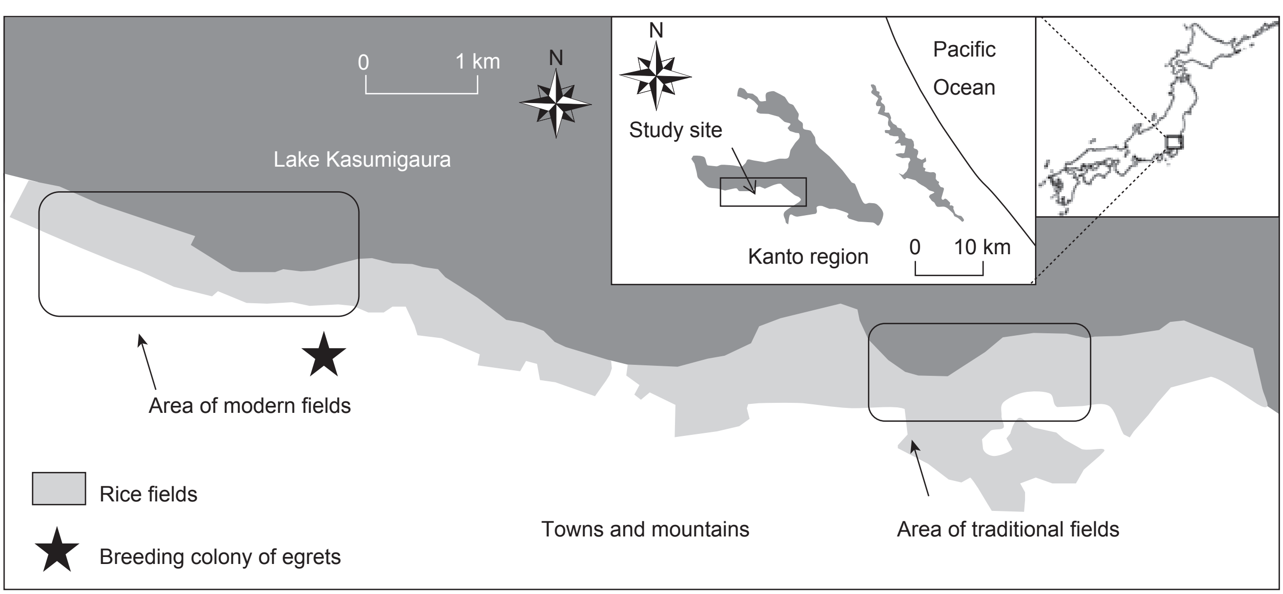

Fig. 1. Study site along the southern shore of Lake Kasumigaura in Ibaraki Prefecture, Kanto region, central Japan (36°02'N, 140°17'E). The 2 areas used for egret and prey surveys are outlined in black. The star indicates the location of the breeding colony of egrets.

results based on the traps seemed to reflect actual patterns in the spatial distribution of the loach at the study site. For other fish, correlations between the 2 measurements were highly variable (r = -0.06-0.84 in each period). Nevertheless, numbers of individuals counted by the traps were 2 and 8 in the modern and traditional fields, and those by the night-time census were 2 and 64, respectively, suggesting that the density of other fish, which was truly low, seemed to be moderately estimated by the minnow traps at the broad scale.

Spatial distribution of egrets

The spatial distribution of foraging egrets was surveyed 2 or 3 days per week from 4 May to 2 July 2008. For each survey, the entire survey route was observed using a car or motorcycle for approximately 1.5 h in the morning when most egrets forage and in the afternoon on 5 and 25 June, days when the prey survey was conducted in the morning. To avoid biases associated with bad weather, surveys were not conducted during rain events. For each survey, 1 or 2 observers using binoculars recorded the location, species, and behavior (foraging or resting) of all individuals found in the study area. Egrets were easily observed because they are large and conspicuous in open rice fields.

Statistical analyses

Spatial overlaps between egrets and their prey at broad and fine spatial scales were investigated using a mixed generalized linear model with a Poisson or negative binomial distribution and log link in the statistical software package R (R Development Core Team 2008). Analyses were conducted for three of the 4 survey periods (late May, early June, and late June); there was no analysis for the early flooding period (early May) because almost no prey were captured. We used different response and explanatory variables at different spatial scales to correspond to the data types in this study. At the broad scale, abundances of egrets and their prey could not be directly compared because only 2 areas were sampled (i.e., traditional and modern fields). Thus, for each predator/prey group, abundances between the 2 areas were compared. The response variable was the number of egrets or numbers in each prey group (tadpoles, loaches, and other fishes) in each field, and the explanatory variable was the area category (area of modern fields = 0, area of traditional fields = 1). To explore the time period of spatial overlap between egrets and their prey, the number of egrets in each field was summed from the day of each prey survey to 1, 5, or 7 days after the survey. For the analysis of prey groups, the abundance (the number of individuals per trap), instead of biomass, was used to satisfy the assumptions of the Poisson regression because a response variable must be a discrete variable. However, the high correlation between the abundance and wet mass of each prey group supported the robustness of the results (Spearman's rank correlation coefficient r > 0.95 for each prey group in each survey period). The logarithm of area (ha) or the number of traps in each field was used as an offset (i.e., a variable that is forced to have a regression coefficient of 1) to allow for differences in survey efforts for egrets and prey, respectively. To control for the non-independence of data due to the 3 repeated surveys (late May, early June, and late June), the survey period was treated as a random variable. The statistical assumptions of the Poisson distribution seemed to be violated only for the tadpole model; the residual deviance divided by the degrees of freedom was > 2.0 in the tadpole model, while they were 0.90-1.40 in the other models. Thus, the number of tadpoles was modeled with a negative binomial distribution.

At the fine scale, abundances of egrets and their prey in each field were directly compared; the response and explanatory variables were the number of egrets and the total wet mass of the 3 prey groups, respectively. The number of egrets in each field was summed from the day of each prey survey to 1, 5, or 7 days after the survey. The logarithm of the area of each field (ha) was used as an offset. To control for the non-independence of the data due to the 3 repeated surveys and the spatially nested samplings, the survey period and the area category (modern = 0, traditional = 1) were treated as random variables. The statistical assumptions of the Poisson distribution did not seem to be violated; the residual deviances divided by the degrees of freedom were 0.73-1.15 for all of the models.

RESULTS

Of the 144 traps set in each survey period, 2-13 traps could not be set up because of low water levels or because they were removed by an unknown 3rd party; thus analyses were performed using data from the remaining traps. In total, traps captured 836 tadpoles, 33 loaches, and 26 fish of other species. Approximately 90% of the tadpoles were the Japanese tree frog *Hyla japonica*, with the remaining being the Tokyo daruma pond frog *Rana porosa.* Fishes other than the loach included the Japanese silver crucian carp *Carassius auratus langsdorfii* and stone moroko *Pseudorasbora parva*. In total, 74 individual Intermediate Egrets were observed in the 48 fields.

At the broader spatial scale, although densities of the aquatic prey groups tended to be larger in the traditional field area than in the modern field area (Fig. 2), a significant difference was not confirmed for the density of tadpoles (Table 1). The density of egrets in each field was significantly higher in the traditional field area than in the modern field area whether integrated from the day of each prey survey or to 1, 5, or 7 d after the survey (Table 1). At the finer spatial scale, there was a significant positive spatial correlation between the density of egrets and the total wet mass of their prey in each field only for a short time period, that is for 1 d (Table 2).

DISCUSSION

Spatial overlaps were observed between the Intermediate Egret and its aquatic prey at both broad and fine spatial scales, and a longer time period was observed for the broad-scale overlap than the fine-scale overlap. These results suggest that hierarchical predator-prey interactions exist in rice paddy landscapes. In the following, potential processes of the spatial overlaps at the 2 spatiotemporal scales are discussed.

At the broad spatial scale, egrets and their prey tended to be more abundant in the traditional field area than in the modern field area during flooding periods, although the spatial pattern in the density of tadpoles was less clear (Table 1, Fig. 2). This possibly indicates that areas of traditional fields are broad-scale patches with relatively abundant prey for egrets. In modern fields, the deep concrete-sided ditches prevent movements of 2 species of frogs (the Japanese brown frog *R. japonica* and the Tokyo daruma pond frog) and small freshwater fishes, including the loach, from the ditches into flooded fields for

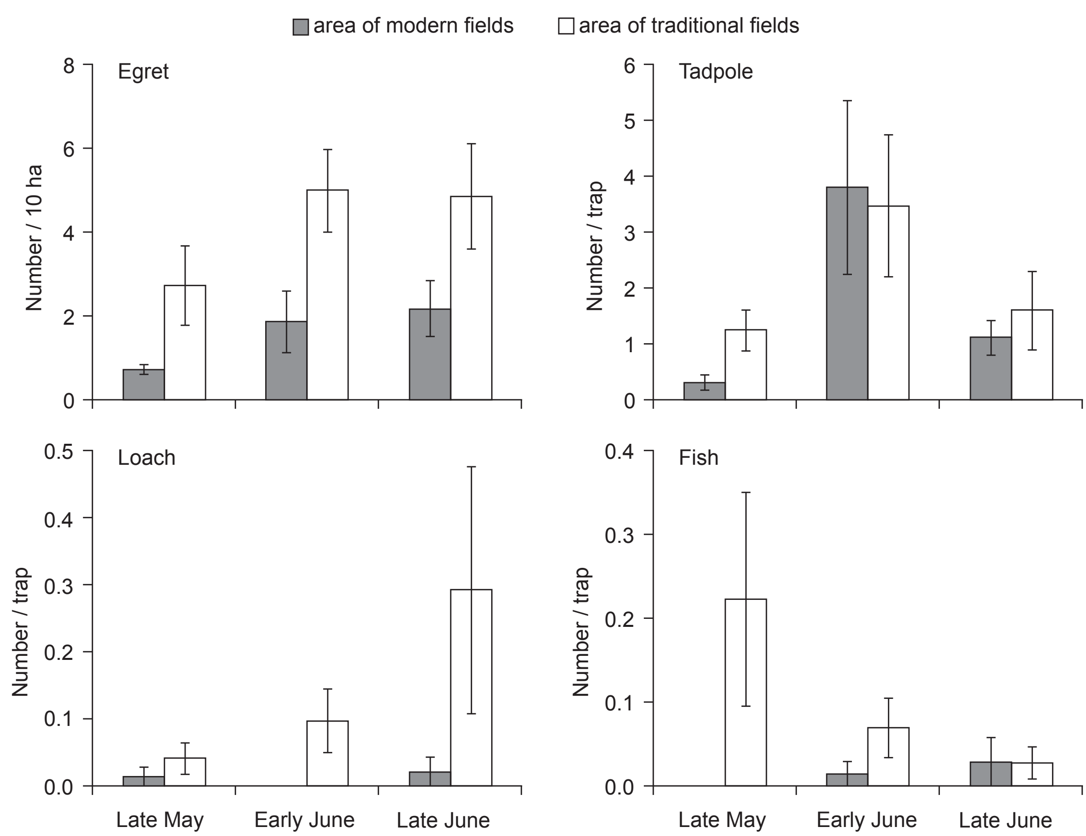

Fig. 2. Densities of the Intermediate Egret and its prey groups (tadpoles, loach, and other fishes) in modern and traditional fields. Values are the mean densities per field; error bars indicate the standard error. *n* = 23-24 for each area during each survey period.

oviposition, and thus reduce their densities (Fujioka and Lane 1997, Lane and Fujioka 1998, Katayama et al. 2011). However, it should be noted that a lack of spatial replicates at this scale makes it difficult to separate effects of other environmental factors. For example, landscape structures (e.g., a proportion of forest cover and width of agricultural fields) may affect abundances and distributions of frogs and egrets (Maeda 2005, Kato et al. 2010). Effects of many landscape-scale factors remain to be revealed in rice-paddy ecosystems (King et al. 2010).

Broad-scale spatial overlap between egrets and their prey was observed at a long temporal scale from a few days to a week (Table 1) and possibly for more than 1 mo (from late May to late June; Fig. 2). Thus, broad-scale patch selection by egrets seemed to be successful despite a large cost in travel and time. Such broad-scale overlaps were frequently reported for large avian predators (e.g., seabirds and waterbirds) and their prey and can result from memories of past foraging trips or from various cues indicating the locations of prey patches such as the presence of other individuals with successful foraging (Fauchald et al. 2000, Davoren et al. 2003, Gawlik and Crozier 2007). In addition, the breeding colony might function as an information center for foraging egrets (Fasola 1982), wherein temporarily unsuccessful individuals that used modern fields obtain knowledge of the location of prey patches from successful ones that used traditional fields, and then aggregate in prey patches at broad scales. These hypotheses should be tested in future

Table 1. Results of generalized linear mixed models used to investigate spatial overlap between Intermediate Egrets and their prey at a broad spatial scale. For analyses of the egrets, the response variable was the number of egrets in each field, which was summed from the day of each prey survey to 1, 5, or 7 d after the survey to explore the time period of the broad-scale overlap. The explanatory variable is the area category (modern fields = 0, traditional fields = 1), and the random variable is the survey period (late May, early June, or late June)

Response variable	Intercept		Explanatory variable (area)		
	Estimated	S.E.	Estimated	S.E.	*p*
Egrets (number/ha)					
1 d	-1.52	0.66	1.01	0.39	< 0.01
5 d	-1.74	0.83	1.60	0.36	< 0.001
7 d	-0.90	0.57	1.28	0.28	< 0.001
Prey group (number/trap)					
Tadpoles	0.19	0.44	0.47	0.32	0.14
Loach	-4.85	0.82	2.72	0.73	< 0.001
Other fishes	-4.34	0.64	2.01	0.62	< 0.005

S.E., standard error.

Table 2. Results of generalized linear mixed models used to investigate spatial overlap between egrets and their prey at a fine spatial scale. As a response variable, the number of egrets was summed from the day of each prey survey to 1, 5, or 7 d after the survey to explore the time period of the fine-scale overlap. The explanatory variable is the total prey mass (g wet weight/trap), and random variables are the categories of survey period and area (modern or traditional field type)

Response variable Egrets (number/ha)	Intercept		Explanatory variable Total prey mass (g wet weight/trap)		
	Estimated	S.E.	Estimated	S.E.	*p*
1 d	-1.23	0.77	0.12	0.05	< 0.05
5 d	-1.04	1.10	0.04	0.05	0.41
7 d	-0.35	0.78	0.05	0.04	0.17

studies.

At a fine spatial scale, although the density of prey was recorded only once each day, it might change even within a day due to biotic (e.g., predation and competition) and abiotic (e.g., agricultural practices) factors operating at fine spatiotemporal scales (Matsushima and Kawata 2005, Amano and Katayama 2009, Kato et al. 2010). Nevertheless, the spatial overlap between egrets and their prey was observed when the density of egrets was summed from the day of each prey survey to 1 d after the survey, but not to 5 or 7 d after the survey (Table 2). This indicates the possibility that (1) the magnitude of within-day changes in prey abundance in each field was not too large to change the spatial distribution of egrets within a day at the fine scale and thus (2) egrets could successfully track changing prey distributions through their fine-scale foraging patch selection at a daily time scale (Amano and Katayama 2009). Causes of slow changes might be that (1) prey movements among rice fields are restricted by earthen banks at field boundaries and thus prey abundances in each field do not rapidly change (e.g., over several hours); (2) the low density of foraging egrets (fewer than 6 individuals per 10 ha on average; Fig. 2) limits the effect of patch depletion; or (3) individual egrets can move among nearby patches (i.e., rice fields) in a foraging trip within several hours (Amano and Katayama 2009) and thus have enough knowledge to determine patch quality. These possibilities should be tested in future studies. We noted that such a fine-scale spatial overlap between predators and prey may be unique in rice paddy landscapes. In pelagic marine systems, for example, many studies reported weak spatial overlap, probably due to rapid changes in prey distributions caused by prey movements (Mehlum et al. 1999, Fauchald et al. 2000, but see Benoit-Bird and Au 2003).

Overall, this study shows patterns of spatial overlap between egrets and their aquatic prey at 2 spatiotemporal scales and the underlying processes potentially affecting these patterns in a rice paddy landscape in Japan. Future studies in rice paddy landscapes should explore what type of agricultural practices affect predator-prey interactions at different scales.

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REFERENCES

Amano T, N Katayama. 2009. Hierarchical decision-making in predators: the influence of foraging experience at more than one spatial and temporal scale. Ecology **90:** 3536-3545.

Benoit-Bird KJ, WWL Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav. Ecol. Sociobiol. **53:** 364-373.

Bernstein C, A Kacelnik, JR Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. J. Anim. Ecol. **57:** 1007-1026.

Bernstein C, A Kacelnik, JR Krebs. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. J. Anim. Ecol. **60:** 205-225.

Davoren GK, WA Montevecchi, JT Anderson. 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol. Monogr. **73:** 463-481.

Donald PF. 2004. Biodiversity impacts of some agricultural commodity production systems. Conserv. Biol. **18:** 17-38.

Fasola M. 1982. Feeding dispersion in the Night Heron *Nycticorax nycticorax* and Little Egret *Egretta garzetta* and the information centre hypothesis. Boll. Zool. **49:** 19-28.

Fauchald P. 1999. Foraging in a hierarchical patch system. Am. Nat. **153:** 603-613.

Fauchald P, KE Erikstad, H Skarsfjord. 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology **81:** 773-783.

Fujioka M, SJ Lane. 1997. The impact of changing irrigation practices in rice fields on frog populations of the Kanto Plain, central Japan. Ecol. Res. **12:** 101-108.

Fujioka M, JW Armacost, H Yoshida, T Maeda. 2001. Value of fallow farmlands as summer habitats for waterbirds in a Japanese rural area. Ecol. Res. **16:** 555-567.

Gawlik DE, GE Crozier. 2007. A test of cues affecting habitat selection by wading birds. Auk **124:** 1075-1082.

Katayama N, D Saitoh, T Amano, T Miyashita. 2011. Effects of modern drainage systems on the spatial distribution of loach in rice ecosystems. Aquatic Conserv. Mar. Freshw. Ecosyst. **21:** 156-164.

Kato N, M Yoshio, R Kobayashi, T Miyashita. 2010. Differential responses of two anuran species breeding in rice fields to landscape composition and spatial scale. Wetlands **30:** 1171-1179.

King S, CS Elphick, D Guadagnin, O Taft, T Amano. 2010.

Effects of landscape features on waterbird use of rice fields. Waterbirds **33(Spec. Publ. 1):** 151-159.
Kotliar NB, JA Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59:** 253-260.
Lane SJ, M Fujioka. 1998. The impact of changes in irrigation practices on the distribution of foraging egrets and herons (Ardeidae) in the rice fields of central Japan. Biol. Conserv. **83:** 221-230.
Maeda T. 2005. Bird use of rice field strips of varying width in the Kanto Plain of central Japan. Agric. Ecosyst. Environ. **105:** 347-351.
Matsushima N, M Kawata. 2005. The choice of oviposition site and the effects of density and oviposition timing on survivorship in *Rana japonica*. Ecol. Res. **20:** 81-86.
Mehlum F, GLJ Hunt, Z Klusek, MB Decker. 1999. Scale-dependent correlations between the abundance of Brunnich's Guillemots and their prey. J. Anim. Ecol. **68:** 60-72.
Osawa S, M Shimada, T Katsuno. 2005. Environmental factors that regulate the density of *Rana porosa porosa* on the levees of flatland paddy fields. J. Rural Plan Assoc. **24:** 91-102. (in Japanese with English summary)
R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Russell RW, GL Hunt, KO Coyle, RT Cooney. 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. Landsc. Ecol. **7:** 195-209.
Sato N, N Maruyama. 1996. Foraging site preference of Intermediate Egrets *Egretta intermedia* during the breeding season on the eastern part of Kanto Plain, Japan. J. Yamashina Inst. Ornithol. **28:** 19-34.
Sato T, A Azuma. 2004. Frogs abundance and environments of levees relationships around paddy fields in alluvial fan. Jpn. J. Inst. Landsc. Architect. **67:** 519-522. (in Japanese with English summary)
Tanigaki N. 2001. Seasonal changes of intake rates and niche overlaps of three egret species in paddy fields. Master's thesis, Univ. of Tsukuba, Tsukuba, Japan.
Wu J, OL Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q. Rev. Biol. **70:** 439-466.