



OPEN Feeding behavior and prey characteristics of great egrets (*Ardea alba*) in eco-friendly and conventional rice fields in South Korea

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Rice fields are important wildlife habitats; however, intensive agricultural practices have reduced the population of farmland birds. As a high-level consumer, the great egret (*Ardea alba*) serves as an indicator of the overall biodiversity of rice fields. However, little is known about the effects of farming methods on the feeding habitat selection of the great egret. Therefore, we examined the influence of eco-friendly and conventional farming methods on prey characteristics and great egret feeding behavior in rice field ecosystems. We employed focal observations and trap-based sampling to quantify prey characteristics and great egret feeding behaviors in eco-friendly and conventional rice fields. Great egrets showed more hunting attempts per minute and a higher intake rate in conventional fields, but feeding efficiency did not differ. Moreover, they consumed larger loaches in eco-friendly fields than in conventional fields. Great egrets exhibited slower feeding behaviors in eco-friendly fields due to the increased handling time of larger prey, such as loaches. Eco-friendly fields supported a higher abundance of larger-sized loaches than conventional fields, indicating their potential for supporting a higher abundance of great egrets. Our findings highlight the importance of sustainable farming practices for the conservation of the great egret.

Keywords great egret, feeding behavior, sustainable agriculture, biodiversity

Agricultural lands are habitats with substantial biodiversity value; however, intensive farming practices have contributed to biodiversity loss^{1–3}. While the habitat value of rice fields is widely acknowledged, they are not a complete substitute for natural wetlands; however, their potential as suitable habitats for wildlife is expanding^{4,5}. Rice fields serve as breeding, stopover, and wintering sites for a variety of waterbird species^{6–9}. Notably, rice fields serve as important habitats for endangered waterbird species such as the Oriental stork (*Ciconia boyciana*), crested ibis (*Nipponia nippon*), and black-faced spoonbill (*Platalea minor*)^{10–12}. Consequently, rice fields are increasingly recognized for their potential to support wildlife conservation efforts. However, since the late 20th century, there has been a steady decline in the number of farmland birds owing to agricultural intensification in several regions worldwide^{13–15}.

Intensive agricultural practices such as tilling and the application of synthetic pesticides and fertilizers may negatively affect the farmland food web^{5,16}. Several studies have investigated the role of sustainable agricultural practices in mitigating biodiversity loss^{17–19}. In particular, research on agricultural ecosystems has focused on the effects of eco-friendly farming practices on biodiversity, such as the degree of eco-friendliness (prohibition of chemical use, slight chemical use, and non-organic fertilizer and chemical use) on biodiversity²⁰, changes in species diversity between eco-friendly and conventional farming based on landscape characteristics^{5,21}, and the effect of organic farming on various bird taxa¹⁵. Compared to conventional farming methods, eco-friendly farming methods support a higher abundance of organisms such as birds, amphibians, fish, and macro-invertebrates, along with a more complex and stable food web^{22–24}.

The great egret (*Ardea alba*) is a representative waterbird species in South Korea, with breeding colonies distributed near rice fields nationwide^{25–27}. As a high-level consumer in the rice field food web, the great

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Variable	Estimate	SE	χ^2	df	p
Intercept	0.503	0.126	62.221	1	<0.001
Number of steps per minute	0.006	0.004	8.059	1	<0.01
Number of hunting attempts per minute	0.126	0.019	5.390	1	<0.05
Number of intakes per minute	0.150	0.027	8.982	1	<0.01
Feeding efficiency	0.109	0.111	1.129	1	0.288

Table 1. Results of generalized linear mixed model analysis of the effects of farming practices on the feeding behaviors of great egrets.

Variable	Eco-friendly field	Conventional field	W	p
Number of steps per minute	19.95 ± 1.01	22.26 ± 1.19	3157	0.307
Number of hunting attempts per minute	2.02 ± 0.15	3.12 ± 0.23	2347	<0.001
Number of intakes per minute	0.7 ± 0.07	1.54 ± 0.18	2591	<0.01
Feeding efficiency	0.38 ± 0.03	0.46 ± 0.04	2956	0.093

Table 2. Comparison of means using the Wilcoxon test (W). Results are presented as mean ± SE.

Variable	Estimate	SE	χ^2	df	p
Intercept	0.509	0.107	53.333	4	<0.001
Prey type	1.661	0.370	0.011	1	0.916
Prey size	0.786	0.079	7.133	2	<0.05
Handling time (s)	0.229	0.080	15.144	1	<0.001

Table 3. Results of generalized linear mixed model analysis of the effects of farming practices on prey type, prey size, and prey-handling time of great egrets.

egret serves as an indicator species for biodiversity. Great egrets are particularly active in rice fields during the transplanting season²⁸. While the timing of breeding varies not only between colonies but also within them, the nestling period in most breeding grounds is during the rice transplanting season²⁷. Additionally, great egrets are observed more frequently in eco-friendly rice fields than in conventional fields during the transplanting season, and they are known to use loaches as a major food source^{15,29}. Moreover, in the case of paddy fields being flooded just before planting, it is generally difficult to observe the effect of pesticide use on the abundance or size of loach populations. This is because water is usually introduced through irrigation channels, and the loaches migrate along with the incoming water^{30,31}. Consequently, great egrets intensify their hunting efforts for prey, such as loaches in rice fields, during the transplanting season in order to meet the increased feeding demands of their chicks²⁸.

The selection of a feeding habitat is crucial as it directly influences the reproductive success of migratory birds, including the great egret, during the breeding season, when the energy requirements of chicks are high^{32–35}. The feeding habitat choice of great egrets is influenced by various factors such as food density, habitat type, water depth, anthropogenic activity, and land use^{26,35–37}. However, only a few studies have investigated the effects of agricultural practices on feeding habitat selection and behavior of the great egret²⁸. Therefore, in this study, we aimed to compare the effects of eco-friendly and conventional rice farming practices on prey characteristics and feeding behavior of the great egret in rice field ecosystems.

Results

Generalized linear mixed model (GLMM) analysis revealed differences in the feeding behaviors of great egrets, excluding feeding efficiency between eco-friendly and conventional fields (Table 1). Specifically, the steps per minute, hunting attempts per minute, and intakes per minute were lower in eco-friendly fields than in conventional fields (Table 1). However, the comparison of means did not demonstrate significant differences in the number of steps per minute (Wilcoxon test, $W = 3157$, $p = 0.307$; Table 2). Notably, the number of intakes per minute in conventional fields was two times higher than that in eco-friendly fields.

Regarding potential prey, prey type did not vary according to field type (eco-friendly and conventional fields), but prey size and handling time varied (Table 3). The majority of the prey of great egrets were loaches (95.5% in eco-friendly fields and 90.2% in conventional fields; Fig. 1). Eco-friendly fields had a higher proportion of large loaches (68.8%), and conventional fields had a higher proportion of small loaches (55.7%; Fig. 2). Additionally, larger prey corresponded to a longer handling time; specifically, great egrets in eco-friendly fields exhibited longer handling time than those in conventional fields [58.14 ± 1.09 s in eco-friendly fields ($n = 64$) and 46.45 ± 2.06 s in conventional fields ($n = 61$); Fig. 3]. Additionally, the abundance of loaches captured per trap was higher in eco-

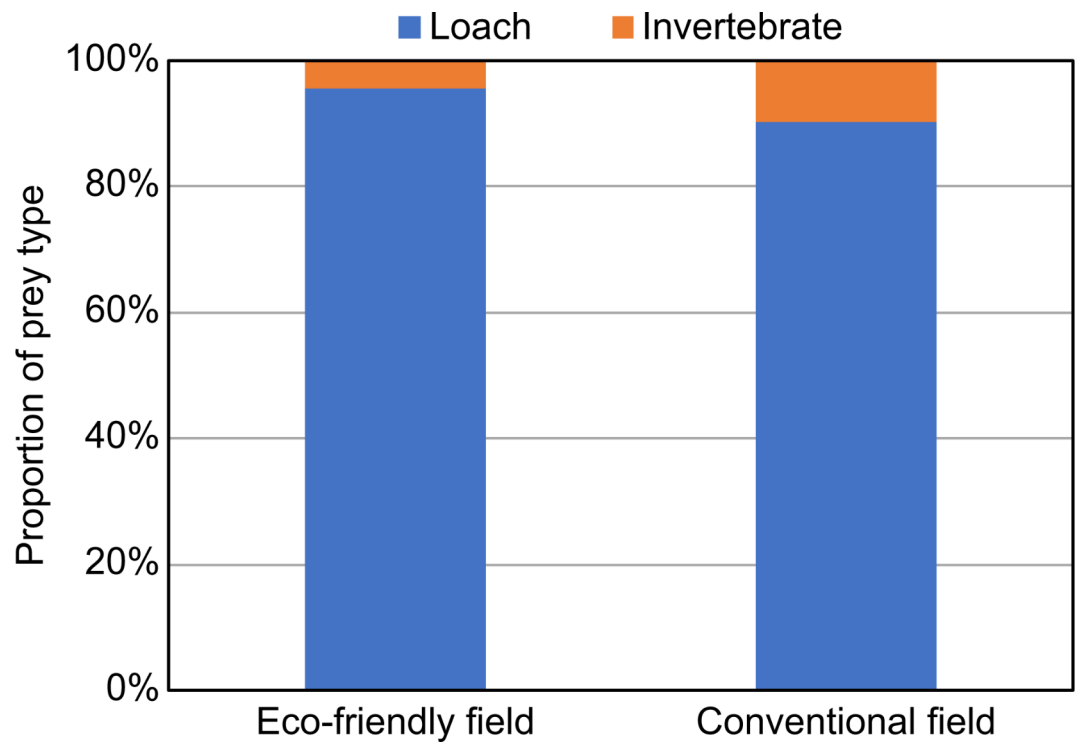


Fig. 1. Proportion of captured prey by type in eco-friendly ($n=64$) and conventional ($n=61$) fields.

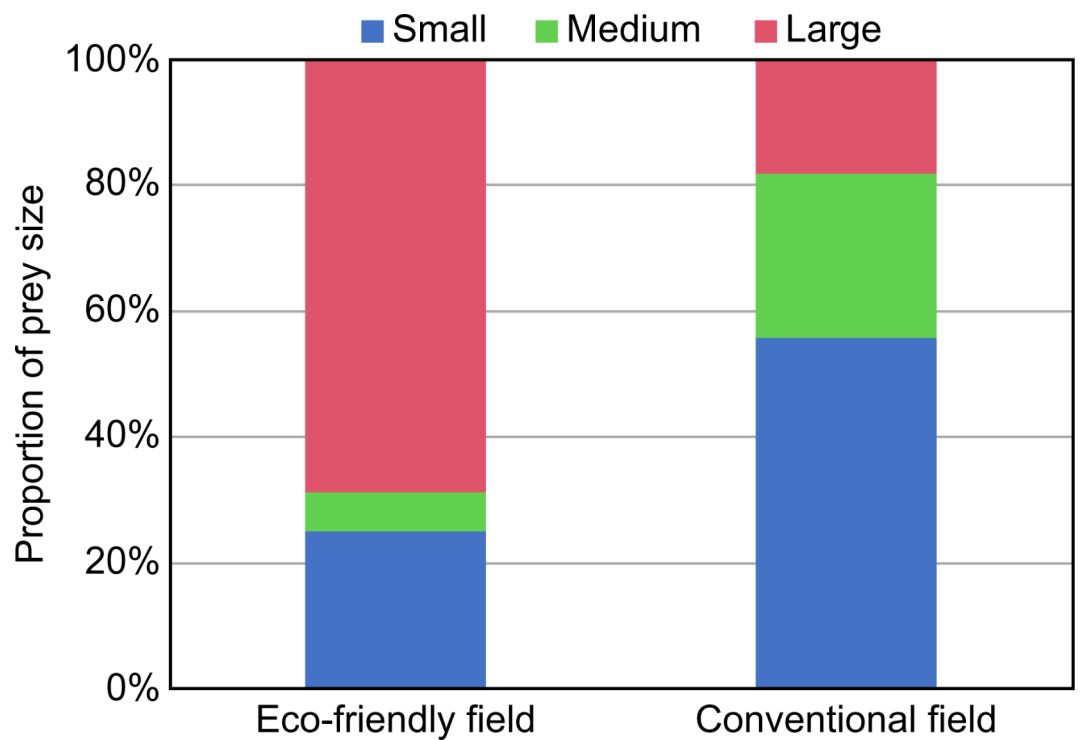


Fig. 2. Proportion of captured prey by size (large, medium, and small) in eco-friendly ($n=64$) and conventional ($n=61$) fields.

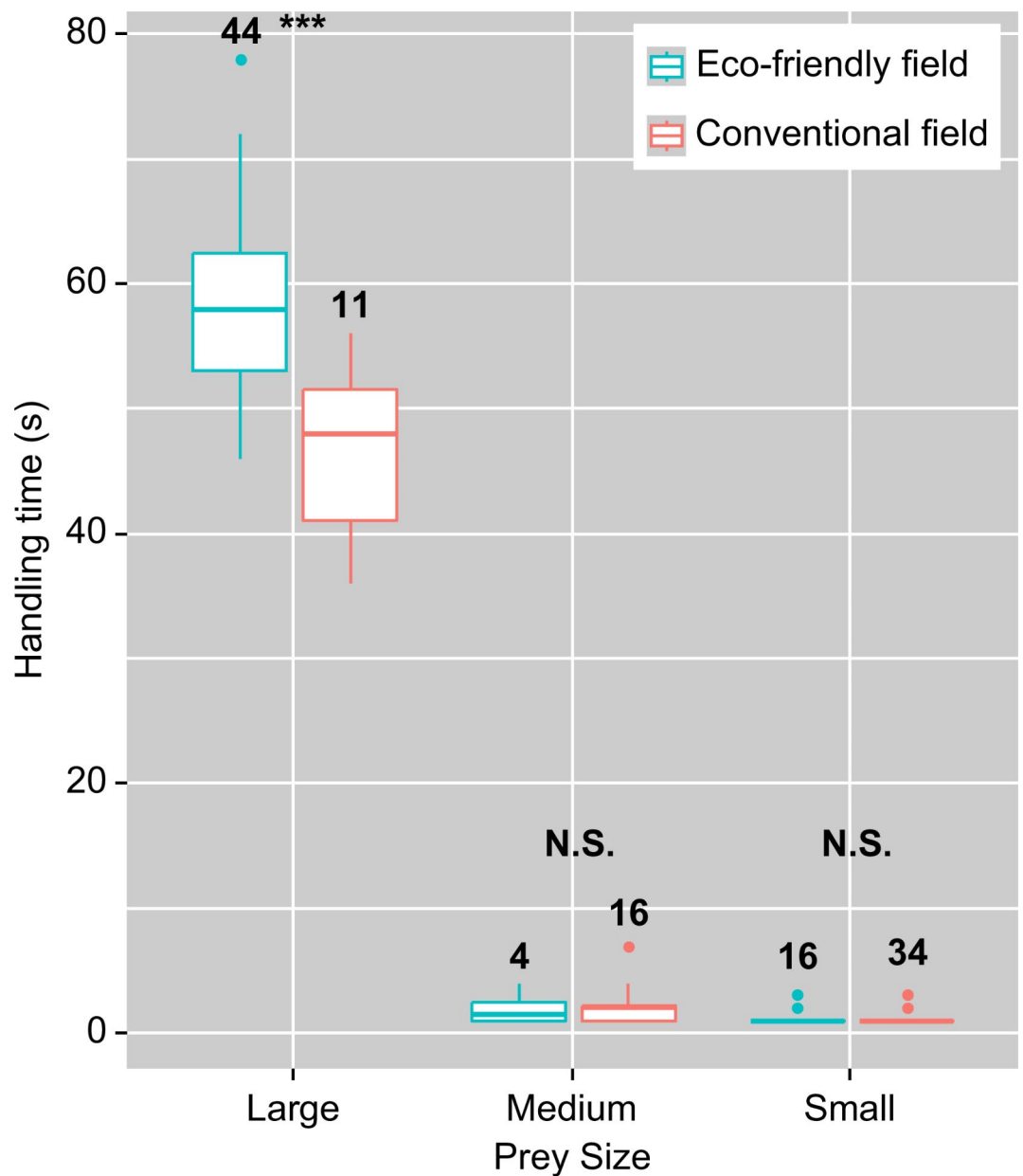


Fig. 3. Multiple boxplots for comparing the median handling time (s) for each prey size in eco-friendly and conventional fields. The boxes represent the interquartile range of handling time, the horizontal line within the box is the median, and whiskers show the range within the upper and lower limits. The numbers above each box plot indicate sample sizes. N.S., not significant; ***, $p < 0.001$.

friendly fields (11.20 ± 2.30 , $n = 30$) than in conventional fields (2.60 ± 1.03 , $n = 30$), and individuals captured in eco-friendly fields were found to be longer [81.42 ± 0.82 mm in eco-friendly fields ($n = 281$) and 65.10 ± 1.10 mm in conventional fields ($n = 84$); Fig. 4].

Discussion

In this study, we compared the feeding behaviors and prey characteristics of great egrets in eco-friendly and conventional rice fields to elucidate the effect of farming practices on rice field ecosystems. Choi et al.¹⁵ reported a higher frequency of great egret sightings in eco-friendly fields than in conventional fields during the transplanting season. Our study also suggests that great egrets use eco-friendly fields more frequently than conventional fields. By analyzing the behavioral traits of great egrets in detail and understanding their relationships with specific food sources such as loaches within rice field ecosystems, our research further corroborates these findings.

In South Korea, the rice transplanting season typically spans late May to early June, coinciding with the fledgling period of great egrets. During this critical phase, considerable foraging efforts of great egrets are directed toward supplying an adequate amount of food for rapidly growing chicks²⁸. In the present study, we analyzed the feeding behavior of great egrets in eco-friendly and conventional fields to determine the effect

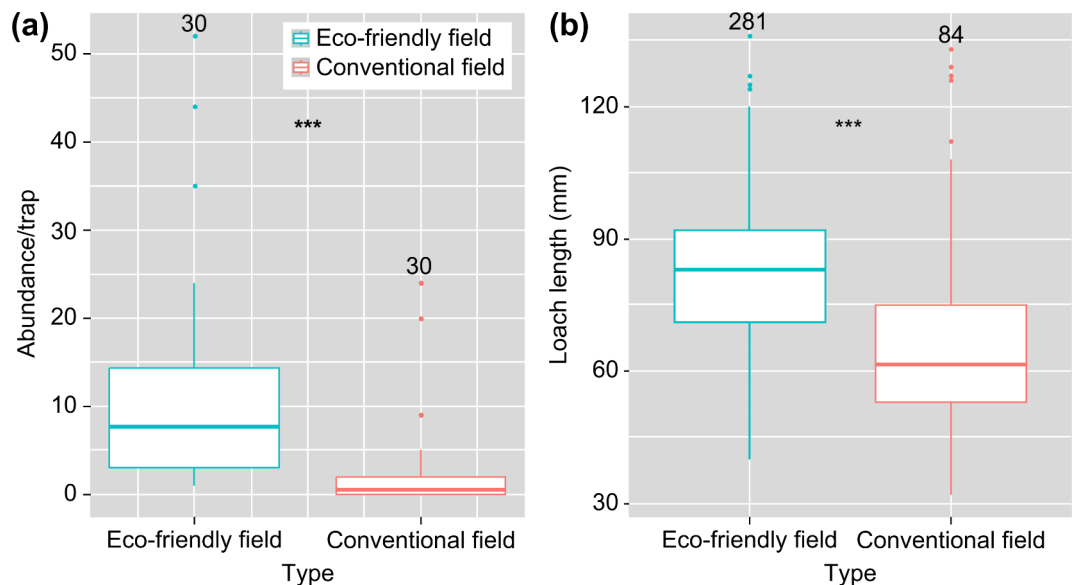


Fig. 4. Box-and-whisker plots depict (a) loach abundance per trap and (b) length of individual loaches in eco-friendly and conventional fields. The interquartile range of both abundance and length is represented by the boxes, with the median indicated by the horizontal line within each box. The whiskers extend to the upper and lower limits, showcasing the range, whereas circles indicate outliers. Sample sizes are denoted above each box plot. N.S., not significant; **, $p < 0.01$; ***, $p < 0.001$.

of farming practices. Handling time according to prey size emerged as an important determinant of feeding behaviors, including the number of steps, hunting attempts, and intakes. Notably, great egrets in eco-friendly fields exhibited slower feeding behaviors, excluding feeding efficiency, than those in conventional fields. This deceleration primarily stems from increased prey-handling time during hunting activities in eco-friendly fields, where larger loaches are more prevalent than in conventional fields. Furthermore, the preference for a stand-and-wait hunting strategy over an active walking strategy was indicative of the overall sluggish hunting behavior of great egrets in eco-friendly fields (personal observation). This phenomenon was particularly evident in areas with abundant large loaches, consistent with the observations of Yamada³⁸. Great egrets tend to target larger loaches owing to their abundance in eco-friendly fields^{39,40}. Our findings align with those of previous studies reporting preferences for larger, more energy-rich prey^{41,42}. The greater abundance of great egrets in eco-friendly fields than in conventional fields²⁴ might be related to the greater abundance of large prey in eco-friendly fields.

Previous studies have reported the presence of numerous tadpoles, alongside loaches and invertebrates, during the establishment of flooded paddies^{6,43,44}. However, in the present study, we solely observed invertebrates and loaches, either through recordings or sampled using traps. The absence of tadpoles is attributable to the limited abundance and variable hatching times (outside the study period) of tadpoles in the surveyed area⁴⁵. Thus, loaches, being the dominant fish species, have emerged as crucial prey for herons and egrets inhabiting rice paddies in South Korea⁴⁶. The spatial distribution of loach populations is influenced by various aspects of modern drainage systems and water management⁴⁷. However, all fields in this study were irrigated with water from the same ditch, thereby reducing variability among different fields. We focused on the effect of farming practices (eco-friendly vs. conventional) on loach distribution. In addition to the greater abundance of loaches in eco-friendly fields, loaches were found to be larger and heavier in eco-friendly fields than in conventional fields^{30,48,49}. Loaches primarily feed on aquatic animals such as Chironomids, Copepods, and Cladocerans^{50–52}. Therefore, they are believed to be more abundant and larger in eco-friendly rice fields, which have a higher presence of these aquatic animals^{53–55}.

While great egrets in both eco-friendly and conventional fields exhibited similar feeding efficiency, they favored larger and heavier loaches in eco-friendly fields. Previous research has indicated lower biomass yield of great egrets in conventional rice fields⁵⁶, highlighting the advantages of eco-friendly fields in providing higher energy returns⁵⁷. Numerous studies have demonstrated the benefits of targeting large prey for energy acquisition^{57–61}. While we did not directly compare the energy gained from handling larger loaches versus smaller ones in this study, considering the energy expenditure for hunting smaller prey, acquiring larger loaches is likely more advantageous for great egrets. Enhanced energy acquisition enables great egrets to provide their chicks with high-energy prey, thereby potentially boosting reproductive success in eco-friendly fields. Moreover, compared to the hunting methods in eco-friendly fields, it is believed that in conventional fields, they compensate for energy acquisition by easily handling smaller loaches and increasing hunting frequency. However, this results in increased movement for hunting, such that eco-friendly fields, in which loaches are more abundant and hunting behavior does not need to involve extensive movement, are considered more beneficial in terms of net energy gain than conventional fields. Further research is needed to accurately compare the energy acquisition between these two types of fields.

The direct collection of loaches using traps and indirect observation of loach-hunting behavior of great egrets suggest a higher abundance and larger size of loaches in eco-friendly fields than in conventional fields. The large size of loaches indicates their good health status, implying that they consume a variety of food resources such as frog eggs, small tadpoles, and small invertebrates^{62–64}. Eco-friendly fields, characterized by minimal pesticide or herbicide usage, have been recognized for their greater abundance and biomass of loaches than those of conventional fields^{30,48,49}.

This study demonstrated the pivotal role of eco-friendly farming practices in maintaining a stable food web within rice fields and highlighted the potential of optimizing rice fields to support wildlife conservation efforts. For example, rice farmers can limit the use of synthetic pesticides and herbicides to adopt more eco-friendly practices. In South Korea, incentives for eco-friendly rice cultivation are provided based on specific criteria, with rice grown using these methods commanding a higher market value⁶⁵. However, the adoption of eco-friendly farming practices has been impeded by factors such as an aging farming population and rural depopulation, leading to their limited adoption in certain regions⁶⁶. Addressing the challenges posed by these factors requires strategic policy interventions. Despite existing payment schemes in South Korea favoring individual farmers, future policies should consider additional incentives for larger areas, such as survey zones, particularly in mechanized rice fields. This strategic approach is critical in addressing evolving agricultural dynamics in response to demographic shifts.

Materials and methods

Study sites

The study sites were located in Seokmun-myeon, Dangjin-gun, Chungcheongnam-do, South Korea (37°02'N, 126°30'E; Fig. 5). The rice fields in this region were reclaimed from construction lands starting in 1979 and developed on 3904 ha as a part of the Large-scale Comprehensive Agricultural Development Project. Initially, rice was cultivated using conventional methods in the entire area, but since 1999, eco-friendly cultivation methods have been increasingly adopted (574.2 ha). In this study, cultivation methods involving minimal to no pesticide use or minimal chemical fertilizer use were considered “eco-friendly,” whereas agricultural practices involving pesticide use were considered “conventional.” In the conventional fields, a pesticide mixture of tiadinil

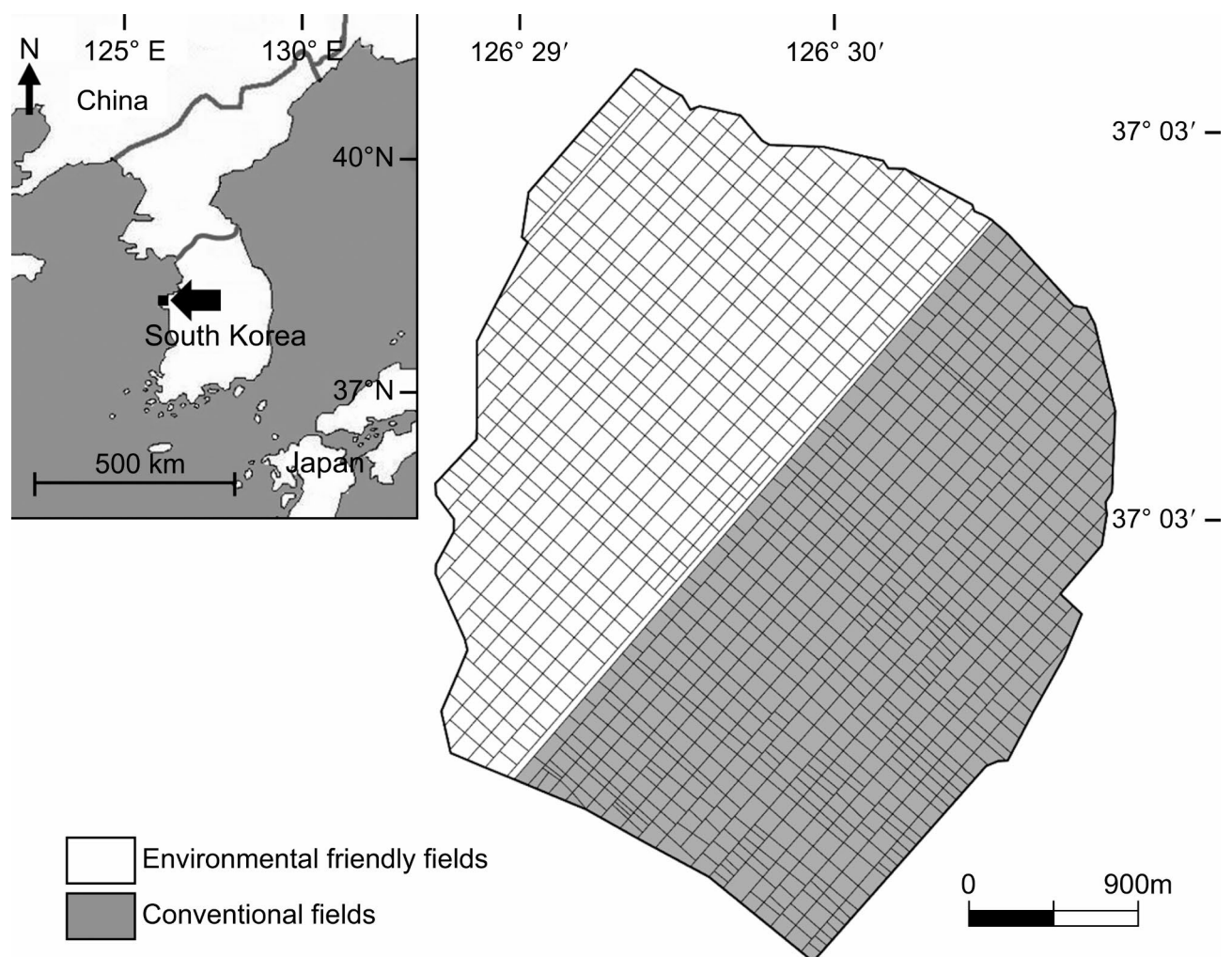


Fig. 5. Map of the study sites. The map was created using Adobe Illustrator 2024.

and clothianidin was used for sterilization in the seedling box, and pesticides containing pyrazosulfuron-ethyl or fentrazmide were used after transplantation. In some eco-friendly paddies, pesticides were applied at a frequency of once per cycle; however, most of the eco-friendly rice fields in this study were pesticide-free. Additionally, management of levees and roads typically differs between eco-friendly and conventional rice fields. While management of conventional rice paddies differs by survey unit, eco-friendly rice paddies are managed on a larger scale by local governments through mechanization. In this study, weeds on the levees and roads of eco-friendly rice fields were either left in place or physically removed using a weeder, whereas those of conventional rice fields were removed using a chemical herbicide. The eco-friendly and conventional rice fields in this study were adjacent to each other, separated by roads, and irrigated by the same ditch. The survey unit, measuring 0.45 ± 0.07 ha (mean $\pm$ standard error), was a standardized field unit enclosed by levees and farm roads. For this study, 446 eco-friendly rice fields and 442 conventional rice fields were selected. To minimize the effect of changes in the survey field, the behavior of the great egret and sampling traps of potential prey were observed in rice fields that had been transplanted from May 30 to June 14, 2016. Moreover, since eco-friendly and conventional rice fields were adjacent to each other along the farm road and could be affected by pesticides, behaviors of great egrets were not observed within 200 m to the left and right of the farm road.

Behavioral observation

We employed a focal sampling method to quantify the feeding behavior, prey types, and prey sizes of great egrets using a camcorder (HMX-S16; SAMSUNG, Suwon, Gyeonggi-do, South Korea) equipped with a 2.2× optical zoom. The feeding behavior of each individual was recorded for 5 min. We documented the feeding behavior by recording the number of steps per minute, the number of hunting attempts per minute, the number of intakes per minute, feeding efficiency, and prey handling time. During the recording of feeding behavior, it was observed that great egrets preyed only on invertebrates (Classes: Bivalvia, Malacostraca, and Insecta) and fish such as loaches (*Misgurnus mizolepis* and *Misgurnus anguillicaudatus*); therefore, prey types were categorized as either invertebrates or loaches. A hunting attempt was defined as the act of capturing prey by dipping the beak into the water, and intake referred to swallowing prey through neck movement or rapid head lifting. Feeding efficiency was calculated by dividing the number of intakes per minute by the number of hunting attempts per minute. Prey handling time was defined as the time from capturing prey to swallowing.

Based on the beak length of a great egret, prey was classified as small (less than one-third the beak size), medium (less than one-half the size), and large (more than one-half the size). When a great egret hunts loaches, it has been observed that loaches wrap around the beak of the great egret in an attempt to escape. This makes it difficult for the great egret to swallow the loach, so it handles the loach until it weakens and can be swallowed. Through this process, the relative total length of the loach can be determined (Supplementary Fig. S1). To minimize the effect of our presence on the behavior of great egrets, we waited for 10–15 min after our arrival before commencing videotaping. Furthermore, as higher water levels may also affect the behavior of great egrets, we selected individuals feeding at water levels of less than half the length of the tarsus. To mitigate the issue of pseudoreplication, we sampled only one individual per field to reduce repeated sampling of the same individual. We collected video recordings of the foraging behavior of 167 individuals (88 individuals in eco-friendly fields and 79 individuals in conventional fields).

Prey sampling

To determine the abundance profiles of potential food sources, sampling was conducted on June 12 and 14, 2016, by placing two types of traps, which can capture both loaches and invertebrates, in each transplantation field: one loach trap and one Mondori trap⁶⁷. Sampling points for potential food sources were randomly selected. Potential prey abundance was assessed exclusively in the transplanted fields. We quantified the potential prey abundance detected per sampling trap.

Each loach trap measured 28 cm in length and 15 cm in diameter (inlet: 2.8 cm). The Mondori trap was constructed by cutting off the inlet of a plastic bottle (2 L) and reattaching it upside down. Prey such as Bivalvia, Malacostraca, and Insecta species can enter the Mondori trap but cannot easily find the exit. The traps were baited with fish meal (Gompyo; Gompyo Ddugbab, Seoul, South Korea) and dried tubifex worms (Vitakraft, Bremen, Germany), and collected 24 h after setup. Thirty fields were sampled per day.

Prey were categorized into two types, loaches and benthic invertebrates, and only those exceeding a length of 1 cm were counted^{46,68}. The number of prey per sample was calculated as the sum of individual prey caught in the loach and Mondori traps. We measured the length of the loaches, and then weighed them. Efforts were made to remove as much moisture as possible using an experimental hand towel before weighing the loaches. The length of loach species was measured by holding the head, stretching the body as much as possible, and fixing the tail. All prey were promptly released back into the fields where they were captured after the measurements. The study is reported in accordance with the ARRIVE guidelines (<https://arriveguidelines.org>), and all fieldwork procedures adhered to the guidelines of the Kyung Hee University Animal Ethics Committee. The study was approved by the Animal Ethics Committee of Kyung Hee University, and the approval number is 2018-HA-028HO.

Statistical analysis

We used GLMMs with binomial (logit) distributions to assess the effects of field type (eco-friendly vs. conventional) on feeding behaviors and prey characteristics of great egret. The explanatory variables were eco-friendly/conventional fields, and the responsible variables were feeding behaviors (steps, hunting, feeding efficiency, and handling time) and prey characteristics (type, size, and abundance). The survey date was designated as a random effect. All statistical analyses were conducted using R version 4.3.0⁶⁹; the “lme4” package⁷⁰ was employed to fit

and analyze the GLMMs, and mean values were compared using the Wilcoxon test (*W*). Results are expressed as mean $\pm$ standard error.

Data availability

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

Green Choi: Data curation, Formal analysis, Writing - original draft, Writing - review & editing; Min Seock Do: Data curation, Writing - original draft, Writing - review & editing; Seok-Jun Son: Data curation, Writing - original draft, Writing - review & editing; Hyung-Kyu Nam: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. All authors provided final approval for publication.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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