Research Paper

J. Ecol. Field Biol. 33(2): 149-155, 2010
DOI: 10.5141/JEFB.2010.33.2.149

JEFB Journal of Ecology and Field Biology

# Feeding activity of cattle egrets and intermediate egrets at different stages of rice culture in Korea

**Yu-Seong Choi[1,2], Sun-Sook Kim[1] and Jeong-Chil Yoo[1,*]**

[1]Korea Institute of Ornithology and Department of Biology, Kyung-Hee University, Seoul 130-701, Korea
[2]Present address: Korea Institute of Oriental White Stork Rehabilitation Research, Cheongwon 363-791, Korea

This study was conducted to investigate the feeding efficiency of the cattle egret (*Bubulcus ibis*) and the intermediate egret (*Ardea intermedia*) in relation to the stage of rice culture during two breeding seasons, 2006 and 2007, in Asan city, Chungcheongnam-do, South Korea. Cattle egrets caught mainly small invertebrate prey (insects and spiders, 98.4%) during all stages of rice cultivation, and had a higher prey capture rate in the plowing stage (14.98 prey/min) than in other stages (2.82-3.51 prey/min). Therefore, the biomass intake rate of cattle egrets was highest in the plowing stage. The intermediate egret captured both loaches (43.4%) and small invertebrates (50.6%). The prey capture rates of intermediate egrets increased gradually from the flooding stage (0.38 prey/min) to the planting stage (1.09 prey/min), and decreased in the growing stage (1.04 prey/min). However, intermediate egrets had the highest biomass intake rates in the plowing stage because more loaches were caught in the plowing stage (0.54 loaches/min) than other stages (0.23-0.36 loaches/min). Consequently, both intermediate egrets and cattle egrets had high energy intakes in the plowing stage and rice fields provided an important feeding habitat for both species.

**Key words:** cattle egrets, feeding activity, intermediate egrets, rice fields, stage of rice culture

## INTRODUCTION

Rice fields are a unique type of man-made seasonally flooded wetland, which support many taxonomic groups of aquatic organisms (González-Solís et al. 1996, Yamazaki et al. 2004). In particular, rice fields play a significant role as alternative habitats for waterbirds, including herons and egrets, providing a substitute for disappearing natural wetland habitats, since they show relatively high prey densities (Fasola and Ruiz 1996, Fasola et al. 1996, Elphick and Oring 1998, Elphick 2000, Maeda 2001). As the value of rice fields for bird conservation is recognized (Ovenden et al. 1998), it has become clear that further studies of bird feeding strategies in rice fields are their responses to changes in rice field use will be valuable for conservation planning.

The foraging ecology of ardeids in rice fields has been studied mostly in the Mediterranean region (Fasola 1986, Hafner et al. 1986, Fasola and Ruiz 1996, Fasola et al. 1996, Kazantzidis and Goutner 1996, Lombardini et al. 2001), with a few additional studies in Japan (Tojo 1996, Lane and Fujioka 1998) and Australia (Richardson et al. 2001, Richardson and Taylor 2003). Although some ardeids forage in rice fields throughout the year, most species use rice fields primarily during their breeding season, when fields are flooded and the prey density is relatively high (e.g., Fasola et al. 1996, Kazantzidis and Goutner 1996, Maeda 2001). Foraging efficiency in rice fields differed among heron species due to differences in prey preferences among ardeids (Tojo 1996, Richardson et al. 2001)



**Received** 31 December 2009, **Accepted** 5 February 2010
***Corresponding Author**
E-mail: jcyoo@khu.ac.kr
Tel: +82-2-961-0849

and differences in prey type and abundance among regions (Fasola et al. 1996, Lane and Fujioka 1998). Therefore, some species may benefit substantially from foraging in rice fields, while other species may obtain little or no benefit (e.g., Campos and Lekuona 2001, Richardson et al. 2001, Richardson and Taylor 2003).

Changes in agricultural practices have significant effects on the distribution and foraging efficiency of ardeids (Hafner et al. 1986, Lane and Fujioka 1998, Tourenq et al. 2003). In particular, insectivorous or carnivorous waterbirds, such as herons and egrets, may be more affected by the physical structures of rice fields and by agricultural treatment methods than seed-eating waterbirds (e.g., ducks, geese and cranes) during winter, because the abundance and richness of animal prey is highly dependent on management regimes such as irrigation practices and pesticide treatments (González-Solís et al. 1996, Fujioka and Lane 1997, Lane and Fujioka 1998, Tourenq et al. 2003, Yamazaki et al. 2004, Wilson et al. 2008).

In Korea, rice fields occupy larger areas of land (55.3% of total agricultural area) than any other crop (based on 2007 data from Korean Statistical Information Service, www.kosis.kr). In general, rice fields are flooded in spring and summer and dry in winter. They may thus play an important role as substitute foraging and nesting wetlands for waterbirds during the spring-summer period (Fasola and Ruiz 1996, Fujioka et al. 2001). Rice fields show dramatic seasonal changes in vegetation and water levels, and therefore the availability of rice fields as feeding habitats for ardeids also varies (Narusue and Uchida 1993, Sato and Maruyama 1996, Maeda 2001, Richardson et al. 2001, Richardson and Taylor 2003).

The cattle egret (*Bubulcus ibis*) and the intermediate egret (*Ardea intermedia*) are common breeding ardeids in Korea and they frequently forage in rice fields (Choi et al. 2007), although other habitats such as grasslands and freshwater marshes are also important feeding habitats (Kushlan and Hancock 2005). The objective of this study was to evaluate the foraging efficiency of two ardeid species at different stages of rice culture during the breeding season.

## MATERIALS AND METHODS

### Study area

The study was conducted in rice fields of Dunpo-myeon and Eumbong-myeon in Asan city, Chungcheongnam-do, South Korea (Fig. 1). The study area is located in northeastern area of 5 km radius from a mixed-species heronry (36°52'15" N, 127°02'10" E), and most feeding egrets in the study area probably breed in the heronry.

In Korea, rice fields are generally flooded for 5-6 months of the year (from April to September), which coincide with the breeding and migrating seasons of waterbirds. Rice cultivation in Korea involves the following stages: flooding and plowing (April and May), rice planting (late May and early June), rice growing (from June to September) and harvesting (October). The height of rice crops peaks in August at about 1 m. Water levels in rice fields are maintained at about 10-20 cm depth throughout the rice growing season (from April to September), after which the water is allowed to dry out for the harvest.

### Methods

We observed feeding activities of cattle egrets and intermediate egrets between May and early July in 2006 and 2007. Daily observations were made from 08:00 to 19:00 h on days with favorable weather conditions (no rain or strong wind). We recorded the feeding activity of each egret using digital video cameras (Sony DCR TRV-20 and DCR HC-40; Sony Electronics Inc., Tokyo, Japan) or via direct observations using binoculars (8×) and a spotting scope (20-60×). One observation bout lasted 4-5 minutes for the intermediate egret and 2-3 minutes for the cattle egret because of their high food intake. We conducted 280 observations totaling 812.3 minutes (average 2.9 min/observation) for cattle egrets and 120 observations totaling 589.7 minutes (average 4.9 min/observation) for intermediate egrets.

The following information was recorded during each observation: rice stage, feeding location within the rice fields (center, edge and levees), duration of observation, type and size of prey items, and number of steps, pecks and captures made. For small prey, successful prey capture was determined by whether the bird exhibited swallowing behaviors. Each of the last three variables was divided by the duration of observation to calculate, each bird's movement rate (steps/min), pecking rate (pecks/min) and capture rate (captures/min). A bird's success rate was calculated as captures/peck. The prey type and size were categorized based on estimated size relative to bill size (Bayer 1985) and taxonomic group, including (1) small invertebrates, including all terrestrial and aquatic insects and spiders; (2) tadpoles; (3) loaches, and (4) others, including earthworms and unidentified prey. Prey biomass (g dry weight) was calculated as the average mass of similar-sized specimens that we collected in the nearest colony. To calculate biomass intake rate per a minute, we divided the total biomass taken by an individual during an observation by the observation time.

We categorized the process of rice culture into four stages (Table 1): (A) flooding, rice fields are flooded by shallow water and are plowed but rice is not planted (from 1 May to 20 May); (B) plowing by tractors (hereafter "plowing"), rice fields are plowing by tractors or farming machines (from 5 May to 20 May)- in this stage the egrets used rice fields even though humans (farmers and observers) were present; (C) rice planting (hereafter "planting"), rice is planted and grows to a height not over 20 cm (from 20 May to 10 June); (D) rice growing (hereafter "growing"), rice height is over 20 cm and plants become dense (from 10 June to 30 July). We observed that egrets generally avoided rice fields when humans were present, but the egrets often sought prey in rice fields during plowing.

All statistical analyses were performed on STATISTICA (StatSoft 2004) following the guidelines of Zar (1999). All feeding activity variables did not follow a normal distribution (Shapiro-Wilk tests). Therefore, comparisons of feeding activities and prey intakes among stages of rice culture were analyzed with non-parametric Kruskal-Wal-

**Table 1.** The schedule of rice culture at the study site in 2006 and 2007

| Stage | Period | Water depth (cm) | Rice height (cm) | Human activity in rice fields |
|---|---|---|---|---|
| Flooding | 1 May - 20 May | 5-10 | 0 | No |
| Plowing | 5 May - 20 May | 5-10 | 0 | Yes |
| Planting | 20 May - 10 June | 15-20 | 15-20 | No |
| Growing | 10 June - 20 July | 15-20 | 20-70 | No |

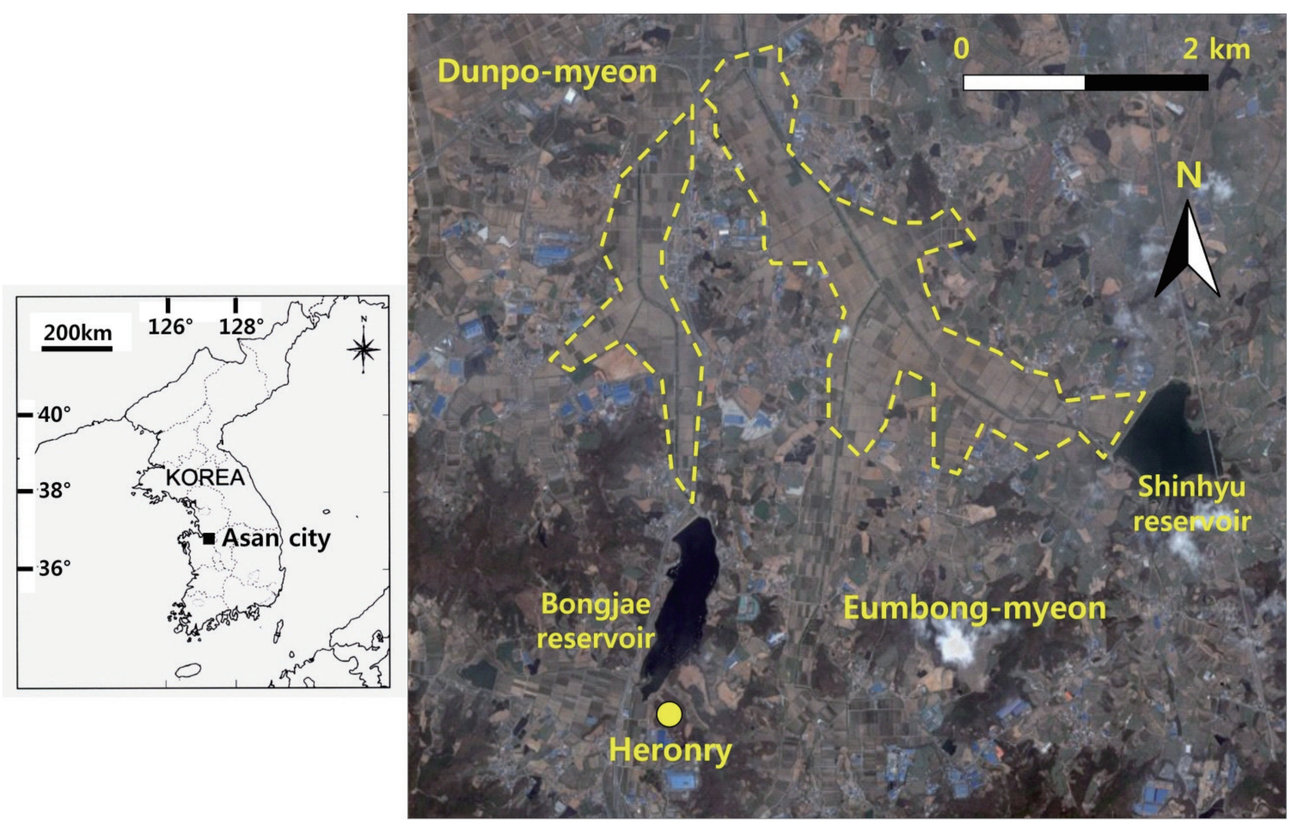


**Fig. 1.** Map of the study area. The dotted lines indicate the boundaries of the rice fields.

lis tests and multiple pairwise comparisons were made with Dunn's test.

## RESULTS

### Cattle egrets

Comparisons of cattle egret foraging activity among the four rice field stages are shown in Table 2. The rate of movement did not show a significant change across the four rice field stages (Kruskal-Wallis test, $H_3$ = 1.47, n.s.). However, the pecking rate ($H_3$ = 177.13, $P$ < 0.001) and capture rate ($H_3$ = 178.90, $P$ < 0.001) were highest in the plowing stage. Pecking and capture rates in the plowing stage were 4-5 times as high as those in other stages. In addition, more attempts were successful in the plowing stage than in other stages ($H_3$ = 36.37, $P$ < 0.001). Finally, biomass intake per minute was highest in the plowing stage ($H_3$ = 184.10, $P$ < 0.001) and was 4 times higher during plowing than during other stages.

In all stages, the main prey items of cattle egrets were small invertebrates such as insects and spiders (98.4%). The number of invertebrate prey captured differed significantly among stages ($H_3$ = 177.30, $P$ < 0.001) (Fig. 2), with the largest numbers captured in the plowing stage (mean = 14.84 prey/min) and lower numbers captured in the other three stages (mean = 2.41-3.48 prey/min). The number of loaches captured increased significantly ($H_3$ = 35.98, $P$ < 0.001) (Fig. 2) from the flooding stage (mean = 0.04 prey/min) to the planting stage (mean = 0.42 prey/min) and then fell again in the growing stage (mean = 0.02 prey/min).

### Intermediate egrets

The feeding efficiency of intermediate egrets also significantly changed across cultivation stages in rice fields (Table 3). Intermediate egrets walked more in the planting stage than in other stages ($H_3$ = 24.87, $P$ < 0.001),

**Table 2.** Feeding efficiency of cattle egrets in different stages of rice field cultivation

| Stage | Steps/min | Pecks/min | Captures/min | Success rate | Biomass/min |
|---|---|---|---|---|---|
| Flooding | 37.98 ± 1.81 (32) | 4.09 ± 0.22$^b$ (34) | 3.51 ± 0.18$^b$ (34) | 0.87 ± 0.02$^b$ (34) | 0.10 ± 0.01$^b$ (34) |
| Plowing | 38.52 ± 1.20 (105) | 15.54 ± 0.72$^a$ (119) | 14.98 ± 0.72$^a$ (119) | 0.96 ± 0.01$^a$ (119) | 0.40 ± 0.02$^a$ (119) |
| Planting | 38.72 ± 1.91 (40) | 3.32 ± 0.24$^b$ (40) | 2.82 ± 0.23$^b$ (40) | 0.85 ± 0.03$^b$ (40) | 0.07 ± 0.01$^b$ (40) |
| Growing | 36.27 ± 1.47 (87) | 3.46 ± 0.16$^b$ (87) | 3.01 ± 0.14$^b$ (87) | 0.89 ± 0.01$^b$ (87) | 0.08 ± 0.00$^b$ (87) |
| Statistics | $H$ = 1.47 NS (0.68) | $H$ = 177.13 $P$ < 0.001 | $H$ = 178.90 $P$ < 0.001 | $H$ = 36.37 $P$ < 0.001 | $H$ = 184.10 $P$ < 0.001 |

Values are represented as mean ± SE and numbers in parentheses are sample sizes. Variables were compared across stages using nonparametric Kruskal-Wallis tests. Stages with the same letter were not significantly different based on multiple comparisons tests using Dunn's test.
NS, not significant.

**Table 3.** Feeding efficiency of intermediate egrets in different stages of rice field cultivation

| Stage | Steps/min | Pecks/min | Captures/min | Success rate | Biomass/min |
|---|---|---|---|---|---|
| Flooding | 16.95 ± 1.77$^{ab}$ (16) | 0.69 ± 0.09$^b$ (19) | 0.38 ± 0.06$^b$ (19) | 0.60 ± 0.08 (19) | 0.04 ± 0.01$^b$ (17) |
| Plowing | 10.75 ± 1.02$^b$ (33) | 1.18 ± 0.21$^{ab}$ (33) | 0.91 ± 0.18$^{ab}$ (33) | 0.78 ± 0.04 (33) | 0.10 ± 0.01$^a$ (32) |
| Planting | 21.84 ± 1.86$^a$ (42) | 1.87 ± 0.22$^a$ (43) | 1.09 ± 0.14$^a$ (43) | 0.67 ± 0.04 (43) | 0.07 ± 0.01$^{ab}$ (41) |
| Growing | 14.43 ± 2.12$^b$ (25) | 1.52 ± 0.33$^{ab}$ (25) | 1.04 ± 0.27$^{ab}$ (25) | 0.71 ± 0.05 (25) | 0.07 ± 0.01$^{ab}$ (24) |
| Statistics | $H$ = 24.87 $P$ < 0.001 | $H$ = 13.19 $P$ < 0.01 | $H$ = 14.38 $P$ < 0.01 | $H$ = 6.29 NS (0.98) | $H$ = 8.27 $P$ < 0.05 |

Values are represented as mean ± SE and numbers in parentheses are sample sizes. Variables were compared across stages using nonparametric Kruskal-Wallis tests. Stages with the same letter were not significantly different based on multiple comparisons tests using Dunn's test.
NS, not significant.

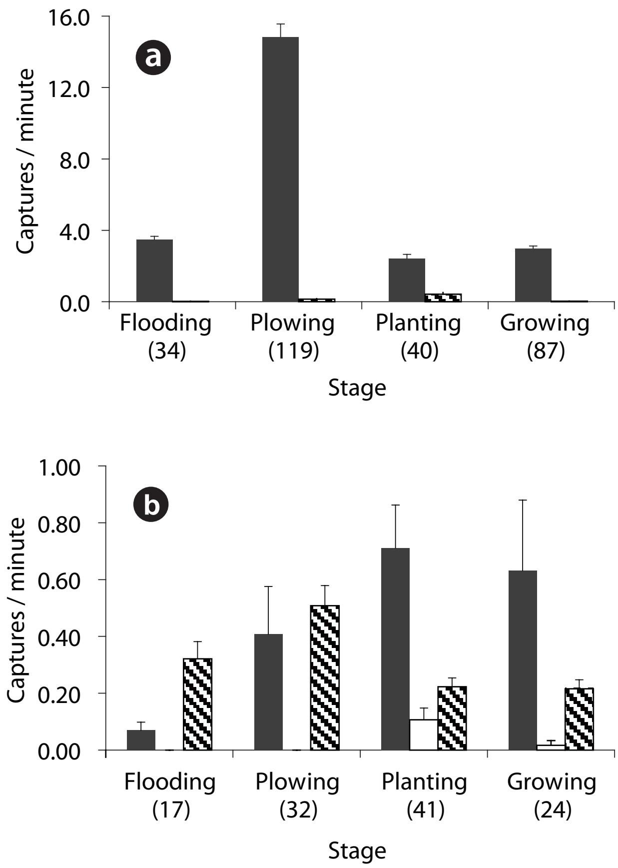


**Fig. 2.** The number of invertebrates (solid bar), tadpoles (open bar) and loaches (hatched bar) captured per minute by cattle egrets (a) and intermediate egrets (b) during each rice field stage. Bars above boxes indicate standard error and numbers in parenthesis are sample sizes. For cattle egrets, tadpoles were excluded as they were never captured.

and pecking and capture rates of intermediate egrets increased gradually from the flooding stage to the planting stage, and then decreased in the growing stage ($H_3$ = 13.19, $P < 0.01$ for pecking rate and $H_3$ = 14.38, $P < 0.01$ for capture rate). The success rate did not significantly differ among stages ($H_3$ = 6.29, n.s.), but intermediate egrets had significantly higher biomass intake in the plowing stage than in other stages ($H_3$ = 8.27, $P < 0.05$).

Intermediate egrets caught mainly small invertebrates (50.6%) and loaches (43.4%), but they also captured a few tadpoles (5.1%). There were significant changes in the numbers of invertebrates ($H_3$ = 14.00, $P < 0.01$), tadpoles ($H_3$ = 10.34, $P < 0.05$) and loaches captured ($H_3$ = 15.00, $P < 0.01$) across rice field stages (Fig. 2). The number of invertebrate prey captured increased from the flooding stage (mean = 0.07 prey/min) to the planting (mean = 0.71 prey/min) and growing (mean = 0.63 prey/min) stages, and intermediate egrets caught more loaches in the plowing stage (mean = 0.54 prey/min) than other stages (mean = 0.23-0.36 prey/min). No tadpoles were captured in the first two stages, but tadpole capture increased significantly in the rice planting stage (mean = 0.11 prey/min).

## DISCUSSION

The cattle egret was the most abundant species feeding in rice fields throughout the study period and its feeding efficiency was higher than those of other ardeids, as has been reported in other studies in rice fields (Tojo 1996, Lombardini et al. 2001, Richardson et al. 2001, Richardson and Taylor 2003). The cattle egret is well adapted to agricultural and disturbed habitats worldwide (Kushlan and Hafner 2000, Kushlan and Hancock 2005), which may be related to their prey preferences; they are mainly insectivores. Rice fields provide an adequate habitat for various arthropod communities (e.g., aquatic and terrestrial insects and spiders) in Korea (Lee et al. 2002) and other countries (González-Solís et al. 1996, Yamazaki et al. 2004, Wilson et al. 2008). Our study showed that cattle egrets in rice fields had the highest feeding rate during the stage of plowing by tractors. Sudden flooding of rice fields can create surges in prey availability for cattle egrets (Lombardini et al. 2001). Moreover, as the flooding rice fields are plowed by tractors, many spiders and insects may be disturbed and may become easy prey for cattle egrets. Cattle egrets often forage beside grazing mammals such as horses or cattle (Dinsmore 1973, Thompson et al. 1982, Burger and Gochfeld 1989, Metz et al. 1991) and machines such a dump trucks and tractors (Burger and Gochfeld 1983) in order to catch the insects disturbed by the larger animal or machine. Thus, cattle egrets seemed to take similar advantage of the tractors, which may have increased prey availability during the early breeding period.

By contrast, the moving, pecking and capture rates of intermediate egrets were relatively low in the plowing stage and tended to increase after rice planting. This variation in feeding activity in rice fields may be related to changes in prey availability (Richardson et al. 2001). In this study, intermediate egrets captured more and larger loaches in the plowing stage than in other stages, although prey captures per unit time were low. Loaches are nocturnal and cryptic fishes and they often hide under the mud in the daytime, which make them difficult to catch. Therefore, plowing of rice fields by tractors may affect the behavior of loaches, making it easier for egrets to find and catch these disturbed loaches, in a manner analogous to the capture of insect prey by cattle egrets. In addition, egrets tended to walk less in the plowing stage, and consequently the capture rate per unit foraging effort was relatively high. However, after the rice planting stage, they shifted their focus from loaches to invertebrates or tadpoles and the capture rate increased because aquatic insects and tadpoles were less mobile and they occurred at higher density. As the rice crops developed and fields became more densely vegetated, it was probably harder to find and catch loaches. Consequently, intermediate egrets had higher energy intakes in the plowing stage in spite of their low overall prey capture rate as they were able to take more loaches during that time.

A high capture rate does not always correspond with high foraging efficiency, since prey types vary in their energetic values (Richardson et al. 2001, Richardson and Taylor 2003). In rice fields, small invertebrates such as insects and spiders are plentiful but have low energetic values. Conversely, loaches have high energetic value but it is hard to find and catch them. In the month of May, which coincides with chick rearing for intermediate egrets and the peak period of egg-laying for cattle egrets in Korea, the energy costs of breeding were high for both species. Therefore the plowing of flooded fields in May might provide an important benefit to ardeids by increasing their prey encounter rates.

In the present study, the foraging efficiency and prey composition of cattle egrets did not vary greatly across the stages of rice cultivation except during the plowing stage, while those of intermediate egrets changed significantly during different stages of rice cultivation. However, intermediate egrets may have compensated for the lower energy intake per prey through more frequent captures of small invertebrates in the rice-growing period. As the availability of rice fields as feeding habitats varies among stages of rice culture, ardeids need to adjust their feeding strategies in response to changes in food availability in rice fields. Our previous studies (Choi et al. 2007, 2008) showed that cattle egrets and intermediate egrets, highly rice-field-dependent foragers, changed to rice banks (or levees) or edge areas as feeding sites and avoided the inner parts of rice fields as the rice crop developed and fields became densely vegetated. At the same time, both species might respond to changes in their feeding habitats by changing their feeding methods and prey types. It is difficult to spot prey in densely vegetated rice fields, which may encourage herons to change feeding sites or methods (Maeda 2001, Richardson et al. 2001). In periods when rice fields are covered with dense vegetation, rice banks provide vegetation gaps suitable for herons foraging on aquatic prey (Sato and Maruyama 1996, Maeda 2001).

It appears that rice fields provide an important feeding habitat for intermediate egrets and cattle egrets in Korea. In particular, rice fields provide the best foraging habitat for cattle egrets and may be contributing to an increase in breeding populations of cattle egrets in Korea since the 1960s. Although the availability of food in rice fields varies across stages of rice culture, ardeids might be able to meet their energy needs by changing their feeding location or style. A more detailed understanding of the factors affecting ardeid foraging decisions is needed to better understand how management regimes (e.g., irrigation practices and pesticide treatments) affect ardeid behavior and the availability of rice fields as feeding sites.

## LITERATURE CITED

Bayer RD. 1985. Bill length of herons and egrets as an estimator of prey size. Colonial Waterbirds 8: 104-109.

Burger J, Gochfeld M. 1983. Behavior of nine avian species at a Florida garbage dump. Colonial Waterbirds 6: 54-63.

Burger J, Gochfeld M. 1989. Age differences in Cattle Egrets *Bubulcus ibis*, foraging with wild ungulates in Kenya. Ardea 77: 201-204.

Campos F, Lekuona JM. 2001. Are rice fields a suitable foraging habitat for Purple Herons during the breeding season? Waterbirds 24: 450-452.

Choi YS, Kwon IK, Yoo JC. 2007. Foraging habitat preferences of herons and egrets. J Ecol Field Biol 30: 237-244.

Choi YS, Kwon IK, Yoo JC. 2008. A study of feeding methods in five species of herons and egrets in Korea. J Ecol Field Biol 31: 147-151.

Dinsmore JJ. 1973. Foraging success of cattle egrets, *Bubulcus ibis*. Am Midl Nat 89: 242-246.

Elphick CS. 2000. Functional equivalency between rice fields and seminatural wetland habitats. Conserv Biol 14: 181-191.

Elphick CS, Oring LW. 1998. Winter management of Californian rice fields for waterbirds. J Appl Ecol 35: 95-108.

Fasola M. 1986. Resource use of foraging herons in agricultural and nonagricultural habitats in Italy. Colonial Waterbirds 9: 139-148.

Fasola M, Ruiz X. 1996. The value of rice fields as substitutes for natural wetlands for waterbirds in the Mediterranean region. Colonial Waterbirds 19 (Special Publication 1): 122-128.

Fasola M, Canova L, Saino N. 1996. Rice fields support a large portion of herons breeding in the Mediterranean region. Colonial Waterbirds 19 (Special Publication 1): 129-134.

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

González-Solís J, Bernadí X, Ruiz X. 1996. Seasonal variation of waterbird prey in the Ebro Delta rice fields. Colonial Waterbirds 19 (Special Publication 1): 135-142.

Hafner H, Dugan PJ, Boy V. 1986 Use of artificial and natural wetlands as feeding sites by Little Egrets (*Egretta garzetta* L.) in the Camarge, southern France. Colonial Waterbirds 9: 149-154.

Kazantzidis S, Goutner V. 1996. Foraging ecology and conservation of feeding habitats of Little Egrets (*Egretta garzetta*) in the Axios River delta, Macedonia, Greece. Colonial Waterbirds 19 (Special Publication 1): 115-121.

Kushlan JA, Hafner H. 2000. Heron Conservation. Academic Press, San Diego, CA.

Kushlan JA, Hancock JA. 2005. The Herons. Oxford University Press, Oxford.

Lane SJ, Fujioka M. 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.

Lee JH, Yun JC, Kim ST, Park HH, Uhm KB. 2002. Arthropod community structures in rice fields in Korea. In: Ecology of Korea (Lee DW, Jin V, Choe JC, Son YH, Yoo SJ, Lee HY, Hong SK, Ihm BS, eds). XIII INTECOL International Congress of Ecology, Seoul, pp 257-269.

Lombardini K, Bennetts RE, Tourenq C. 2001. Foraging success and foraging habitat use by Cattle Egrets and Little Egrets in the Camargue, France. Condor 103: 38-44.

Maeda T. 2001. Patterns of bird abundance and habitat use in rice fields of the Kanto Plain, central Japan. Ecol Res 16: 569-585.

Metz KJ, Prior KA, Mallory ML. 1991. Do cattle egrets gain information from conspecifics when foraging? Oecologia 86: 57-61.

Narusue M, Uchida H.1993. The effect of structural changes of paddy fields on foraging egrets. Strix 12: 121-130.

Ormerod SJ, Watkinson AR. 2000. Editor's introduction: birds and agriculture. J Appl Ecol 37: 699-705.

Ovenden GN, Swash AR, Smallshire D. 1998. Agri-environmental schemes and their contribution to the conservation of biodiversity in England. J Appl Ecol 35: 955-960.

Richardson AJ, Taylor IR. 2003. Are rice fields in southeastern Australia an adequate substitute for natural wetlands as foraging areas for egrets? Waterbirds 26: 353-363.

Richardson AJ, Taylor IR, Growns JE. 2001. The foraging ecology of egrets in rice fields in southern New South Wales, Australia. Waterbirds 24: 255-264.

Sato N, Maruyama N. 1996. Foraging site preference of Intermediate Egrets *Egretta intermedia* during the breeding season in the eastern part of the Kanto Plain, Japan. J Yamashina Inst Ornithol 28: 19-34.

StatSoft. 2004. STATISTICA for Windows. Version 7. StatSoft, Inc., Tulsa, OK.

Thompson CF, Lanyon SM, Thompson KM. 1982. The influence of foraging benefits on association of Cattle Egrets (*Bubulcus ibis*) with cattle. Oecologia 52: 167-170.

Tojo H. 1996. Habitat selection, foraging behaviour and prey of five heron species in Japan. Jap J Ornithol 45: 141-158.

Tourenq C, Sadoul N, Beck N, Mesléard F, Martin JL. 2003. Effects of cropping practices on the use of rice fields by waterbirds in the Camargue, France. Agr Ecosyst Environ 95: 543-549.

Wilson AL, Watts RJ, Stevens MM. 2008. Effects of different management regimes on aquatic macroinvertebrate diversity in Australian rice fields. Ecol Res 23: 565-572.

Yamazaki M, Hamada Y, Kamimoto N, Momii T, Kimura M. 2004. Composition and structure of aquatic organism communities in various water conditions of a paddy field. Ecol Res 19: 645-653.

Zar JH. 1999. Biostatistical Analysis. 4th ed. Prentice Hall International, London.