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Grey Heron (*Ardea cinerea*) Expansion Promotes the Persistence of Mixed-species Heron Colonies

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Abstract.—Range expansion of native as well as exotic species often causes effects on the original species; however, not all range expansions are negative for breeding colonies consisting of mixed species. The Grey Heron (*Ardea cinerea*) has increased and expanded its distribution in Japan in the last 20 years. Its solitary and early nesting habits may facilitate establishment and persistence of colonies of mixed heron species. To examine whether the addition of Grey Herons has affected colony persistence and the number of established and abandoned colonies, 16 years of monitoring data from before and after the expansion of Grey Herons around Ibaraki Prefecture in Japan were analyzed. Most newly established colonies were without Grey Herons before their expansion, but more than half of the established colonies contained Grey Herons after the expansion. The number of colony abandonments decreased after the Grey Heron expansion and most of these occurred in colonies that were without Grey Herons both before and after the expansion. Persistence periods were longer in colonies with Grey Herons than in colonies without Grey Herons. The expansion of Grey Herons into mixed heron colonies has promoted the persistence of mixed heron colonies, and local populations of colonial herons seemed to gain the benefit of colony sustainability.
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Key words.—*Ardea cinerea*, breeding site selection, Grey Heron, range expansion.

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The introduction and spread of exotic species has become a global ecological and conservation crisis as invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Elton 1958; Vitousek *et al.* 1996; Wilcove *et al.* 1998; Gurevitch and Padilla 2004). Negative effects of invasive species on native communities have been reported, particularly for invasive species with expansions that were driven by human transport and commerce (Ruiz *et al.* 1997; Mack *et al.* 2000). Similar problems can occur with range expansion of indigenous species (Rahel and Olden 2008; Rahel *et al.* 2008). Expanding species can cause interspecific competition for food or nesting-habitat, especially where those species breed in spatially limited areas as in the mixed-species colonies of seabirds (Burger and Shisler 1978; Trivelpiece and Volkman 1979; Quintana and Yorio 1998). Moreover, in terrestrial areas, the expansion of Cattle Egrets (*Bubulcus ibis*) has caused direct competition with other heron and egret species for nest sites and nesting materials because the aggressiveness and highly gregarious nature of Cattle Egrets has excluded other species from high-quality nest sites (Burger 1978; Dami *et al.* 2006).

In Japan, the distribution range and population size of the Grey Heron (*Ardea cinerea*, Ardeidae) markedly increased over a span of 20 years (Environmental Agency of Japan 1994; Matsunaga *et al.* 2000; Sasaki 2001). Grey Herons are native wading birds that exist throughout temperate Europe, Africa and Asia (Kushlan and Hancock 2005). Their distribution in Japan around the 1950s to 1970s was limited (Kurata and Higuchi 1972; Sawara *et al.* 1994; Fig. 1A), and the species composition of heron colonies, except in Hokkaido, were mainly all or some of other five Ardeidae species (Wild Bird Society of Japan 1981; Environmental Agency of Japan 1994). Since then, Grey Herons have markedly increased in range and population size, and have begun to breed in both coastal and inland areas throughout Japan (Environmental Agency of Japan 1994; Matsunaga *et al.* 2000; Sasaki 2001; Fig. 1B). In this study, we expected that the incorporation of Grey Herons into mixed-species heron colonies may facilitate the establishment and persistence of colonies because they are skilled at establishing new colonies.

Grey Herons have the most solitary habits of the six colonial heron species in Japan

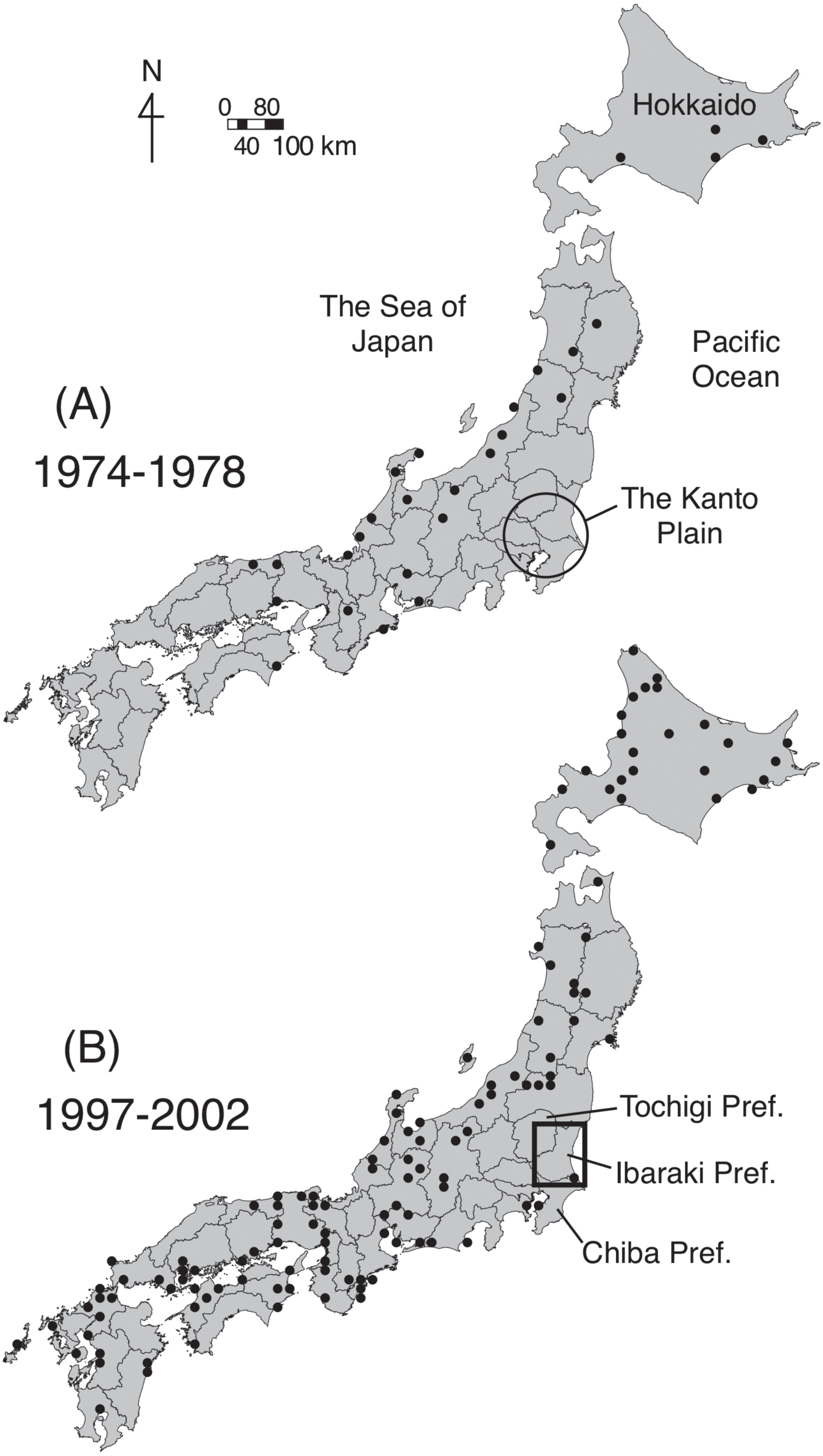

Figure 1. Map of the breeding distributions of Grey Herons in Japan during (A) 1974-1978 and (B) 1997-2002 (modified from Biodiversity Center of Japan 2004). Dots show the grids in which breeding activities of Grey Herons were confirmed in least one breeding season. The square region in (B) shows the area of this study.

(Environmental Agency of Japan 1994). While Grey Herons are primarily a colonial nesting species, they also often breed in small, single-species colonies of 2-10 nests (Environmental Agency of Japan 1994; Kushlan and Hancock 2005). Grey Herons have the potential to establish new colonies without relying on existing colonies established by other species. Grey Herons arrive at colony sites and begin nesting about a month before the other species. This may serve as a cue for the other, later-arriving species in choosing their colony site (Seppänen *et al.* 2007). If a colony site has degraded and become unsuitable for breeding, Grey Herons may choose an alternative location near the former site, and, hence, the mixed-species colony can persist.

To clarify whether the recent population increase and expansion of Grey Herons have affected interspecific dependency in regards to colony site choice, we analyzed 16 years of monitoring data for mixed-species colonies around Ibaraki Prefecture, Japan, that include periods before and after the expansion of Grey Herons. We hypothesized that if Grey Herons had begun to take an initiative in establishing colonies and other species had begun to follow them in colony-site selection, more colonies including Grey Heron individuals would have been newly established and persisted longer than colonies without Grey Heron populations. We focused on three colony states (establishment, persistence and abandonment) and evaluated: 1) the changes in the number of establishment and abandonment events of colonies before and after the expansion of Grey Herons; and 2) the differences in the persistence periods of colonies between those with and without Grey Heron populations.

METHODS

Study Area and Species

This study focused on the eastern part of the Kanto Plain in central Japan (35° 47′ N to 36° 50′ N, 139° 46′ E to 140° 47′ E), which includes the whole of Ibaraki Prefecture and parts of Tochigi and Chiba Prefectures (Fig. 1B; see Fig. 1 in Mashiko and Toquenaga 2013 for the distribution of colonies). The north is mountainous and not suitable for herons and egrets to breed and forage. The remainder of the area is extensive, flat lowlands with large areas along rivers being used for rice production. Forest and residential areas are scattered throughout the region. Lotus fields are scattered near Lake Kasumigaura. Rice and lotus fields and their irrigation ditches support large numbers of foraging herons and egrets (Sato and Maruyama 1996; Lane and Fujioka 1998; Maeda 2001).

Each year, Grey Herons, Great Egrets (*A. alba*), Intermediate Egrets (*Egretta intermedia*), Little Egrets (*E. garzetta*), Cattle Egrets and Black-crowned Night Herons (*Nycticorax nycticorax*) breed in colonies in bamboo thickets, trees, or a mixture of both. The breeding season of the birds in this area is from March to August, but there is considerable variation in the onset of breeding among the six species. Grey Herons arrive first in March, and Great Egrets, Little Egrets and Black-crowned Night Herons arrive in April; these species are residents and wanderers and some individuals winter in this area. Finally, the migrant species arrive, Intermediate Egrets in late April and Cattle Egrets by early May (Mashiko and Toquenaga 2013).

Colony Data

Colony sites in the study area have been recorded over the last 30 years (Koshida 2007). From 2002 to 2012, colony size and number of individuals of constituent species for each colony were estimated by aerial photographs and ground surveys (Mashiko and Toquenaga (2013) for 2002-2011 and continuous surveys for 2012 using the same methodology). For data before 2001, binary values (0: absence, 1: presence) for constituent species are available. The species compositions of almost all colonies that existed earlier than 2002 were reported in earlier studies (Fujioka *et al.* 2001; Koshida 2007); these data were obtained by observing the nesting activities or inbound and outbound movements of each species in the colonies from the ground.

Every year, colony locations were confirmed by checking the places where colonies had been located in previous years because an average of 75% of colony sites were formed at the same sites as in the previous year. When a colony was abandoned, checks were made to determine whether other colonies had formed nearby. To minimize missing information for colonies, we used local literature and personal information from local observers especially during periods in which surveys by the authors were not intensive.

From these data, we determined a study period that ranged from before to after the expansion of Grey Herons in the study area. Until 1999, Grey Herons had nested with the other five species in only one colony (the dot in the square region in Fig. 1B; corresponding to colony 3, Fig. 2). All of the other colonies in our study area were composed of five species and excluded Grey Herons. The first colony established by Grey Herons alone was recorded in 2005 (colony 35, Fig. 2; Mashiko and Toquenaga 2013). Thus, we defined 2005 as the beginning of the increase and expansion of Grey Herons in the study area. Since our data extended to 2012, and for a balanced pre/post examination, we compared

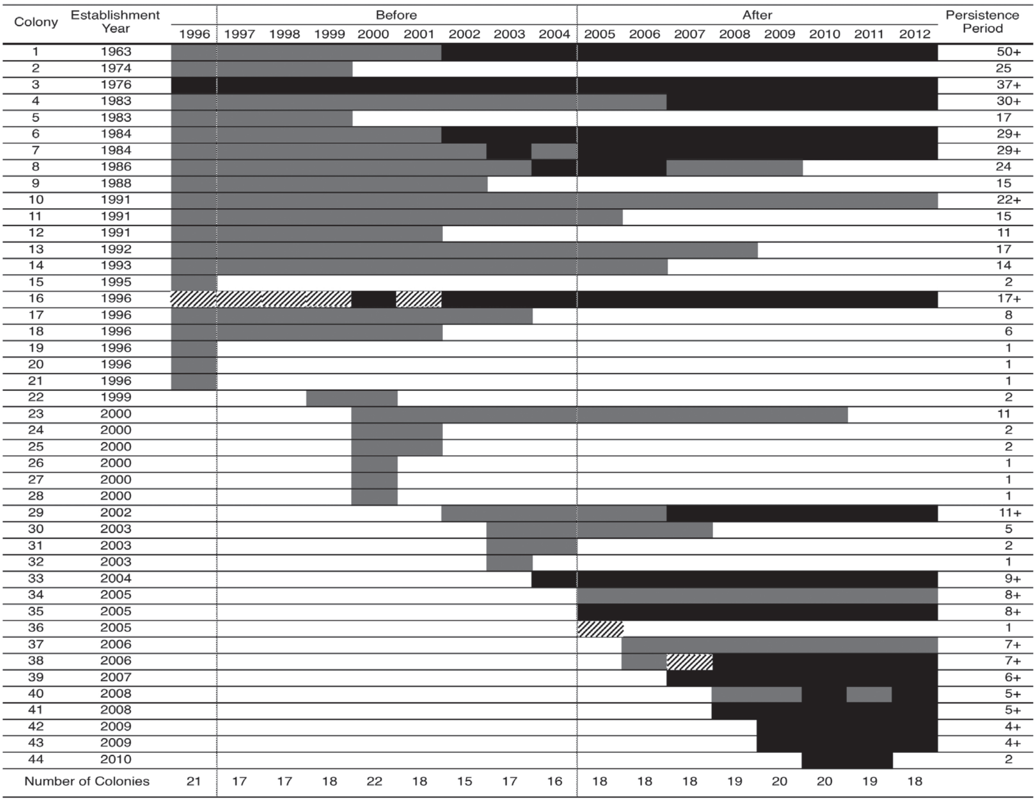

Figure 2. Establishment year, binary-state species composition, and the persistence period of 44 observed colonies from 1996 to 2012. Gray bars show the colonies without Grey Herons, black bars show the colonies with Grey Herons, and hatched bars show the colonies for which binary-state species composition data were not available because of the shortage of observation records. "+" in the persistence period represents censored observations, i.e., an abandonment event was not observed before the end of our study period. Colonies in 1996 were only used to count the number of abandoned colonies in 1997.

data for 8 years before (1997 to 2004) and after (2005 to 2012) this expansion. The mean population size of Grey Herons per colony in the study area in 2012 was 188 individuals, which was 9.6 times larger than that of 2004 (Fig. 3).

From 1997 to 2012, between 15 and 22 (18.1 ± 0.4 SE) annual colonies were observed every year, and a total of 40 colonies were recorded (Fig. 2). Each colony can be characterized by three states: establishment, persistence and abandonment. To determine the years in which these three states occurred for each colony, we considered colony-site shifts. When a colony site was abandoned due to vegetation loss through natural causes or felling, herons and egrets often re-established their colony nearby. In such cases, we assumed that the abandoned and the newly established sites could be considered the same colony despite being at slightly different locations. The maximum distance for a colony-site shift was determined to be half of the mean nearest-neighbor distance of colony sites (Mashiko and Toquenaga 2013). Since two neighboring colony sites were separated by an average of 12.78 ± 1.85 km every year, the maximum site-shift distance was defined as 6.39 km. A colony was deemed to have been established when a new colony site was located where there had been no colony site within a radius of 6.39 km in the previous year. A colony was deemed to have been abandoned when no new colony site was located within a radius of 6.39 km in the next year. The persistence period is the duration between establishment and abandonment.

In this study, we evaluated the incorporation of Grey Herons into heron colonies using binary values for the existence of Grey Herons: with or without Grey Herons in the species compositions of the colonies. The five constituent species other than the Grey Heron were combined because they were included in 88% of all recorded mixed-species colonies.

Statistical Analyses

To detect whether the number of establishment and abandonment events of colonies had changed before and after the expansion of Grey Herons, we performed a 2×2 chi-squared test. To analyze the colony

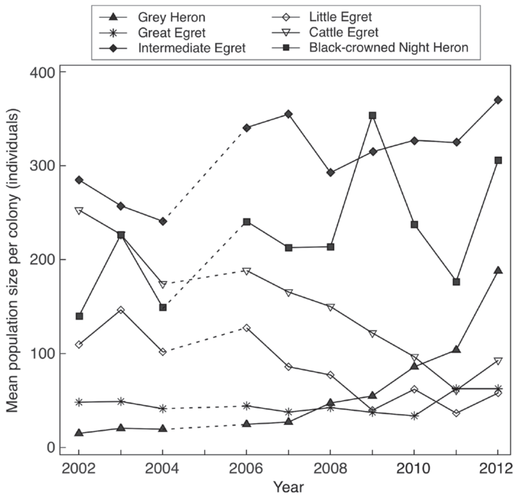

Figure 3. Changes in mean population size per colony of six species of herons and egrets in the study area from 2002 to 2012. The year 2005 is not shown because the population censuses based on a combination of aerial and ground surveys were limited to only five out of 18 colonies.

establishments, we counted the number of establishment events and categorized them into two classes: with or without Grey Heron populations in the first year of the colony. To analyze the colony abandonments, we counted the number of abandonment events according to the year when the abandonment was recorded. For abandonment events in 1997, we referred to the data for the four colonies that existed in 1996 (colonies 15, 19, 20, and 21, Fig. 2). Then we focused on the binary-state species composition during the persistence periods of those abandoned colonies and classified them into four categories: Grey Herons existed throughout the persistence period (Grey Heron throughout: T), Grey Herons joined after the establishment of colonies (Grey Heron post-establishment: P), Grey Herons never joined (Grey Heron nonexistent: N), and Grey Herons had joined the colony but disappeared before abandonment (Grey Heron disappeared: D).

To examine whether the incorporation of Grey Herons affected the length of persistence periods of colonies, we classified all colonies into the same four categories as those in the analysis of abandonment (T, P, N and D) and compared their survival curves. Since the datasets for persistence periods contained censored data (Fig. 2), non-parametric survival curves were estimated with the Kaplan-Meier method for each category. Differences between the curves were evaluated with the log-rank test (Kleinbaum 1996). The persistence periods for all colonies were obtained from Koshida (2007) for colonies before 2001, Mashiko and Toquenaga (2013) for those from 2002-2011 and colony data for those in 2012 (M. Mashiko and Y. Toquenaga, unpubl. data). For 17 colonies that had been established before 1997, we assigned actual persistence periods rather than those limited to our study interval (1997-2012). The persistence periods ranged from 1 to 50 years (Fig. 2).

Since there was only one colony for which the binary-state species composition data was not available (colony 36, Fig. 2), 39 colonies during 1997 to 2012 were used to analyze the establishment and persistence periods, and 43 colonies, including four colonies in 1996, were used to analyze the abandonment events. All statistical analyses were conducted using Program R (R Development Core Team 2013).

Results

Changes in the number of colony establishment events showed an increasing pattern in colonies with Grey Herons, but a decreasing pattern in colonies without Grey Herons (Fig. 4A). The total number of colony establishment events declined only by two after the Grey Heron expansion (Fig. 4A), whereas the number of colonies established with Grey Herons significantly increased after the expansion ($\chi^2 = 6.712$, $P = 0.019$). Before 2004, only one colony (colony 33, Fig. 2) included Grey Herons in its establishment year, but this colony consisted of all six heron species in Japan. It was not clear whether the Grey Heron led the establishment of this colony because of the lack of information from its onset. Conversely, after 2005, the establishment of six colonies (colonies 35, 39, 41-44; Fig. 2) was obviously led by Grey Herons. Five of these (all except colony 41) were established by Grey Herons. Colony 41 was relatively small and dominated by Grey Herons (12 nests); they gathered at the colony site from the very beginning of the breeding season, and a smaller number of Black-crowned Night Herons (4 nests) were observed during the late breeding season. Grey Herons established their colonies irrespective of the existence of the other species, but the other heron species almost ceased establishing their own colonies.

The number of abandonment events had an unchanged pattern in the colonies with Grey Herons and a decreasing pattern in colonies without Grey Herons (Fig. 4B). For colonies with Grey Herons, there has been one abandonment event in each of the T and D categories since 2005, and no

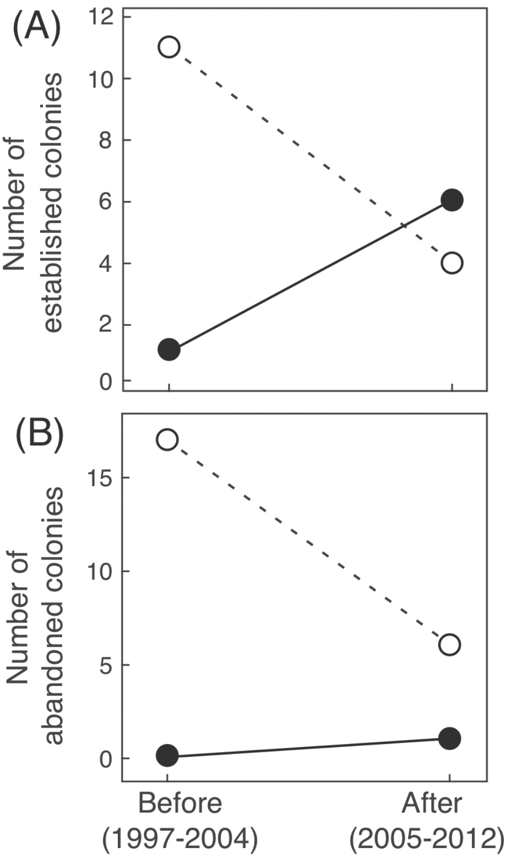

Figure 4. Number of (A) establishments and (B) abandonments of colonies before and after the expansion of Grey Herons. In (A), open circles with a dashed line represent the colonies without Grey Herons, and filled circles with a solid line represent the colonies with Grey Herons in the establishment year. In (B), open circles with a dashed line represent colonies that Grey Herons never joined during the persistence period (N). Filled circles with a solid line represent two categories: Grey Herons existed throughout the persistence period (T), and Grey Herons had existed but disappeared (D). Since these two categories exhibited the same increasing pattern, these two lines are completely overlaid.

abandonment events in category P. For colonies without Grey Herons, the proportion of abandonments of colonies that Grey Herons never joined (N) did not differ before and after the Grey Heron expansion ($\chi^2 = 2.534$, $P = 0.298$). The total number of abandonment events decreased dramatically, nearly halved, after the Grey Heron expansion.

Among the four categories (T, P, N, and D), we excluded D in the following analysis of the persistence period because category D included only a single colony and, hence, was not suitable for the survival analysis. Survival curves differed between the T and N categories: persistence periods of colonies with Grey Herons throughout their persistence period were much longer than those of colonies that Grey Herons never joined ($\chi^2 = 4.7$, $P = 0.030$; Figs. 5A and 5C). Sur-

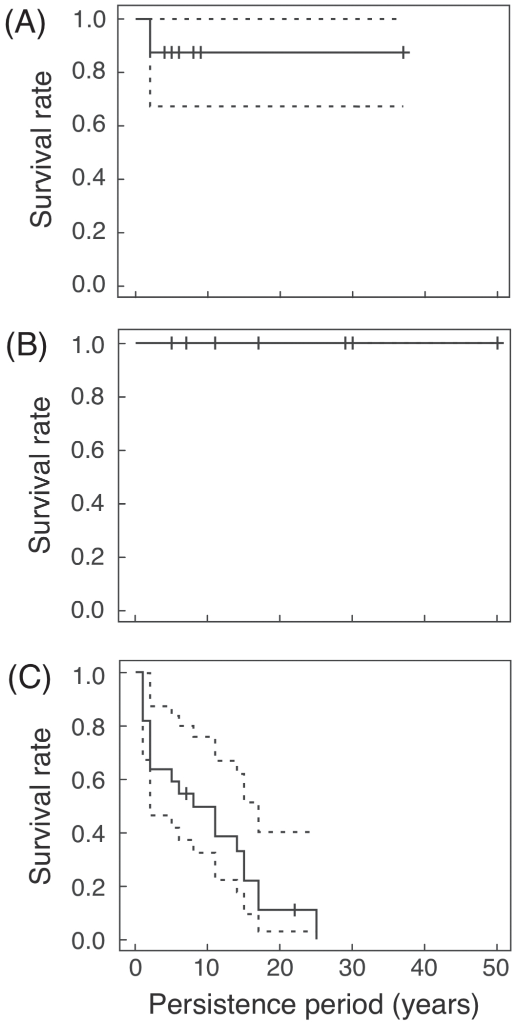

Figure 5: Survival curves (solid lines) for three patterns of the existence of Grey Herons during the persistence period of colonies using the Kaplan-Meier estimate with 95% confidence interval (dashed lines). In (A), Grey Herons existed throughout the persistence period (T; *n* = 8); in (B), Grey Herons joined already existing colonies (P; *n* = 8); and in (C), Grey Herons never joined (N; *n* = 22). Vertical bars represent the censored observations.

vival curves also differed between the P and N categories: persistence periods of colonies joined by Grey Herons were much longer than those of colonies that Grey Herons never joined ($\chi^2 = 14.2$, $P < 0.001$; Figs. 5B and 5C). Survival curves did not drop for decades for colonies with Grey Herons. Conversely, survival curves for colonies without Grey Herons continuously decreased, and those colonies lasted 25 years at most.

DISCUSSION

The distribution range of Grey Herons has clearly increased in Japan since the 1990s, but currently there is no conclusive explanation for the cause of the expansion. The introduction of largemouth bass (*Micropterus psalmodies*) and smallmouth bass (*M. dolomieu*) in lakes and rivers in the 1980s and 1990s for leisure fishing (Kaneko and Wakabayashi 1998) may be providing Grey Herons with their preferred feeding choice (large fish) even inland, but there are no quantitative data to support this hypothesis. In Hokkaido, Matsunaga *et al.* (2000) suggested that recent climatic warming and increases in aquaculture have provided the species with additional food resources. It is not known whether the increase of the Grey Heron in other more temperate parts of Japan also depends on these factors, but the species' ability to respond quickly to changes in food availability (Adams and Mitchell 1995; Jakubas 2004) would be expected to boost populations.

Two ecological features of Grey Herons, the highest rate of solitariness and the earliest arrival order among the six species of herons and egrets, are likely to contribute to the establishment of colonies. Its solitary habits would enable this species to newly establish small, single-species colonies. In fact, all six colonies containing Grey Herons established after 2005 were relatively small and made up of only Grey Herons or dominated by them (Mashiko and Toquenaga 2013). Moreover, their arrival time at the beginning of the breeding season, which is the earliest of the six species, enables them to choose colony sites independently. Thus, Grey Herons began to take over the role of vanguard for establishing colonies at locations where no herons or egrets have bred in the past.

The presence of Grey Herons allowed the other five heron species in Japan to adopt a new strategy for colony site selection: joining colonies established by Grey Herons at the very beginning of a breeding season. This new strategy has been adopted since 2005 when Grey Herons began to increase and expand in the study area. This strategy becomes optimal when identifying resources or establishing a colony costs more than scrounging or following a pioneer species (Ohtsuka and Toquenaga 2009a, 2009b).

In Japan, the Great Egret, Intermediate Egret, Little Egret, and Cattle Egret have never formed single-species colonies consisting of less than 50 individuals (Environmental Agency of Japan 1994). Among them, the Cattle Egret, an especially gregarious species (Kushlan and Hancock 2005), often relies on the nesting activities of other species as a stimulus for their own nesting and breeding (Rice 1956; Dusi and Dusi 1968; Westerskov 1974; Belzer and Lombardi 1989). The addition of Grey Herons has stimulated other gregarious species in choosing their breeding-colony sites, and this may provide some insight into the conservation of mixed-species heron colonies.

This pioneer/follower relationship among the constituent species of mixed-species colonies also explains the present results for abandonment and persistence period. Abandonment of colonies was sometimes caused by the disappearance (either through natural death or felling) of nesting vegetation. When individual herons and egrets are confronted with these situations, they can either establish a new colony near the previous one or abandon the site and join another colony that has already been established by other individuals but is located far from their previous site. Trees and bamboo thickets are abundant and exist throughout the study area. It is easier for Grey Herons to establish new colonies, but not so for more gregarious species. When Grey Herons establish a new colony in the vicinity of past colonies of other species, the remaining species often join that colony. Consequently, a past colony is not abandoned, but persists for at least another year. This may be the reason colonies perpetuated the Grey Heron hegemony once they became a constituent species.

In both colonial and terrestrial birds, it has been demonstrated that individuals of earlier-arriving species can be used as informants by the later-arriving species (e.g., Dusi and Dusi 1968; Westerskov 1974; Mönkkönen *et al.* 1990, 1999; Thomson *et al.* 2003). However, using the presence of other individuals as a cue is not always beneficial; consequences would vary depending on the types of interspecific relationships that develop from the ecological features of constituent species, such as arrival order, aggressive behavior and predation. Interspecific interaction has important consequences on community ecology and conservation (Seppänen *et al.* 2007). The ecological features of an expanding species are crucial factors in determining whether they infringe upon or are suitable for co-colonization, especially when they share the same resources.

In our case, direct negative interspecific interaction, such as predation and aggressive behavior, was not observed between Grey Herons and the other five species. Thus, Grey Heron expansion has led to a positive consequence: local populations of colonial herons and egrets seem to have gained the benefit of colony sustainability. The positive consequences for heron colonies led by Grey Heron expansion are unique and contradict the negative effects of expanding species on communities for which there has been extensive reporting (Mack *et al.* 2000). However, this does not necessarily indicate that the incorporation of Grey Herons has led to an increase in the population size of the five species formerly dominant in Japan. In fact, population sizes of Little Egrets and Cattle Egrets have decreased since 2002 in our study area (Fig. 3); however, the factors contributing to this decrease in population size are not yet clear. Relatively little is known about the effects of rapidly changing numbers and distribution of one species against another (cf. Burger 1978; Werschkul 1978; Dami *et al.* 2006). It remains a challenge for future studies to determine whether the expansion of Grey Herons has negative impacts on other species by reducing their reproductive success.

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