

Doctoral Thesis

**Population dynamics and individual life of  
the colony-breeding Grey Heron *Ardea cinerea*  
in suburban Tokyo**

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## Abstract

The density-dependent processes that limit the colony size of colonially-breeding birds such as herons and egrets remain unclear, because it is difficult to monitor colonies from the first year of their establishment, and most previous studies have considered mixed-species colonies. In the present study, single-species colonies of the Grey Heron (*Ardea cinerea*) were observed from the first year of their establishment for 16 years in suburban Tokyo. Colony size increased after establishment, illustrating a saturation curve. The breeding duration (days from nest building to fledging by a pair) increased, but the number of fledglings per nest decreased, with colony size. The reproductive season in each year began earlier and there was greater variation in the timing of individual breeding when the colony size was larger. The prolonged duration until nursing by early breeders of the colony suggests that herons at the beginning of the new breeding season exist in an unsteady state with one another, likely owing to interactions with immigrant individuals. Such density-dependent interference may affect reproductive success and limit the colony size of Grey Herons.

Colonial birds have two confront problems to breed, which colonies that they attend and where they nest within the colony. In this study, the nest site selection by Grey Herons was examined. They tended to nest on the trees near the ridge of the hill. In the studied colony, the cherry (*Prunus jamasakura*) and oak (*Quercus serrata*) trees were often used. The nest height from the ground ranged from 7.8 to 22.2 m with the mean of 12.7 m. The nests were located from 42.7 to 100% of tree height with the mean of 83.1% (N=66, SD=14.0). Nesting at higher may provide safety from ground predators. The number of chicks fledged ranged 0 to 4 with the mean of 1.68 per attempted nest, and not correlated with any nest site characteristics such as nest height, tree diameter, and tree height. The effect of the horizontal distribution of nests on the breeding success was also undetected and it was unlikely that the peripheral nests were more vulnerable than the central ones. Thus, the reason why Grey Herons colonize at breeding was not explained by predation avoidance function, suggesting the other colony function of mate attraction and finding or information center to search efficient hunting sites.

Site fidelity to the colony and breeding histories of individual Grey Herons were examined by intensive and long-term (9 years) observations of 50 fledglings and 19 adult birds banded with color-patterned rings. In total, 38 (76.0%) of 50 marked



fledglings were never resighted in the natal colony. Of the 12 returned birds, 4 (33.3%) began to breed at 2-years-old, 2 (16.7%) began to breed at 3-years-old, 1 (8.3%) began to breed at 4-years-old, and 5 (41.7%) never bred. Two birds survived after 9 years from fledging. In total, 18 (94.7%) of 19 adult birds were resighted in the next breeding season and most of them (15/18) bred there. Birds tend to stay at the same breeding colony once they have returned. Some birds exhibited site fidelity to the breeding nest every year but others did not. Four pairs, with both birds marked, remained in a pair bond every year until one of them was lost. The number of chicks fledged per nest did not change with the age of the parent. Two broods in the same breeding season were observed in 7 (9.0%) of 78 nests, in which at least one parent was marked. The maximum number of fledglings produced by a single male over the 9 years was 22. Of 23 birds that were resident for more than 2 years, 4 birds (all females) continued to stay at the colony site after the breeding season. However, 19 (8 males, 3 females, 8 unsexed) left the colony after the late breeding season and were observed in outside locations, particularly at fixed feeding sites. The maximum distance of resighted, marked fledglings was 1,580 km southwest of the colony, 54 days after release.

In Grey Heron, thus, individual behavior and performance in the colony affect the whole colony dynamics. Benefit of colony breeding in suburban Tokyo, where predation pressure is now weak, may be efficient and continuous mate searching for their long lives despite being density-dependent processes in the colony when it reaches high density.

## 1. General introduction

Hérons and egrets nest in a colony, reaching to hundreds or thousands of pairs, in relatively limited areas and in high density. Herons and egrets are usually one of the large birds and attract much attention to their population fluctuation and limitation, because it is easier to estimate the number of breeding pairs in colony breeding birds than in the non-colony breeders. Population fluctuation may be caused by several factors that are not mutually exclusive. In the review by Butler (1994), he concluded as follows. First, there is little unequivocal evidence that density-dependent factors regulate most wading bird populations. Intraspecific competition for breeding sites, colony-sites, and food supplies appears to be unimportant in determining the reproductive success or survival in most wading bird species. Second, it is unclear whether food limits the number of breeding pairs through density-dependent processes. Density-independent factors are also important to fluctuate population. Unpredictable factors such as cold weather, high winds, human impacts, disease, and food shortage can explain reduced breeding success and increased mortality in wading birds in some regions without invoking density-dependent mechanisms (Butler 1994).

The evolution of colonial breeding in birds has been explained by the information center hypothesis (Ward and Zahavi 1973; Krebs 1974), the antipredator hypothesis (Patterson 1965), and the mate attraction and finding hypothesis (Simpson et al. 1987; Draulans 1988). The information center hypothesis predicts that neighbors within a colony benefit from the opportunity to follow each other to suitable feeding sites. The antipredator hypothesis predicts that clustering of nests provides protection against predators, particularly for central individuals. The mate attraction and finding hypothesis predicts that finding a new mate or relocating a previous mate may be facilitated.

The hypothesis that colonial breeding facilitates the finding of unpredictable food items is still resolved well. In this hypothesis, colonially breeding herons feed in some groups. In most cases of heron feeding, however, they do solitarily (Hancock and Kushlan 1984).

In the antipredator hypothesis, possible advantages include early warning, mobbing, and predator swamping via breeding synchrony (Rodgers 1987a). The Yellow Bittern *Ixobrychus sinensis* makes a nest at about 1 m on the water surface and has two

breeding systems, solitarily and colonially, in central Japan (Ueda 1996). Predation rates observed in 1991-1993 are always higher (40-93%) in solitary nests than in colonial nests (8-38%). In this area, therefore, the colony breeding is beneficial to avoid predation particularly by terrestrial predators such as weasels and snakes. However, colonial breeding also incurs a disadvantage in predation risks, as the colony is highly obvious via auditory (calls of adults and young), olfactory (birds themselves, guano, and dropped food items), and visual (large, often light colored species flying in and out of the site) cues to predators (Rodgers 1987a). If the breeding is more or less synchronous, any potential swamping of predators via breeding synchrony is reduced (Rodgers 1987b). Thus, it has been questioned in some cases whether colonial breeding by herons reduces the risk of predation (Krebs 1978; van Vesseem and Draulans 1986b). Nests in heronries are not easily accessible when formed on trees. However, predation by Goshawks *Accipiter gentilis* and raccoons *Procyon lotor* is increased by colonial breeding (Mertens 1951; Pratt and Winkler 1985).

The mate attraction and finding hypothesis is that birds are easier in finding of the mate when they gather to the narrow area at the beginning of the breeding period than they do solitarily. Most herons chose new nest sites and new mates each year. The colony may therefore serve as an assembly site for mate finding. Mate finding and avoidance of predation are more likely to explain coloniality in Great Blue Herons than are advantages associated with finding food (Simpson et al. 1987). In the densely-gathered breeding system, however, intra and inter-specific competition for nest sites and food resources is sometimes demerit to colonial birds as mentioned above.

In this study, to simplify the factors affecting density-dependent processes of colony breeders, a single-species colony of Grey Herons (*Ardea cinerea* L.) was selected and monitored for 16 years beginning at its establishment. First, by monitoring this colony, I investigated (1) the long-term population fluctuation patterns, (2) density-dependent phenomena based on individual breeding behavior and reproductive successes, and (3) density-independent factors such that how winter temperatures affect colony size and individual breeding behavior. Next, to know the colony formation of this single-species colony, I examined (1) nest site selection by Grey Herons comparing between nested and un-nested trees standing in the colony area in species, diameter, and height and (2) the effect of spatial distribution of nests on breeding success under the hypothesis that the central part of colony is safety but periphery is risky for nest predation. Finally, to

trace individual behavior and reproductive success for longtime, individually banded Grey Herons were observed intensively for 9 years in the same colony. In this long term individual monitoring allowed me to examine (1) the degree of fidelity to the breeding colony, the nesting site in the colony, and the feeding site in the non-breeding period, (2) post-natal migration patterns after fledging, and (3) the lifetime reproductive parameters. All these data could illustrate the dynamics of the Grey Heron colony from the viewpoint of individual performance among the colony members, which suggested the importance of social factors such as individual interactions particularly at the beginning of breeding seasons that repeated every year.

## 2. Study species and study site

### 2-1. Study species

The Grey Heron (*Ardea cinerea* L.) is a large grey-colored heron having white and black stripes (Fig. 2-1) belonging to the tribe Ardeini, subfamily Ardeinae, and family Ardeidae (so called as wading or ciconiiform birds) (Table 2-1). In the world, 42 species are known in the subfamily Ardeinae that consists of three tribes Ardeini (22 species), Egrettini (14 species), and Nycticoraxini (Table 2-1). The breeding range of Grey Herons covers most of the Old World south of the Arctic Circle, including Europe, Africa, Asia, and East Indies islands to Wallace's Line (Kushlan and Hancock 2005). After the breeding season, generally when the young can fly, Grey Herons disperse in all directions (Kushlan and Hancock 2005). Therefore, in the non-breeding range expands to outside of the breeding range. Grey Herons are sedentary and widely distributed in Japan (Committee for Check-list of Japanese Birds 2000). The distribution range is recently expanding to north (Wild Bird Society of Japan 1994). In Hokkaido, northern Japan, only 6 colonies were recorded in 1960, but 53 colonies in 1999, although the mean number of nests per colony decreased from 171 before 1980 to 48 after 1980, and inland colonies increased after 1980 (coastal colonies dominated before 1980) (Matsunaga et al. 2000).

Grey Herons feed on a variety of aquatic animals such as fish, amphibians, crustaceans, insects, and worms (Kushlan and Hancock 2005). Their feeding technique is usually standing (Fig. 2-2). Their feeding sites are ponds, lakes, rivers, marshes, and seashores (tidal shallow bays), but often use artificial water environments such as rice fields, fish farms, parks, and dams (Fig. 2-3) (Sawara et al. 1990). First-year Grey Herons are less successful at feeding than are adults when prey density is low, due to lower encounter rates with potential prey, but at very high prey densities both age classes perform in a similar way (Draulans 1987).

In Japan, Sawara et al. (1994) reported their diets at 18 colony sites across Japan. Of all regurgitated 220 items, 76% were fish (most freshwater species, but some sea species), 12% were crustaceans, and others were frogs, water beetles, mollusks, annelids, and only one *Microtus* mammal. This result shows that the diets of Grey Herons dominate fish and crustaceans in Japan in contrast to European results that they

feed on also small mammals, *Arvicola terrestris*, *Microtus* voles, and *Mustela erminea*, and birds (often chicks), *Gallinula chloropus*, *Fulica atra*, *Vanellus vanellus*, *Anas platyrhynchos*, *Aythya fuligula*, *Larus ridibundus* and *Haematopus ostralegus* (Owen 1955; Giles 1981; Marquiss and Leitch 1990; Jakubas and Mioduszezewska 2005), although Grey Herons using tidal and estuary areas as hunting sites eat mostly fishes (Cook 1978b; Draulans and Hannon 1988). Coci Herons in Argentina also feed on a great amount of small mammals (rodents), *Ctenomys talarum* and *Myocastor coypus* (Pretelli et al. 2012).

The Grey Heron is a typical colonial breeder, although often in small colonies of 2-10 nests to a thousand of pairs (Kushlan and Hancock 2005). Such a heron colony is called as a heronry. The heronry is classified into two categories, single- and mixed-species heronries. Grey Herons breed often in the mixed-species heronries with other species of herons and egrets. In Japan, the single-species colonies or those with Black-crowned Night Herons are found in northern part, but the colonies include more species of herons and egrets in southern part, such as Little Egrets, Intermediate Egrets, and Cattle Egrets, or other water birds such as Common Cormorants (*Phalacrocorax carbo*) (Sawara et al. 1994).

Grey Herons does not show distinct sexual differences in size and plumage. After mating the pair care eggs and nestlings. During incubation and the period of bare for small chicks, one of a pair generally stays in the nest. When chicks are older, parents visit their nest only for short periods to feed the chicks (van Vessem and Draulans 1986c).

## **2-2. Study sites**

Three colonies in suburban Tokyo are studied (Fig. 2-4). These colonies could be monitored from their establishments. The first colony was formed on the hilltop at Renkoji, Tama-shi, Tokyo (35°39'N, 139°28'E) in 1996. This site locates near the Oguri-gawa River that just joins the Tama-gawa River. The colony (250 m in the major axis, 80 m in the minor axis) was in a small wood surrounded by houses in a newly built town (Fig. 2-5). The wood consisted of mainly *Quercus acutissima* and *Q. serrata*, and some *Pinus densiflora*.

The second colony studied was located within the Tama Zoological Park, Hino-shi,

Tokyo (35°38'N, 139°24'E). In this zoo, several woods are remained and wild Grey Herons have established the colony from 2000. The colony (290 m in the major axis, 220 m in the minor axis) was in a small wood consisting of *Quercus acutissima*, *Q. serrata*, *Carpinus tschonoskii*, *Prunus jamasakura*, and *Pinus densiflora* (Fig. 2-6). They often use the water sites in the caged area of rearing animals for hunting sites (Fig. 2-3).

The third was the colony formed in a small wood at Ozenji, Kawasaki-shi, Kanagawa Prefecture (35°35'N, 139°31'E). This includes the neighboring two subcolonies (100 m × 80 m and 70 m × 30 m) with the intercolonial distance of 300 m. The vegetation was *Quercus acutissima*, *Q. serrata*, *Prunus jamasakura*, and planted *Cryptomeria japonica* (Fig. 2-7).

These colonies observed were all single-species heronries consisting of Grey Herons, although Sugita (2001) reported that the colony of the Tama Zoological Park included at least 13 nests of Black-crowned Night Herons at establishment of Grey Heron colony in 2000.

Table 2-1. A list of wading birds (=Ciconiiformes) belonging to subfamily Ardeinae in the world (modified from Kushlan and Hancock 2005).

No.	English name	Genus	Species	Author	Tribe	Weight (g)	Distribution	Japanese residents and Japanese name
1	Grey Heron	<i>Ardea</i>	<i>cinerea</i>	Linnaeus, 1758	Ardeini	1020-2073	Europe, Africa, Asia, East Indies islands to Wallace's Line	アオサギ
2	Great Blue Heron	<i>Ardea</i>	<i>herodias</i>	Linnaeus, 1758	Ardeini	2200-2500	North to Central America	
3	Cocoi Heron	<i>Ardea</i>	<i>cocoi</i>	Linnaeus, 1766	Ardeini	1900-1980	South America	
4	White-necked Heron	<i>Ardea</i>	<i>pacifica</i>	Latham, 1801	Ardeini	650-860	Australia	
5	Great Egret	<i>Ardea</i>	<i>alba</i>	Linnaeus, 1758	Ardeini	930-1700	North, Central and South America, Europe, Africa, and north Asia	ダイサギ
6	Eastern Great Egret	<i>Ardea</i>	<i>modesta</i>	Gray, 1831	Ardeini	760-970	south and east Asia and Australasia	
7	Intermediate Egret	<i>Ardea</i>	<i>intermedia</i>	Wagler, 1829	Ardeini	400-500	Africa, southeast and east Asia, and Australia	チュウサギ
8	Black-headed Heron	<i>Ardea</i>	<i>melanocephala</i>	Vigors et Children, 1826	Ardeini	710-1650	Africa	
9	Malagasy Heron	<i>Ardea</i>	<i>humbloti</i>	Milne-Edwards et Grandidier 1885	Ardeini	no data	Madagascar and Comoro islands	
10	White-bellied Heron	<i>Ardea</i>	<i>insignis</i>	Hume, 1878	Ardeini	no data	northern India to northern Myanmar	
11	Sumatran Heron	<i>Ardea</i>	<i>sumatrana</i>	Raffles, 1822	Ardeini	1300-2600	south east Asia to Australia	
12	Goliath Heron	<i>Ardea</i>	<i>goliath</i>	Cretzchmar, 1826	Ardeini	4300-4468	mainly Africa	
13	Purple Heron	<i>Ardea</i>	<i>purpurea</i>	Linnaeus, 1766	Ardeini	525-1345	Europe, Africa, and Asia	ムラサキサギ
14	Cattle Egret	<i>Ardea</i>	<i>ibis</i>	Linnaeus, 1758	Ardeini	270-510	North and South America, Europe, Africa, Asia, and Australia	アマサギ
15	Green Heron	<i>Butorides</i>	<i>virescens</i>	(Linnaeus, 1758)	Ardeini	200-250	North to Central America	
16	Striated Heron	<i>Butorides</i>	<i>striatus</i>	(Linnaeus, 1758)	Ardeini	193-235	South America, Africa, Madagascar, India, south and east Asia, and Australia	ササゴイ
17	Squacco Heron	<i>Ardeola</i>	<i>rallouides</i>	(Scopoli, 1769)	Ardeini	230-370	Europe, Africa, Madagascar, and Iran	
18	Indian Pond Heron	<i>Ardeola</i>	<i>grayii</i>	Sykes, 1832	Ardeini	230-276	India	
19	Chinese Pond Heron	<i>Ardeola</i>	<i>bacchus</i>	(Bonaparte, 1855)	Ardeini	no data	east Asia to Indonesia	アカガシラサギ
20	Javan Pond Heron	<i>Ardeola</i>	<i>speciosa</i>	(Horsfield, 1821)	Ardeini	no data	southern Asia to Indonesia	
21	Malagasy Pond Heron	<i>Ardeola</i>	<i>idea</i>	(Hartlaub, 1860)	Ardeini	no data	Madagascar and east Africa	
22	Rufous Bellied Heron	<i>Ardeola</i>	<i>rufiventris</i>	(Sundevall, 1851)	Ardeini	no data	central Africa	
23	Reddish Egret	<i>Egretta</i>	<i>rufescens</i>	(Gmelin, 1789)	Egrettini	700-850	south North America to north South America	
24	Pied Heron	<i>Egretta</i>	<i>picata</i>	(Goold, 1845)	Egrettini	225-280	northern Australia and East Indies	
25	Slaty Egret	<i>Egretta</i>	<i>vinaceigula</i>	(Sharpe, 1895)	Egrettini	250-340	south central Africa	
26	Black Heron	<i>Egretta</i>	<i>ardesiaca</i>	(Wagler, 1827)	Egrettini	270-390	Africa and Madagascar	
27	Tricolored Heron	<i>Egretta</i>	<i>tricolor</i>	(Pl. Statius-Muller, 1776)	Egrettini	200-415	North to South America	
28	White-faced Heron	<i>Egretta</i>	<i>novaeollandiae</i>	(Latham, 1790)	Egrettini	500-550	Australia and East Indies	
29	Little Blue Heron	<i>Egretta</i>	<i>caerulea</i>	(Linnaeus, 1758)	Egrettini	296-410	North to South America	
30	Snowy Egret	<i>Egretta</i>	<i>thula</i>	(Molina, 1782)	Egrettini	around 370	North to South America	
31	Little Egret	<i>Egretta</i>	<i>garzetta</i>	(Linnaeus, 1766)	Egrettini	300-710	Europe, Africa, Madafascar, Asia, East Indies, and Australia	コサギ
32	Chinese Egret	<i>Egretta</i>	<i>eulophotes</i>	(Swinhoe, 1860)	Egrettini	390-540	Japan, Far East Russia and coastal China	カラシラサギ
33	Eastern Reef Heron	<i>Egretta</i>	<i>sacra</i>	(Gmelin, 1789)	Egrettini	330-700	east Asia to Australia	クロサギ
34	Whistling Heron	<i>Syrigma</i>	<i>sibilatrix</i>	(Temminck, 1824)	Egrettini	521-546	South America	
35	Capped Heron	<i>Ptilherodius</i>	<i>pileatus</i>	(Boddaert, 1783)	Egrettini	518-591	north South America	
36	Yellow-crowned Night Heron	<i>Nyctinassa</i>	<i>violacea</i>	(Linnaeus, 1758)	Egrettini	649-716	North to South America	
37	Black-crowned Night Heron	<i>Nycticorax</i>	<i>nycticorax</i>	(Linnaeus, 1758)	Nycticoraxini	727-1014	North to South America, Europe, Africa, and Asia	ゴイサギ
38	Rufous Night Heron	<i>Nycticorax</i>	<i>caledonicus</i>	(Gmelin, 1789)	Nycticoraxini	810-1014	Indonesia to Australia	
39	White-backed Night Heron	<i>Nycticorax</i>	<i>leuconotus</i>	(Wagler, 1827)	Nycticoraxini	no data	Africa	
40	White-eared Night Heron	<i>Gorsachius</i>	<i>magnificus</i>	(Ogilvie-Grant, 1899)	Nycticoraxini	no data	southeast China and Vietnam	
41	Japanese Night Heron	<i>Gorsachius</i>	<i>goisagi</i>	(Temminck, 1835)	Nycticoraxini	no data	Japan, south China, Indonesia, and Philippines	ミゾゴイ
42	Malayan Night Heron	<i>Gorsachius</i>	<i>melanolophus</i>	(Raffles, 1822)	Nycticoraxini	417-450	India, and south China to Indonesia	ズグロミゾゴイ





**Fig. 2-1.** Wild Grey Heron (*Ardea cinerea*) living in Tama Zoological Park. This individual has steel and color rings in his legs.

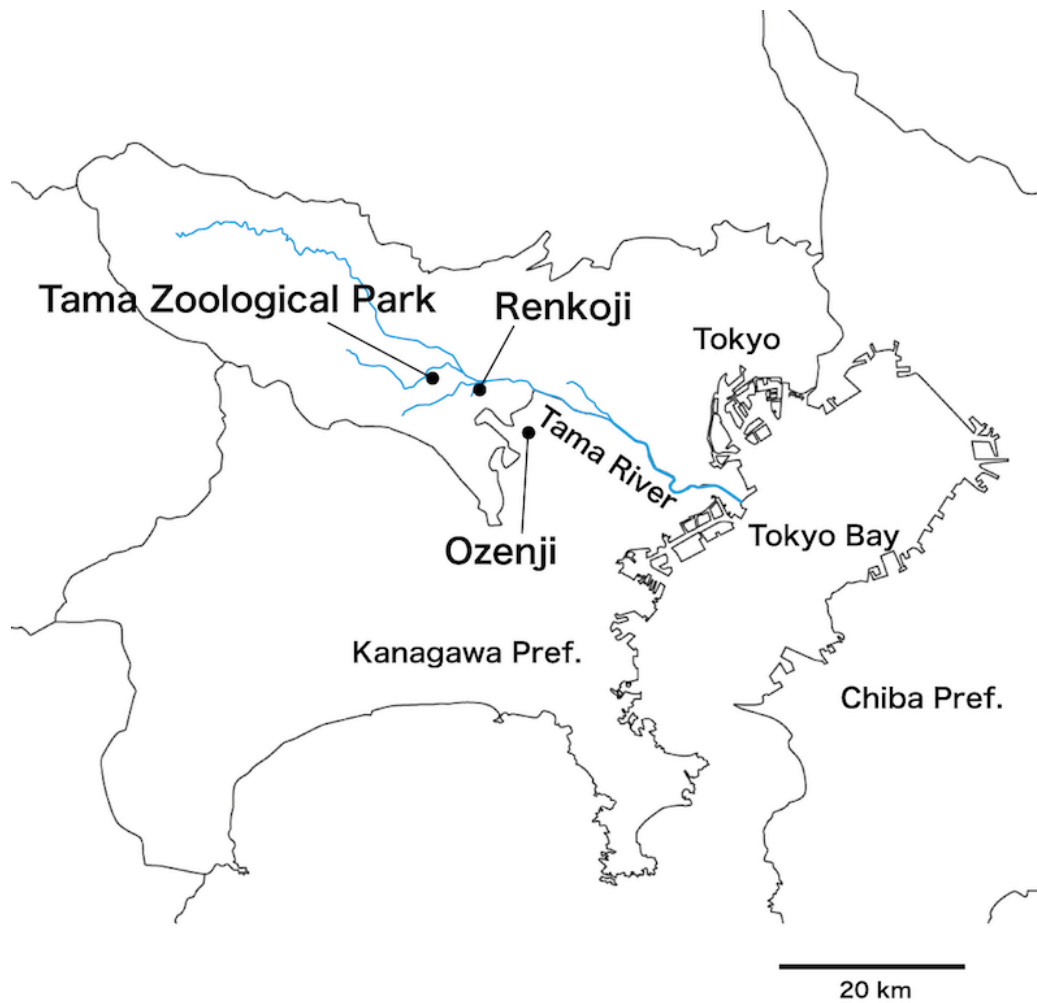


**Fig. 2-2.** Wild Grey Heron (*Ardea cinerea*) standing to capture aquatic preys in a pond.





**Fig. 2-3.** Wild Grey Heron (*Ardea cinerea*) just capturing a fish in the artificial pond in Tama Zoological Park. This individual has steel and color rings in his legs.

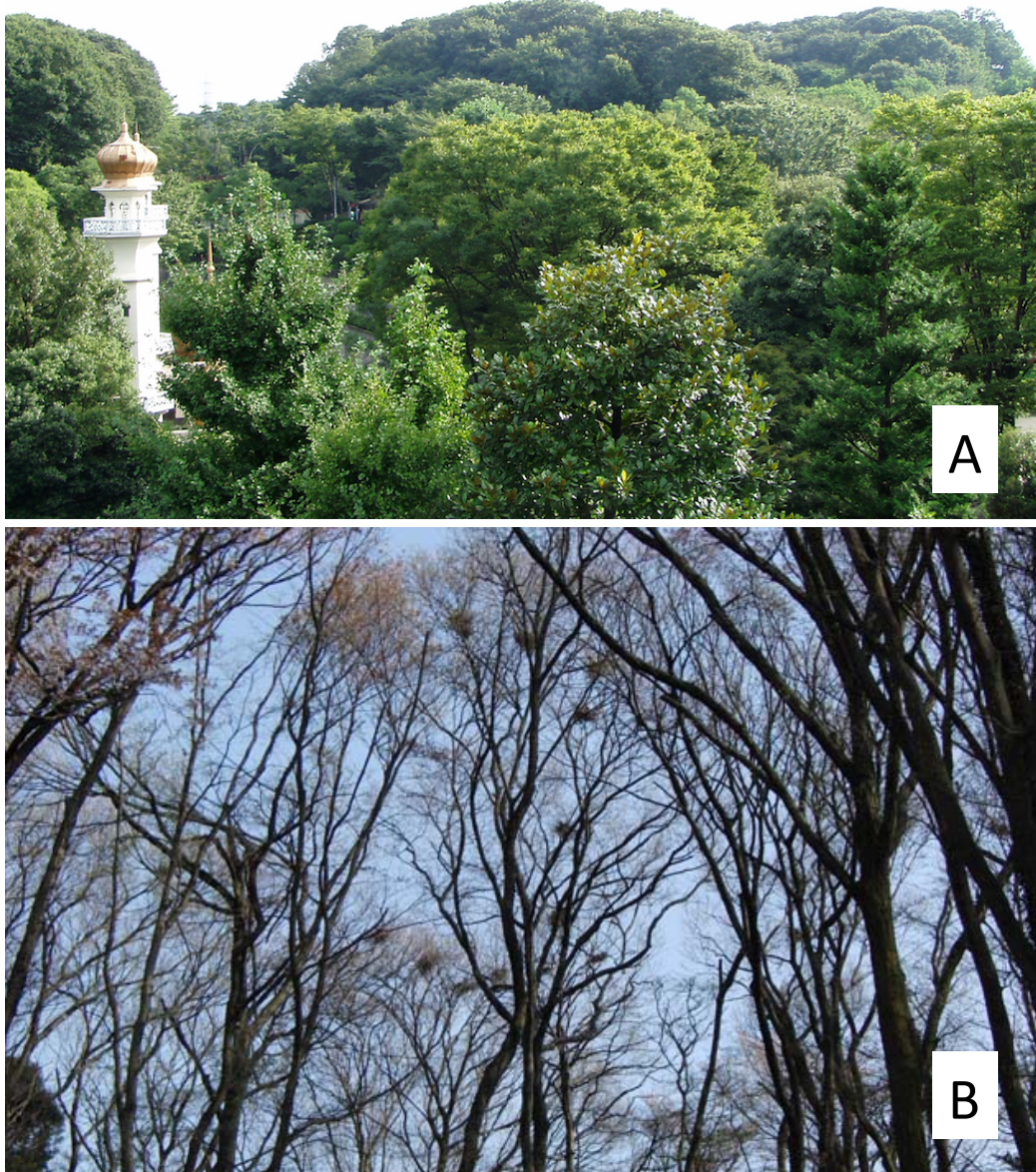


**Fig. 2-4.** Three colonies of the wild Grey Heron (*Ardea cinerea*) observed in this study; Renkoji, Tama Zoological park, and Ozenji.



**Fig. 2-5.** A colony of the wild Grey Heron (*Ardea cinerea*) established at Renkoji, Tama-shi, Tokyo. The colony is formed at the hill slope surrounded by a newly built town near the Oguri-gawa River.





**Fig. 2-6.** A colony of the wild Grey Heron (*Ardea cinerea*) established at Tama Zoological Park, Hino-shi, Tokyo. The colony is formed at the hill top within the park. A, summer; B, winter.



**Fig. 2-7.** A colony of the wild Grey Heron (*Ardea cinerea*) established at Ozenji, Kawasaki-shi, Kanagawa Prefecture. The colony is formed at the hill top near artificial ponds.



### 3. Colony development and density-dependent processes

#### 3-1. Introduction

Wading birds such as herons and egrets nest in colonies in relatively limited areas and at high density, often reaching hundreds or thousands of pairs (Kushlan and Hancock 2005). Herons and egrets are usually quite large birds, and the dynamics of their population attract much attention, as estimating the number of breeding pairs is easier in colony-breeding birds than in non-colony breeders. Population fluctuations may be caused by density-dependent and density-independent processes, although the two are not mutually exclusive.

Density dependence is a negative feedback between population growth rate and population density (Newton 1998). In a White Heron (*Egretta alba*) colony, the mean number of fledglings per nest decreased as the number of nests in the colony increased, suggesting a density-dependent response (Miller 2001). The first egg-laying date was delayed when colony size was large in a Purple Heron (*Ardea purpurea*) colony (Barbraud et al. 2001). However, little unequivocal evidence shows that density-dependent factors regulate population fluctuations of wading birds, because intraspecific competition for breeding sites, colony sites, and food sources appears to be unimportant in determining the reproductive success or survival in most species (Butler 1994; Lande et al. 2002). Instead of tracking yearly changes in a single colony, inter-colonial comparisons in the same year are useful to detect density-dependent processes, and such comparisons have been conducted in herons and egrets. Results have shown that final breeding success is negatively correlated with colony size in Grey Herons (*Ardea cinerea*) in Belgium (van Vessem and Draulans 1986b) and Great Blue Herons (*Ardea herodias*) in Canada (Butler et al. 1995). However, in Grey Herons in northern Poland, breeding success increases with colony size (Jakubas 2005). Different conditions within each colony habitat, such as the distance to feeding sites and predation risks, may cause opposing results for the relationship between colony size and breeding success.

Density-independent factors have also been suggested to affect population fluctuations of herons and egrets. Unpredictable factors such as cold weather, high winds, disease, food shortage, and human impacts can explain reduced breeding success



and increased mortality in some regions without invoking density-dependent mechanisms (Lopez-Ornat and Ramo 1992; Butler 1994; Kirsch et al. 2008). In particular, winter temperature is known to affect populations of herons and egrets via increased mortality (Stafford 1971; North 1979; North and Morgan 1979; van der Molen et al. 1982; Fasola et al. 2010). Winter temperature also affects the onset of the breeding season in Grey Herons (Walmsley 1975; Marion 1989; Campos and Fernandez-Cruz 1991; Jakubas 2011).

Short-term studies are suboptimal for detecting the effects of density on the dynamics of wading bird populations, because birds are long-lived and breed annually (Kushlan and Hancock 2005). Even in the several long-term studies conducted to date, census data were not recorded beginning at colony establishment but began with mature colonies (e.g., Stafford 1971; Lopez-Ornat and Ramo 1992; Kushlan and Hafner 2000; Hafner et al. 2001; Kelly et al. 2007; Kirsch et al. 2008; Ismail and Rahman 2012). The tendency of wading birds to form mixed-species groups has posed another difficulty for detecting density-dependent processes in colony size regulation; in these cases, both intra- and interspecific interactions affect individual behavior and survival (Bennetts et al. 2000; Dami et al. 2006).

In the present study, to simplify the factors affecting density-dependent processes of colony breeders, a single-species colony of Grey Herons was selected and monitored for 16 years beginning at its establishment. I investigated the long-term population fluctuation patterns in this colony and examined density-dependent phenomena based on individual breeding behavior and reproductive successes in the colony. With respect to density-independent factors, I examined how winter temperatures affect colony size and individual breeding behavior.

## **3-2. Materials and methods**

### **3-2-1. Study sites**

In 1996, a breeding colony of Grey Herons became established at a hillside at Renkoji in suburban Tokyo (35°39'N, 139°28'E); this was selected as a long-term monitoring site. This site is located near the Oguri-gawa River where it just joins the Tama-gawa River. The colony (250 m along the major axis, 80 m along the minor axis)

was located in a small area of woods surrounded by houses in a newly built town. The woods mainly consisted of *Quercus serrata* and *Q. acutissima* and some *Pinus densiflora*. In 2000, however, the colony abandoned this site and relocated to a new breeding site on a hilltop in Tama Zoological Park (35°38'N, 139°24'E), located about 5 km west of Renkoji along the Tama-gawa River. In the zoo, woods are patchily distributed, and the Grey Herons use an area (290 m along the major axis, 220 m along the minor axis) consisting of *Quercus serrata*, *Q. acutissima*, *Carpinus tschonoskii*, *Prunus jamasakura*, and *Pinus densiflora*. In 2008, a new colony had been established at Ozenji, Kawasaki-shi, Kanagawa Prefecture (35°35'N, 139°31'E). This included the neighboring two subcolonies (100 m × 80 m and 70 m × 30 m) with the intercolonial distance of 300 m. The vegetation was *Quercus serrata*, *Q. acutissima*, *Prunus jamasakura*, and *Cryptomeria japonica*.

### 3-2-2. Observations

After colony establishment was first noted at Renkoji in mid 1996 (Shirai 1999), the herons were observed systematically beginning the next year (1997) using binoculars (×10) and a spotting scope (×20–60; TSN-1, Kowa, Nagoya). Herons that stayed in their nests were identified to species. I monitored the typical behavior of breeding individuals (standing, nest building, incubation, or guarding) and the number and body size of chicks (small, medium, or large), if present, at intervals of 3–7 days in 1997 and every 7–10 days in 1998–2000. In 2000, the 49 breeding pairs of this colony had disappeared by late April, and no herons were observed afterwards. However, 14 pairs were observed making nests in Tama Zoological Park from late March in 2000. Therefore, I continued to census this consecutive colony at intervals of 7–10 days in 2001, but at intervals of 3–4 days in 2002–2008 and 7 days in 2009–2011. From the census data, the breeding and nursing durations of each nest were calculated as the period from the day that nest-building behavior was first recorded until fledging was completed (all fledglings disappeared in the nest) and the period from ending incubation (judged from continuous standing of parents) to complete fledging, respectively. If predation occurred in the field, the predators were identified and recorded. At the Ozenji colony, I checked only the number of nests used in the breeding season.

To examine the effects of winter temperature on population fluctuations and the

timing of breeding, air temperatures were used from public data recorded by the automated meteorological data acquisition system of the Japan Meteorological Agency at Fuchu, Tokyo (35°41'N, 139°29'E), located 8.4 km northeast from Tama Zoological Park. The minimum value among the mean 10-day temperatures recorded from 1 December to 31 January was used as the coldness value starting the breeding season in each year.

Some unintended effects of observations on breeding heron behavior have been identified (Goering and Cherry 1971; Frederick and Collopy 1989), particularly researcher visits to colonies during nest-building and early incubation, leading to abandonment of nests (Tremblay and Ellison 1979). Artificial effects on heron behavior may be negligible in this study because census observations were made carefully and far from the nests to avoid disturbing the herons and because the nests were so high in the trees that any eggs in the nests were not examined.

### **3-3. Results**

In 2001 and 2002, eight and two pairs of Black-crowned Night Herons (*Nycticorax nycticorax*) were found, respectively, in the Tama Zoological Park Grey Heron colony. Sugita (2001) also reported that the colony at the park included at least 13 nests of Black-crowned Night Herons in 2000. In all other years, only Grey Herons nested within the colony. The number of nests used by the pairs increased annually after colony establishment at Renkoji but tended to become saturated after about 10 years (Fig. 3-1). The Ozenji colony was also increased gradually after 4 years from colony establishment (Fig. 3-1).

The mean duration of breeding by each pair ranged from 99.1 to 129.0 days and the mean duration of nursing ranged from 53.6 to 67.8 days (Table 3-1). The proportion of successful nests that fledged was 62.6–85.3%, excluding all that were unsuccessful by abandonment of the site in 2000 (Table 3-1). The maximum number of fledglings was four, and the mean number of fledglings per successful nests ranged from 1.8 to 3.1 (Table 3-1). The date that the first pair(s) began to breed in the colony differed from year to year, ranging from 4 January to 3 March (Table 3-1). The mean start date of breeding by pairs also differed yearly, and the coefficient of variation (CV) in the start date of colony members ranged from 20.8% to 55.6% (Table 3-1).

For the effect of colony size on breeding parameters (Fig. 3-2), breeding duration increased with colony size, but nursing duration was not correlated with colony size. Colony size did not affect the proportion of successful nests, but the mean number of fledglings per successful nest decreased with colony size. As the colony size increased, the date of the first breeding became earlier and variation in the timing of the onset of breeding by individual pairs was higher.

In terms of the relationships between the date that each pair began breeding and the duration of breeding or nursing (Fig. 3-3, Table 3-2), breeding duration was usually longer in early breeders than in herons that began to breed later in a season. However, the nursing duration did not differ as greatly between earlier and later breeding pairs, suggesting that the duration until nursing was elongated in earlier breeders. In most years, the number of fledglings decreased as the date of the onset of breeding was delayed (Fig. 3-4, Table 3-2).

Air temperatures were warmer (4.0–5.4°C in mean temperature for a period of 10 days of the coldest period) at the beginning of breeding in 2000, 2002, 2004, 2007, and 2009, but were colder (1.9–2.9°C) in 1998, 2001, 2003, 2006, and 2011, compared to temperatures in 1997, 1999, 2005, 2008, and 2010 (3.6–3.9°C). However, winter temperature was unlikely to explain yearly changes in colony size (Fig. 3-1). Moreover, the two groups of warmer and colder years did not significantly differ in the date of the onset of breeding of the colony (t-test;  $t = 0.70$ ,  $df = 8$ ,  $P = 0.70$ ), the CV in individual breeding date ( $t = 1.14$ ,  $df = 7$ ,  $P = 0.29$ ), or other reproductive traits (breeding duration:  $t = 0.04$ ,  $df = 7$ ,  $P = 0.97$ ; nursing duration:  $t = 0.22$ ,  $df = 7$ ,  $P = 0.83$ ; number of successful nests:  $t = 0.51$ ,  $df = 7$ ,  $P = 0.63$ ; number of fledglings per successful nest:  $t = 0.43$ ,  $df = 7$ ,  $P = 0.68$ ).

Predation rarely occurred during the censuses. The observed predators of eggs and chicks were the Japanese rat snake *Elaphe climacophora* ( $N = 1$ ) and the jungle crow *Corvus macrorhynchos* ( $N = 14$ ).

### **3-4. Discussion**

#### **3-4-1. Density dependence**

The Renkoji site was abandoned 4 years after establishment and the colony

relocated to a new site in Tama Zoological Park close to Renkoji along the Tama-gawa River. Higher rates of nest mortality lead to significant decreases in colony size, and breeding colony distributions often shift in association with these reductions in colony size (Boulinier 1996; Danchin et al. 1998). For example, a colony of Great Blue Herons at Pender Harbour, British Columbia, abandoned their site after 2 years of high predation by Ravens (*Corvus corax*), Bald Eagles (*Haliaeetus leucocephalus*), and probably raccoons (*Procyon lotor*) (Simpson et al. 1987; Butler et al. 1995). Heavy predation may thus force colony abandonment by herons. In the study population, however, predation was rarely observed. The snake *Elaphe climacophora* and the crow *Corvus macrorhynchos* were the only predators of eggs and chicks recorded in the present study. Colony nesting of birds sometimes damage vegetation, mainly by altering soil nutrient concentration (Ishida 1996; Mun 1997). Vegetation degradation may cause shifting the colony site (Ogasawara et al. 1982). In this study, however, obvious change in vegetation occurred for 16 years even at the central part of colonies. Thus, the cause of the relocation of the colony remains unknown.

In the present study, the colony size increased yearly after establishment and later became saturated (Fig. 3-1), similar to the patterns reported for Grey Herons in two Spanish colonies (Fernández-Cruz and Campos 1993; Prosper and Hafner 1996). Density-dependent processes may be important factors causing such a demographic pattern. The mean clutch size and fledglings per successful nest have been reported to be 3.3–4.2 and 2.1–3.9, respectively, for Grey Herons (Kim and Koo 2009b). In the present study, fledglings per successful nest ranged from 1.8 to 3.1 with a mean of 2.2 (SD = 0.3, N = 14), but the fledgling number decreased with colony size (Fig. 3-2d), suggesting a density-dependent response. In a study on White Herons in New Zealand, the mean number of fledglings per nest also decreased as the number of nests in the colony increased (Miller 2001). In the present study, the timing of breeding may have also been density dependent because the breeding duration became longer (Figure 2a), the reproductive season occurred earlier (Fig. 3-2e), and variation among individuals increased (Fig. 3-2f) as the colony size increased. The tendency to delay the initial egg-laying date when colony size is large has also been reported for Purple Herons in southern France (Barbraud et al. 2001).

The mechanisms of density dependence in demography involve both extrinsic (food) and intrinsic (social behavior) factors (Bretagnolle et al. 2008). Increased feeding

visits by parents (i.e., higher food availability to chicks) decreases chick mortality of Grey Herons (Jakubas 2005). The nursing duration of Grey Herons, particularly when nursing small chicks, becomes longer when the frequency of returns to the nest decreases, likely because of less food availability at hunting sites (van Vessem and Draulans 1986a). In a field experiment using food supplements, Great Blue Herons showed increased clutch size and fledging success but no difference in the seasonal timing of nesting (Powell 1983). Thus, competition for limited food is a possible source of density dependence. However, the effect of food availability on colony size is usually difficult to detect, because food searching areas used by colony members cannot be tracked completely. In Portugal, Cattle Egret (*Bubulcus ibis*) colonies reportedly depend on areas of dry pasture and crops within a 5 km radius of the colony center, and Little Egrets (*Egretta garzetta*) depend on the presence of freshwater and saltwater habitats within a 5 km area (Farinha and Leita0 1996). Estimating the amount of available food over such a wide range of habitat would be difficult.

Social factors involved in density dependence may be direct behavioral interference among colony members. In herons and egrets, intraspecific interactions may be critical in courtship and nesting (Kushlan and Hancock 2005; McCrimmon 1978). In the present study, earlier breeders took a longer period of time until nursing (i.e., the period from nest building to completed egg incubation) than did later breeders (Fig. 3-3). The prolonged pre-nursing duration may have been caused by unstable states of colony members at the beginning of the breeding season. During this period, interference is expected to be frequent and intense, because the colony includes many unfamiliar birds that have arrived and joined the colony that year. To confirm this interference hypothesis, quantitative data examining the relationship between interference frequency and colony size are needed.

Despite these possible intense interactions in the early breeding season, the number of fledged chicks was greater for earlier breeders than for later breeders (Fig. 3-4). A similar decline in the number of fledglings with a later date of the onset of breeding was observed for Grey Herons in Poland, although not every year (Jakubas 2011). Brood size is often larger in earlier breeders within a reproductive season in birds (Lack 1954), as observed in Grey Herons (Creutz 1975; van Vessem and Draulans 1986b; van Vessem 1991) and other heron and egret species (Rodgers 1980, 1987b; Ranglack et al. 1991). On the other hand, mean brood size increases with the age of parents (Baxter

1994; Thomas et al. 1999). Older individuals may be more successful in acquiring nest sites of good quality and have more experience in parental care (Thomas et al. 1995, 1999). In the present study, these age effects could not be assessed. In the future, to discriminate the effects of the age of parents and the timing of breeding on reproductive success, the age of the Grey Herons must be determined by marking individuals.

### **3-4-2. Density independence**

Unpredictable factors can explain reduced breeding success and increased mortality in some regions without invoking density-dependent mechanisms (Lopez-Ornat and Ramo 1992; Butler 1994; Kirsch et al. 2008). For example, in a study conducted in the Yucatan Peninsula, most herons and egrets failed to reproduce because of food shortages caused by exceptionally heavy rains and flooding of their lowland habitats (Lopez-Ornat and Ramo 1992).

Another well-known density-independent process that can reduce population size in herons and egrets is unpredicted severely low temperatures in winter. The Grey Heron population in England and Wales usually numbers 4500–4800, but after severe winters, it decreases to around 3000 (Stafford 1971). In particular, winter (January to March) temperature strongly affects the survival rate of first-year Grey Herons in England, as estimated by the annual recovery of banded nestlings from 1955 to 1974 (North 1979; North and Morgan 1979). In those studies, in a year when temperatures reached about 1°C, few young birds survived, whereas during years with winter temperatures above 6°C, more than half survived. A large number of Grey Herons also died during a cold spell in January and February 1976 in the Netherlands (van der Molen et al. 1982). In northwest Italy, Grey Herons increased following an increase in winter temperature (Fasola et al. 2010). In France, however, the survival of yearling Little Egrets did not appear to be affected by winter severity (Hafner et al. 1998).

In the present 16-year study, winter temperature was unlikely to explain yearly variation in reproductive parameters. In Poland, Grey Herons in inland colonies begin to breed later than those in coastal colonies, because spring air temperatures are lower and ice cover is present on feeding sites for a longer duration in inland locations (Jakubas 2011). Thus, accessibility of feeding sites (lack of ice cover) in spring is an important factor affecting the onset of breeding. However, in suburban Tokyo, winter

temperatures are relatively mild and rarely fall below 0°C (Fig. 3-5). Therefore, annual differences in the onset of breeding are not likely related to temperature, as in the case of Little Egrets in France (Hafner et al. 1998).



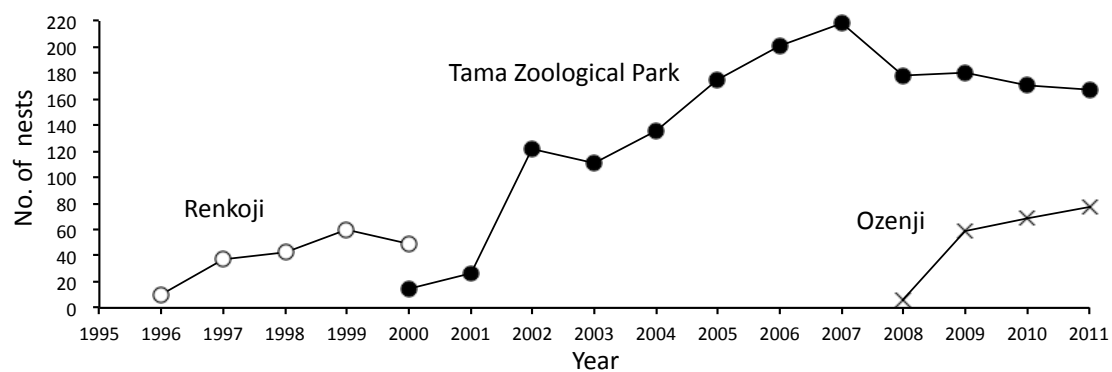
Table 3-1. Mean values of the breeding duration, nursing duration, number of fledglings per successful nest, and date starting breeding in each nest. The proportion of successful nests to fledge and the date of the first breeding in the colony are also shown.

Colony	Year	No of nests used	Breeding duration (days)			Nursing duration (days)			Successful nests		No. of fledglings/successful nest			Date of the first breeding in the colony <sup>a</sup>	Date of the beginning of each nest breeding			
			Mean	SD	N	Mean	SD	N	%	N	Mean	SD	N		Mean	SD	CV (%)	N
Renkoji	1996	10																
Renkoji	1997	37	102.5	6.9	19	67.3	17.1	15	85.3	34	3.1	0.7	29	48	78.1	26.4	33.8	34
Renkoji	1998	43	106.7	14.7	24	58.6	16.3	24	92.1	38	2.5	0.9	35	62	74.9	18.1	24.1	33
Renkoji	1999	60	106.6	16.0	20	64.6	17.0	20	64.4	45	2.2	0.7	29	62	79.6	16.5	20.8	58
Renkoji	2000 <sup>a</sup>	49			0			0	0.0	49			0	47				0
Tama Zoo	2000	14																
Tama Zoo	2001	26	114.6	15.0	15	65.9	16.8	7	85.0	20	1.9	0.7	17	45	83.8	18.0	21.5	25
Tama Zoo	2002	122	99.1	16.2	56	57.3	12.1	43	70.7	92	2.1	0.9	65	49	75.5	22.1	29.3	78
Tama Zoo	2003	111	113.4	15.5	82	64.6	11.0	76	82.5	103	2.5	0.8	85	42	75.9	26.0	34.3	106
Tama Zoo	2004	136	111.1	19.2	79	60.6	17.6	77	79.5	122	2.4	0.9	97	26	72.1	29.2	40.6	135
Tama Zoo	2005	175	120.9	22.1	112	60.4	13.4	95	81.5	157	2.1	0.8	128	4	64.3	35.8	55.6	156
Tama Zoo	2006	201	123.8	21.1	102	61.7	14.5	89	82.6	182	2.0	0.8	114	12	68.6	27.4	39.9	195
Tama Zoo	2007	218	126.6	21.3	125	63.4	17.4	106	79.9	174	2.1	0.8	139	35	69.4	29.2	42.0	208
Tama Zoo	2008	178	114.3	16.9	102	59.3	11.6	96	75.8	149	2.0	0.8	113	27	67.4	21.2	31.4	166
Tama Zoo	2009	180	129.0	21.1	105	67.8	16.7	85	79.1	153	1.8	0.6	121	23	57.0	24.4	42.8	183
Tama Zoo	2010	171	125.9	21.3	117	53.6	17.4	113	77.7	157	1.9	0.6	122	31	67.9	20.9	30.8	155
Tama Zoo	2011	167	125.2	24.7	93	63.3	18.5	99	79.3	150	2.0	0.8	119	38	73.6	31.2	42.4	130
Ozenji	2008	6																
Ozenji	2009	59																
Ozenji	2010	69																
Ozenji	2011	77																

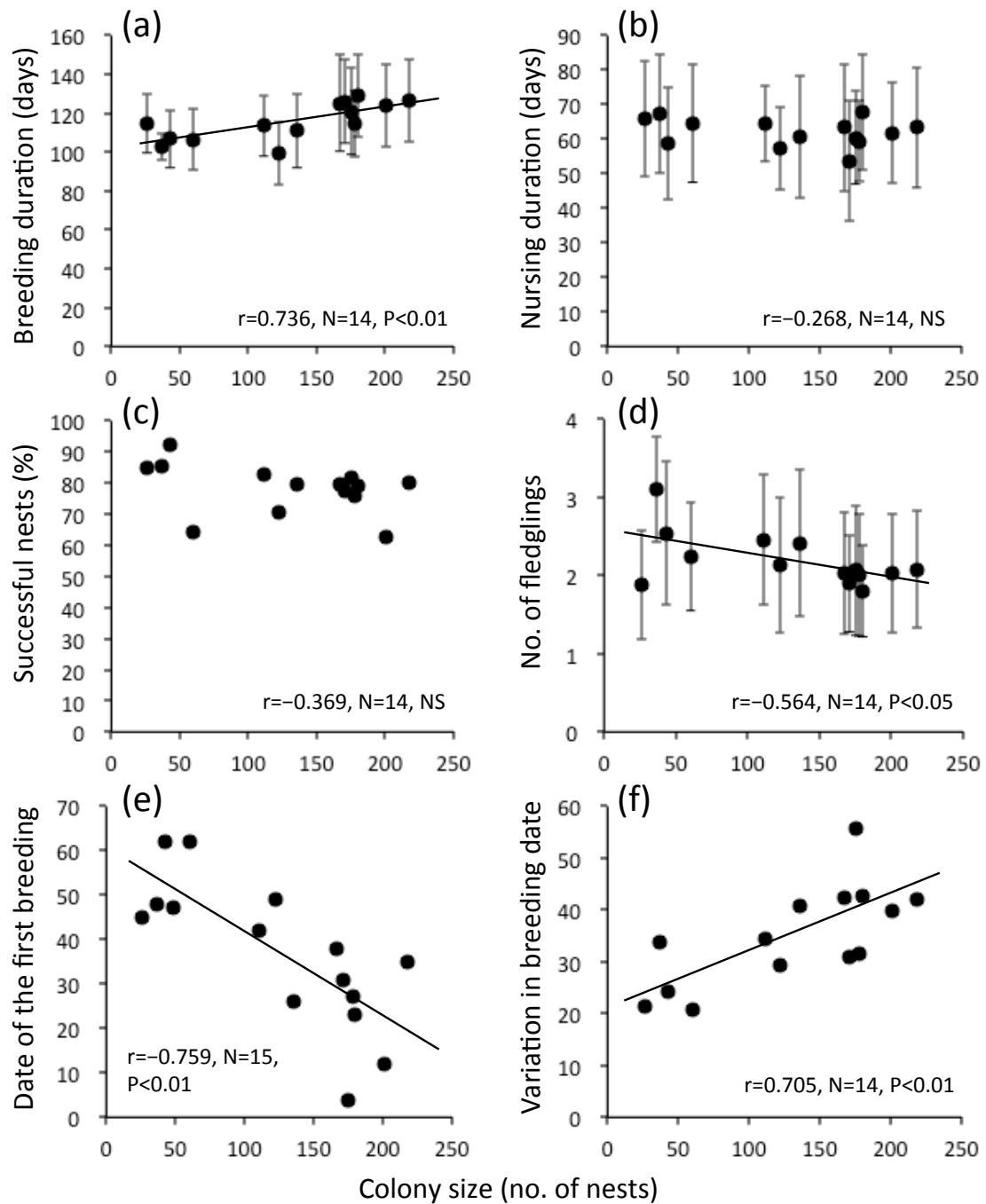
a. all nests were abandoned in this year; b. date is presented by days from January 1th in each year.

Table 3-2. Correlation coefficients between the date of starting breeding and the breeding duration, the nursing duration, or the number of fledglings in each nest. NS,  $P>0.05$ ; \*,  $P<0.05$ ; \*\*,  $P<0.01$ ; \*\*\*,  $P<0.001$ .

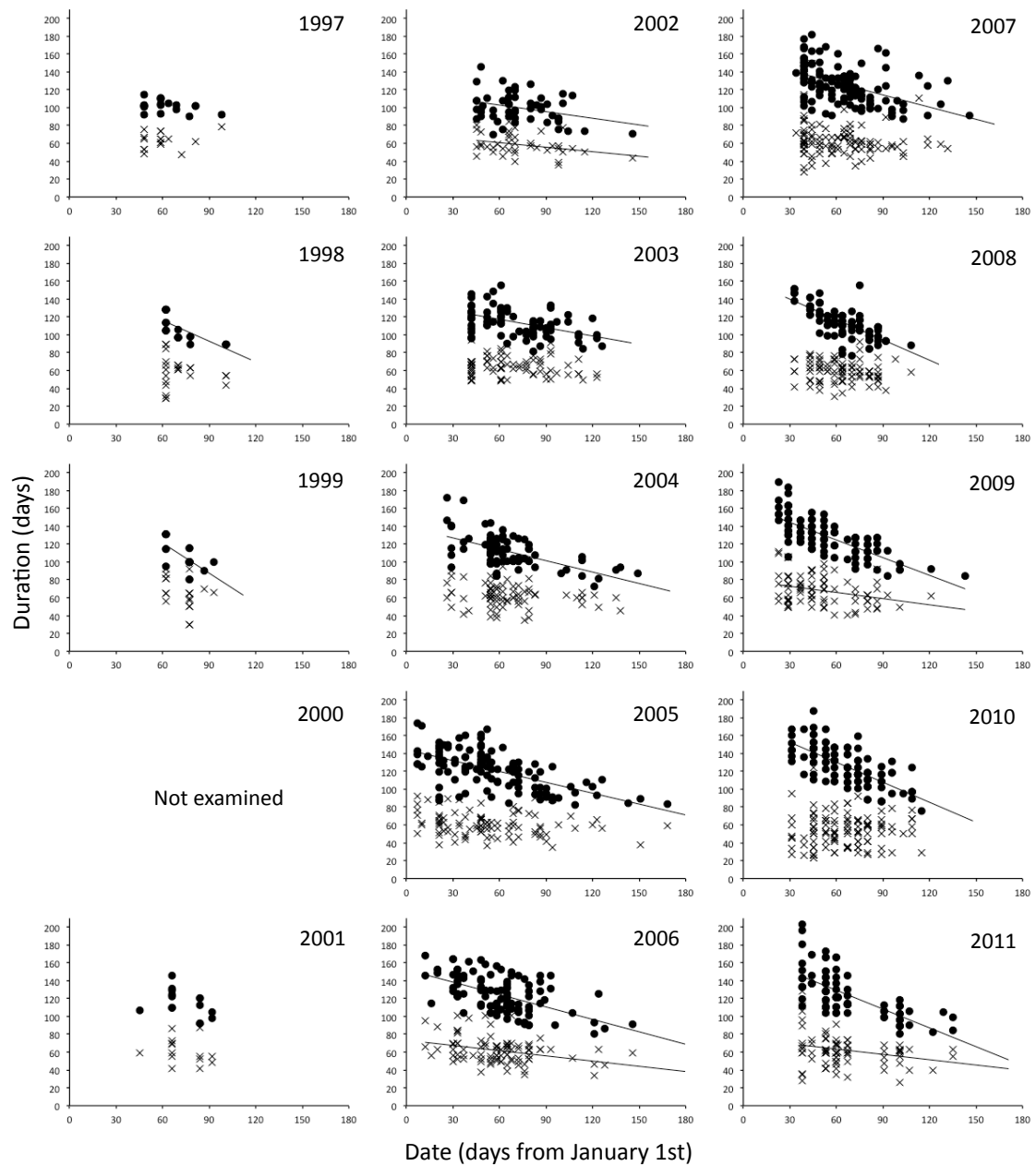
Colony	Year	Breeding duration			Nursing duration			No. of fledglings		
		<i>r</i>	<i>N</i>	<i>P</i>	<i>r</i>	<i>N</i>	<i>P</i>	<i>r</i>	<i>N</i>	<i>P</i>
Renkoji	1996									
Renkoji	1997	-0.376	19	NS	0.285	16	NS	-0.495	30	**
Renkoji	1998	-0.751	24	***	-0.135	24	NS	-0.048	30	NS
Renkoji	1999	-0.647	20	**	-0.350	19	NS	-0.013	37	NS
Renkoji	2000									
Tama Zoo	2000									
Tama Zoo	2001	-0.422	15	NS	-0.233	14	NS	-0.591	19	**
Tama Zoo	2002	-0.329	54	*	-0.323	40	*	-0.327	78	**
Tama Zoo	2003	-0.475	79	***	-0.121	74	NS	-0.233	100	*
Tama Zoo	2004	-0.589	78	***	-0.213	76	NS	-0.218	117	*
Tama Zoo	2005	-0.614	111	***	-0.203	94	NS	-0.178	150	*
Tama Zoo	2006	-0.548	102	***	-0.342	89	**	-0.287	180	**
Tama Zoo	2007	-0.500	125	***	-0.118	106	NS	-0.311	170	***
Tama Zoo	2008	-0.743	101	***	-0.136	95	NS	-0.252	143	**
Tama Zoo	2009	-0.751	105	***	-0.311	84	**	-0.267	137	**
Tama Zoo	2010	-0.709	117	***	0.032	110	NS	-0.110	150	NS
Tama Zoo	2011	-0.702	93	***	-0.255	87	*	-0.307	120	*



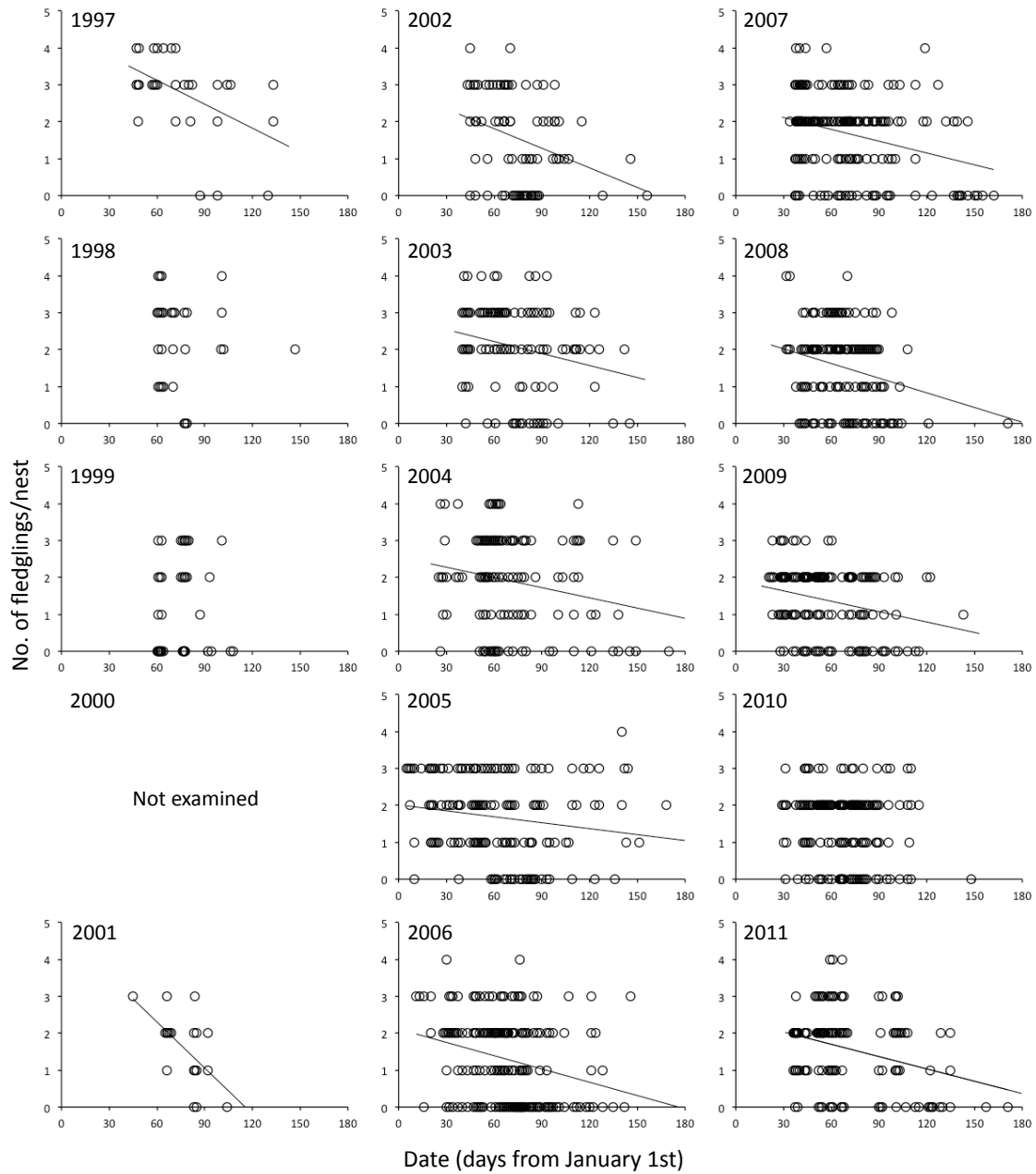
**Fig. 3-1.** Yearly changes in the number of nests in the Renkoji, Tama Zoological Park, and Ozenji colonies. In 2000, the Renkoji site was abandoned, and a new colony was established at the Tama Zoological Park close to Renkoji.



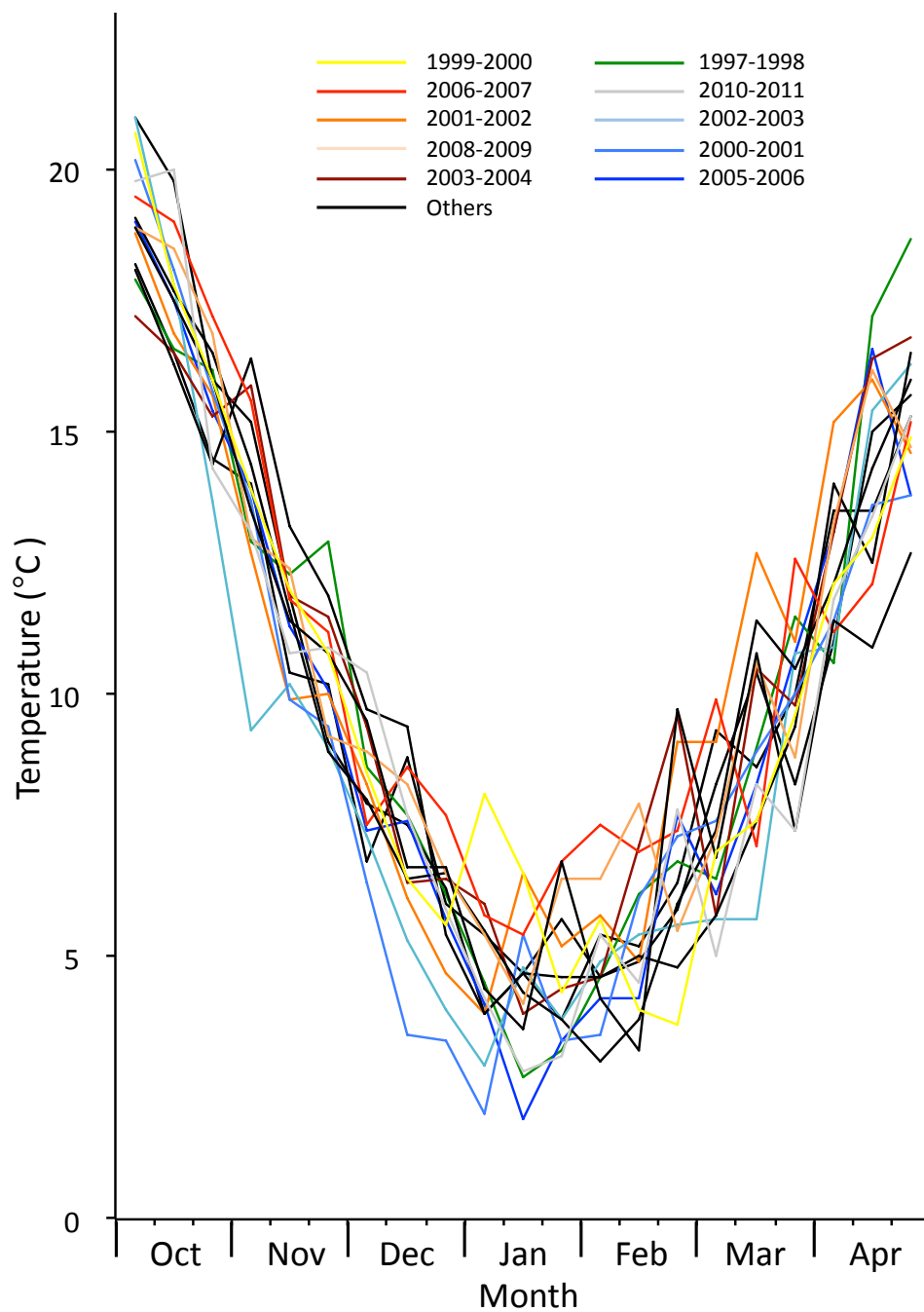
**Fig. 3-2.** Relationships between colony size and (a) breeding duration, (b) nursing duration, (c) proportion of successfully fledged nests, (d) number of fledglings per successful nest, (e) date of the first breeding in the colony, and (f) coefficient of variation in the date of the onset of breeding by individuals. Bars indicate  $\pm$  SD.



**Fig. 3-3.** Breeding (•) or nursing (x) durations of each pair of Grey Herons in relation to the date of the beginning of breeding in each year. Regression lines are shown when the correlation coefficients are statistically significant (see Table 3-2).



**Fig. 3-4.** Number of fledglings per nest in relation to the date of the beginning of breeding in each nest. Regression lines are shown when the correlation coefficients are statistically significant (see Table 3-2).



**Fig. 3-5.** Mean air temperatures in the early, mid, and late periods of each month from 1996 to 2011. The temperatures were recorded by the automated meteorological data acquisition system (Japan Meteorological Agency) at Fuchu, Tokyo, locating 8.4 km northeast from Tama Zoological Park. Reddish and bluish lines indicate warmer and colder winters, respectively.

## **4. Nest site selection and breeding success**

### **4-1. Introduction**

Hérons and egrets are colonial breeders, often hundreds or thousands of birds gather in the colony (Kushlan and Hancock 2005). However, they do not occupy all their nesting habitat, and some colony-sites seems lie vacant (Jenni 1969; McCrimmon 1978; van Vesseem and Draulans 1986b; Gibbs et al. 1987). Because there appear to be large amounts of similar, unused habitats around the colony, social factors are more important in colony formation than environmental factors (Krebs 1974). Adaptive significance of colonial breeding in birds has been discussed from the information center hypothesis (e.g. Ward and Zahavi 1973; Krebs 1974), the mate attraction and finding hypothesis (e.g. Simpson et al. 1987; Draulans 1988), and the antipredator hypothesis (e.g. Patterson 1965).

The information center hypothesis predicts that neighbors within a colony benefit from the opportunity to follow each other to suitable feeding sites. However, it is still resolved well that colonial breeding facilitates the finding of unpredictable food items in the field. This hypothesis also predicts that colonially breeding birds feed in some groups. In daily flight activity, the first-year Grey Herons tended to leave the heronry shortly after another bird more frequently than the adults did (van Vesseem and Draulans 1987a). Synchronization of activity may facilitate the finding of foraging areas, even if not following successful birds, as increasing the probability to reach good hunting sites (van Vesseem and Draulans 1987a). However, in most cases of heron and egret feeding, they do solitarily (Hancock and Kushlan 1984). The mate attraction and finding hypothesis predicts that finding a new mate or relocating a previous mate may be facilitated. Most herons chose new nest sites and new mates each year. The colony may therefore serve as an assembly site for mate finding (Simpson et al. 1987). In the antipredator hypothesis, possible advantages include early warning, mobbing, and predator swamping via breeding colonially and synchrony (Rodgers 1987a). However, colonial breeding incurs a disadvantage in predation risks via auditory (calls of adults and young), olfactory (birds themselves, guano, and dropped food items), and visual (large, often light colored species flying in and out of the site) cues to predators (Rodgers 1987a). Thus, it has been questioned in some cases whether colonial breeding



by herons and egrets reduces the risk of predation (Krebs 1978; van Vesseem and Draulans 1986b).

Within the same colony, herons and egrets do not nest randomly. Vertical and horizontal separation in nest sites usually occurs (Jenni 1969; Kurata and Higuchi 1972; Maxwell and Kale 1977; Burger 1978b; McCrimmon 1978; Fasola and Alieri 1992; Ando 1993; Kazantzidis et al. 1997; Thomas and Hafner 2000; Hilaluddin et al. 2003; Dami et al. 2006; Bertolino and Gola 2008; Si Bachir et al. 2008; Kim and Koo 2009a, b; Nedjah et al. 2010; Park et al. 2011). Here, the antipredator hypothesis to maintain the colonial breeding in the narrow area predicts the difference in breeding success according to the spatial distribution of nests within the same colony; lower breeding success for periphery (or satellite) nesters than central ones (Minias et al. 2012). However, only three studies examined this hypothesis in herons and egrets. Two studies obtained the negative results; pairs nesting in the center of the colony did not fledge more chicks than pairs nesting at the edge in Grey Herons (*Ardea cinerea*) (van Vesseem and Draulans 1986b) and in Great Egrets (*Ardea alba*), Intermediate Egrets (*Ardea intermedia*), Little Egrets (*Egretta garzetta*), and Cattle Egrets (*Ardea ibis*) (Baxter 1994), and the other study obtained some positive effects on Great Blue Herons (*Ardea herodias*) (Simpson et al. 1987).

In this study, first, nest site selection by Grey Herons was studied in the single-species heronry located in suburban Tokyo. All nested trees and un-nested trees standing in the colony area were compared in species, diameter, and height. Second, the effect of spatial distribution of nests on breeding success was examined. For this, the number of chicks fledged was recorded by intensive census of all breeding nests in this colony.

#### **4-2. Materials and methods**

The breeding colony in Tama Zoological Park in suburban Tokyo (35°38'N, 139°24'E) has been studied from the next year of its establishment in 2000. In this zoo, several natural woods and water sites are included and wild Grey Herons used them freely. This colony was a single-species heronry, although included at least 13 nests of Black-crowned Night Herons (*Nycticorax nycticorax*) just on establishment (Sugita 2001). In the breeding season (January to September) in 2002, nests were searched in

the colony and mapped for nest identification. When bred, I recorded the parent behaviors (standing, nest building, incubating, or guarding) and the number and body size (small, medium, or large) of chicks, using a binocular ( $\times 10$ ) and/or a spotting scope ( $\times 20-60$ , TSN-1, Kowa Co. Ltd., Japan). Census intervals in the colony were 3-4 days. From these observations, the number of chicks fledged could be estimated for most nests in the colony.

After ending the breeding season in 2002, all trees of more than 50 mm in the diameter at the breast height (DBH) were numbered and identified to species in the area covering the colony, 180 m  $\times$  230 m (Fig. 4-1A). Tree height from the ground was also recorded. All trees were plotted on the map in 1/500 scale, from which the altitude of the ground of each tree was measured. The lowest altitude was 132 m in the studied area. Thus, the relative height of each tree was calculated as (tree height + altitude at the ground of each tree) – 132. The nest height was measured from the ground to the nest, but it was impossible in 5 of 71 nests. At this time, the height and DBH of each nested tree were also measured and the nest height/tree height ratio (%) was calculated. In analyses, first, the characteristics of the nested trees were compared with un-nested trees. Next, the effects of vertical and horizontal distribution of nests on the breeding success were examined. Because the breeding data were taken every year after 2002 by census at 3-4 days intervals until 2008 and 7 days intervals in 2009-2011, it was possible to examine the relationships between the horizontal distribution of nests and the breeding success in these 10 years. The nest site was presented as the distance from the center of the colony area (115 m north and 90 m east in Fig. 4-1).

### **4-3. Results**

#### **4-3-1. Nest site characteristics**

Grey Herons nested on 36 of 967 trees in the colony (Table 4-1). Nests were found mainly on *Prunus jamasakura* (including a few unidentified *Prunus*) and *Quercus serrata*. The mean number of nests per tree was 3.1 (N=14, SD=2.6) in *P. jamasakura*, 1.3 (N=18, SD=0.5) in *Q. serrata*, and 1 in other 3 tree species (for all trees, 2.0 nests/tree, N=36, SD=1.9). Nested trees were distributed on ridges of the hill despite being different tree species (Fig. 4-1).

Grey Herons nested on the trees of more than 162 mm in DBH (Fig. 4-2A). Among these trees (>162 mm DBH), the tree height from the ground did not differ between un-nested and nested trees (Fig. 4-2B; Mann-Whitney U-test,  $z=1.07$ ,  $N_1=718$ ,  $N_2=36$ ,  $P=0.25$ ), but the relative tree height from the lowest altitude 132 m in the colony area differed between the un-nested and nested trees (Fig. 4-2C;  $z=5.50$ ,  $N_1=718$ ,  $N_2=36$ ,  $P<0.0001$ ). These results coincided with the tendency that the nested trees were distributed on ridges of the hill (Fig. 4-1). The nest height from the ground ranged from 7.8 to 22.2 m, with the mean of 12.7 m ( $N=66$ ,  $SD=3.1$ ). The nests were located from 42.7 to 100% of tree height, with the mean of 83.1% ( $N=66$ ,  $SD=14.0$ ).

#### **4-3-2. Breeding success at each nest**

The number of chicks fledged was confirmed in 57 nests. The mean number of fledglings was 1.68 ( $N=57$ ,  $SD=1.20$ ) per attempted nests, of which 75.4% was successful to fledge with the mean of 2.23 fledglings/nest ( $N=43$ ,  $SD=0.81$ ). There was no statistically significant effect of tree diameter at the breast height (Fig. 3A;  $r=0.01$ ,  $d.f.=55$ ,  $P>0.05$ ), relative nest height from the lowest altitude in the colony site (Fig. 4-3B;  $r=-0.04$ ,  $d.f.=55$ ,  $P>0.05$ ), and nest height on the breeding success (Fig. 4-3C;  $r=-0.151$ ,  $d.f.=55$ ,  $P>0.05$ ).

The periphery/center effect of nest sites on breeding success was examined for the data after 2002. The nests in the colony gradually increased after 2002, and reached maximum in 2007. After that the number of nests per colony was kept around 180. The mean number of fledglings per attempted nest was 1.98 ( $N=86$ ,  $SD=1.25$ ) in 2003, 1.82 ( $N=111$ ,  $SD=1.29$ ) in 2004, 1.66 ( $N=152$ ,  $SD=1.09$ ) in 2005, 1.24 ( $N=173$ ,  $SD=1.13$ ) in 2006, 1.66 ( $N=161$ ,  $SD=1.08$ ) in 2007, 1.45 ( $N=132$ ,  $SD=1.09$ ) in 2008, 1.42 ( $N=130$ ,  $SD=0.89$ ) in 2009, 1.51 ( $N=128$ ,  $SD=0.95$ ) in 2010, and 1.54 ( $N=125$ ,  $SD=1.06$ ) in 2011. The successful nests in fledging were 80.2%, 77.5%, 81.6%, 62.4%, 79.5%, 73.5%, 79.2%, 79.7%, and 78.4%, and the chicks fledged per successful nest were 2.46 ( $N=69$ ,  $SD=0.85$ ), 2.35 ( $N=86$ ,  $SD=0.94$ ), 2.03 ( $N=124$ ,  $SD=0.84$ ), 1.98 ( $N=108$ ,  $SD=0.75$ ), 2.09 ( $N=128$ ,  $SD=0.75$ ), 1.98 ( $N=97$ ,  $SD=0.76$ ), 1.79 ( $N=103$ ,  $SD=0.57$ ), 1.89 ( $N=102$ ,  $SD=0.63$ ), and 1.97 ( $N=98$ ,  $SD=0.77$ ), respectively. Peripheral nests placed on more than 100 m from the center of the colony increased after 2002 to 2006 (Fig. 4-4). However, there was no significant correlation between nest location (distance

from the center of the colony) and breeding success (number of chicks fledged per attempted nest) (Fig. 4-4;  $r=-0.224$  to  $0.185$ ,  $P>0.05$  in any year).

#### 4-4. Discussion

Within the same colony, herons and egrets do not nest randomly (Table 4-2). In the mixed-species heronries, vertical and horizontal separation in nest sites occurs; usually larger species nests are higher in the vegetation than smaller species (Jenni 1969; Kurata and Higuchi 1972; Maxwell and Kale 1977; Burger 1978b; McCrimmon 1978; Fasola and Alieri 1992; Ando 1993; Kazantzidis et al. 1997; Kim and Koo 2009a; Park et al. 2011). In addition to species-specific preference, intra- and inter-specific competition for nest sites may act on such a stratification of nest sites (Burger 1978b). Intra-specific interaction for nest sites is detected in the single-species colony. Si Bachir et al. (2008) reported that the first pairs of Cattle Egrets showed a preference for the more protected positions (on the highest trees, with the highest position, and nearest to the trunk) and fledged the highest number of chicks because of protecting against a strong wind, although this may be associated with a concomitant decline in quality of individuals. Inter-specific competition in the mixed-species heronry is suggested by the fact that nests of Black-crowned Night Herons are found on tall trees when no other species exist in the colony, but on understory when Grey Herons coexist (Bertolino and Gola 2008). Increased number of Grey Herons nesting in reeds had a significant negative impact on the breeding population of Purple Herons (*Ardea purpurea*) using also reeds as nest sites (Thomas and Hafner 2000). Thus, Grey Herons alter nest sites of Black-crowned Night Herons and Purple Herons. Aggressive species may exclude other species from the suitable nest sites in herons and egrets (Burger 1978b; Dami et al. 2006). In southern France, nest displacements of Little Egrets by Cattle Egrets usually occurred following aggressive interactions between the two species and therefore Little Egrets are rarely found at the sections with high Cattle Egret density, which are usually formed at the central part of colonies (Dami et al. 2006). Similar interference is also suggested in Cattle Egrets/Little Egrets colonies in India (Hilaluddin et al. 2003). Thus, nest site displacement of Little Egrets by more aggressive Cattle Egrets causes negative association between the nest success of Little Egrets and the proportion of Cattle Egrets in a given colony (Bennetts et al. 2000). On the other hand, interspecific separation is

not confirmed in Atlantic Coast heronries including 2-6 species where vegetation height chiefly limits nest height (Beaver et al. 1980). Vegetation-limited nesting height is also reported in Purple Herons at northeastern Algeria (Nedjah et al. 2010).

In the same colony (mixed-species heronries), Grey Herons (the largest species) nest on higher trees than other heron and egret species. Moreover, Grey Herons sometimes alter nest sites of other species. In the single-species colony, as shown in this study, Grey Herons nested on the tree located near the hilltop, rather than selecting the taller trees. The tree species is usually not an important factor in nest site selection by herons and egrets (e.g., Ayas 2008). In my study colony, Grey Herons tended to nest on the cherry (*Prunus jamasakura*) and oak (*Quercus serrata*) trees.

Van Vessem and Draulans (1986b) summarized the hypotheses to explain the colony formation of birds. The anti-predator hypothesis predicts that birds breeding solitarily or in small colonies should suffer more from nest predation than birds breeding in large colonies, that birds breeding at the edge of a colony should suffer higher losses than birds breeding in the center, and that synchronization of breeding reduces the risk of predation. The food finding hypothesis, on the other hand, predicts that increasing colony size, and increasing degree of breeding synchronization improve the probability of discovering suitable foraging areas, and, consequently, chick survival of individual pairs. Draulans (1988) emphasized that the mate attraction and finding is another function of colonial breeding.

Among these hypotheses, I tested different breeding success according to the spatial distribution of nests within the same colony; lower breeding success for periphery (or satellite) nesters than central ones (Minias et al. 2012). Nest survival is related to nesting sites in the colony in herons (Post 1990). Simpson et al. (1987) showed some advantage in nesting at the central part of the Great Blue Heron colony because the mean distance from the center of the colony differed between the nests failed by predation (farther from the center) and those succeeded in fledging (closer to the center). However, pairs nesting in the center of the colony did not fledge more chicks than pairs nesting at the edge in Grey Herons (van Vessem and Draulans 1986b). Baxter (1994) found no evidence to suggest that nesting in trees distant from the colony edge had any effect on mean fledging success of Great Egrets, Intermediate Egrets, Little Egrets, and Cattle Egrets in their mixed colony. Nesting in the center of the colony may not give any extra protection from avian predators, which may swoop down from above nest

trees (Baxter 1988). Grey Herons in my study also showed no conspicuous difference in the breeding success according to the nest location in the colony. Nests in heronries are not easily accessible by ground predators when formed on tall trees and where predation does not occur always from the periphery of the colony as in the case of the colonies established on the ground. Therefore, the periphery/center effect in predation risk is weakened in canopy-breeding colonial birds.

Colonial breeding incurs a disadvantage in predation risks is the colony is highly obvious via auditory (calls of adults and young), olfactory (birds themselves, guano, and dropped food items), and visual (large, often light colored species flying in and out of the site) cues to predators (Rodgers 1987a). Intensive predation once noticed by the predators is observed in the breeding colonies (Rodgers 1987a). Thus, it has been questioned in some cases whether colonial breeding by herons and egrets reduces the risk of predation. In the future, to know the reason why Grey Herons gather in the colony to breed, we must examine other colony functions, mate attraction and finding or information center to search efficient hunting sites.

Table 4-1. Trees available in the colony area and those nested by Grey Herons.

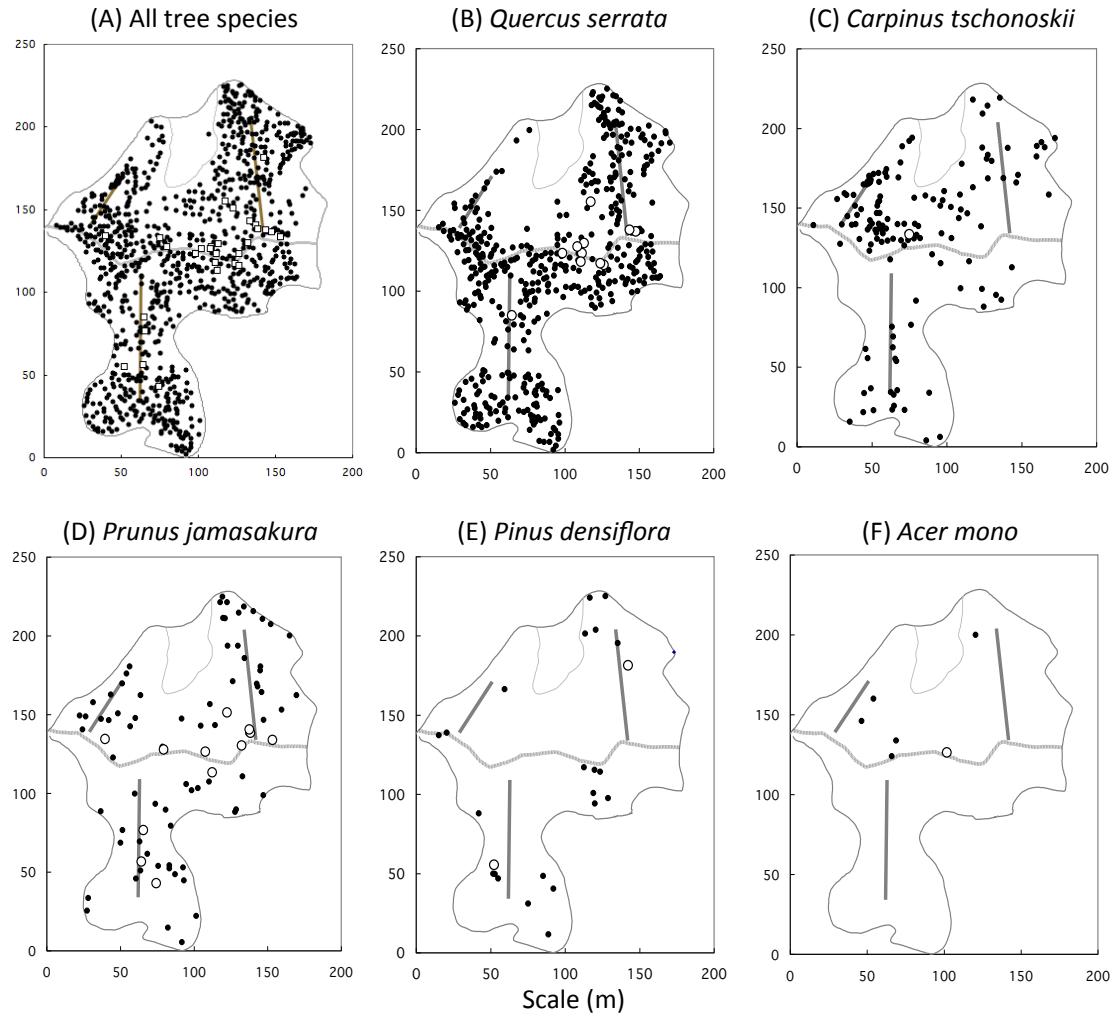
Tree species	Available	Nested	No. of nests
<i>Quercus serrata</i>	516	18	23
<i>Carpinus tschonoskii</i> <sup>a</sup>	152	1	1
<i>Prunus jamasakura</i> <sup>b</sup>	102	14	44
<i>Styrax japonica</i>	43		
<i>Styrax obassia</i>	27		
<i>Pinus densiflora</i>	26	2	2
<i>Ilex macropoda</i>	10		
<i>Ilex crenata</i>	7		
<i>Cryptomeria japonica</i>	7		
<i>Acer mono</i>	6	1	1
<i>Quercus acutissima</i>	6		
<i>Eurya japonica</i>	6		
<i>Chamaecyparis pisifera</i>	5		
<i>Quercus glauca</i>	4		
<i>Robinia pseudoacacia</i>	4		
<i>Rhus sylvestris</i>	4		
<i>Fagara ailanthoides</i>	3		
<i>Cornus brachypoda</i>	3		
<i>Lagerstroemia indica</i>	3		
<i>Albizia julibrissin</i>	3		
<i>Chamaecyparis obtusa</i>	3		
<i>Magnolia obovata</i>	3		
<i>Clethra barbinervis</i>	3		
<i>Acer palmatum</i>	2		
<i>Fraxinus sieboldiana</i>	2		
<i>Cornus controversa</i>	2		
<i>Fraxinus lanuginosa</i>	1		
<i>Mallotus japonicus</i>	1		
<i>Ulmus parvifolia</i>	1		
<i>Meliosma myriantha</i>	1		
<i>Acea crataegifolium</i>	1		
<i>Juglans ailanthifolia</i>	1		
<i>Diospyros kaki</i>	1		
<i>Carpinus japonica</i>	1		
<i>Castanea crenata</i>	1		
<i>Alnus hirsuta</i>	1		
<i>Magnolia kobus</i>	1		
<i>Castanopsis cuspidata</i>	1		
<i>Rhus javanica</i>	1		
<i>Alnus borealis</i>	1		
<i>Celtis sinensis</i>	1		
Total	967	36	71

a, including 9 *C. laxiflora*b, including 22 unidentified *Prunus*

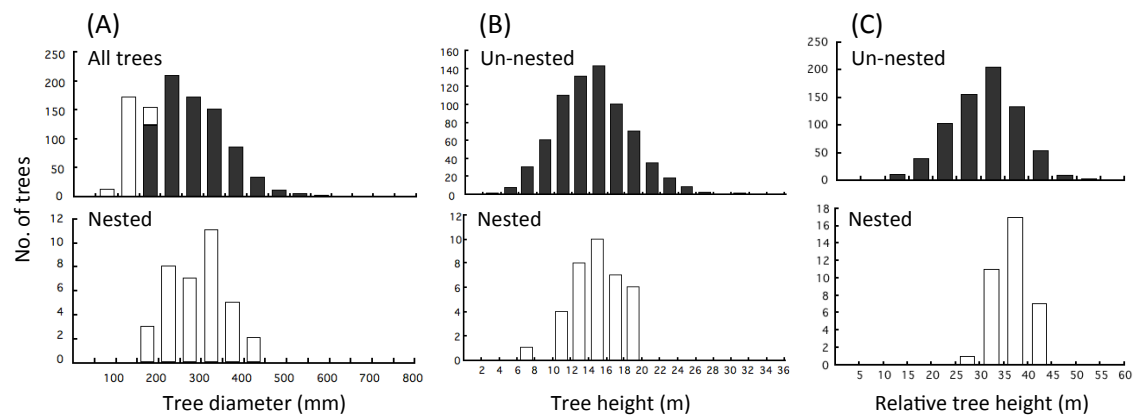
Table 4-2. Nest site selection by herons and egrets.

Heronry	Species examined	Site	Methods	References	Selectivity/trend	Factors affecting nest site selection
3 species/c olony (1 colony)	Black-crowned Night Heron	northwestern Italy	16 years comparison of nest height in the same colony	Bertolino & Gola 2008	Nests are seen on tall black locusts when no other species exist in the colony but on understory hawthorn and black elderberry when Little Egrets and Grey Herons increased in the colony, particularly Grey Herons. Grey Herons (14.6 m), Black-crowned Night Herons (5.0 m).	Interspecific interaction in mixed-species heronry (by Grey Herons)
5 species/c olony (36 colonies)	all species	Italy	nest height comparison among colonies with different species combinations	Fasola & Alieri 1992	Vertical alignment of species; Grey Herons at the highest levels, Black-crowned Night Herons, Little Egrets, and Squacco Herons at the intermediate levels, and Purple Herons at the lowest levels.	Species specific preference
6 species/c olony (1 colony)	all species	western Japan	nest height and tree species	Ando 1993	Nest height; Grey Herons (9.4 m) and Great Egrets (9.5 m) highest, Black-crowned Night Herons (8.7 m) intermediate, Little Egrets (6.0 m), Cattle Egrets (7.5 m) and Intermediate Egrets (7.6 m) lower. In tall alder woods, Night Herons and Little Egrets responded to the presence of Grey Herons by nesting at a lower height than when they were the only two species in the colonies.	Species specific but similar preference
3 species/c olony (1 colony)	all species	northwestern Korea	nest height and the distance from the trunk	Kim & Koo 2009a	Grey Herons (8.4 m) and Black-crowned Night Herons (8.5 m) nested higher than Little Egrets (6.4 m). Black-crowned Night Herons nested more distant from the tree trunk than the others.	Species specific but similar preference
3 species/c olony (1 colony)	Grey Heron	northwestern Korea	comparison among trees with single or other herons' nests	Kim & Koo 2009b	No difference in nest height (8.4-8.7 m) and the distance from the tree trunk despite coexisting with other species.	No interspecific interaction (to Grey Herons)
6 species/c olony (1 colony)	all species	Korea	nest height comparison	Park et al. 2011	Vertical stratification.	Species specific preference
2 species/c olony (2 colonies)	Little Egret	southern France	behavioral observation and comparison among sections within the colony	Dami et al. 2006	Cattle Egrets displace the Little Egret nest sites and Cattle Egrets occupy the central part of colony while Little Egrets use the peripheral part of colony as nesting.	Interspecific interaction in mixed-species heronry (by Cattle Egrets)
3 species/c olony (1 colony)	all species	Turkey	tree species selection	Ayas 2008	No selection of tree species to nest in willow and poplar forest by Black-crowned Night Herons, Grey Herons, and Little Egrets	Not selected by tree species in the same colony
2 species/c olony (1 colony)	all species	Greece	nest height comparison	Kazantzidis et al. 1997	Black-crowned Night Herons (4.2 m) nest higher than Little Egrets (3.5 m).	Species specific preference?
single species/c olony (6 colonies)	Purple Heron	northeastern Algeria	nest height comparison among colonies with different vegetations	Nedjah et al. 2010	Nests are higher in willow colonies (1.0 m) than reed or lesser reed-mace colonies (0 m).	Nest site selection limited by vegetation (available tree species)
single species/c olony (1 colony)	Cattle Egret	Algeria	temporal pattern of nesting within a breeding season	Si Bachir et al. 2008	First arriving bird (14 m) nests at the highest trees close to the tree trunk, but later birds (7 m) nest lower and away from the tree trunk. Breeding success is higher in birds nesting higher and closer to the tree trunk.	Intraspecific interaction. Correlation between nest site and breeding success
2-6 species/c olony (6 colonies)	all species	Atlantic Coast in northeastern USA	comparison of nest position among 5 mixed-species colonies	Beaver et al. 1980	Variation in nest sites between colonies are greater than between species. Snowy Egrets (0.1-2.2 m), Louisiana Herons (0.1-1.0 m), Little Blue Herons (1.5 m), Black-crowned Night Herons (1.3-2.6 m), Great Egrets (1.7 m).	Colony vegetation affects nest site selection.
4 species/c olony (1 colony)	Grey Heron and Black-crowned Night Heron	western Japan	nest height	Kurata & Higuchi 1972	Grey Herons nested higher (mostly >7 m, max 13 m) than Black-crowned Night Herons (2-6 m). Tree species are not selected.	Species specific preference
4 species/c olony (1 colony)	all species	Australia	nest position from the edge of colony and fledging success	Baxter 1994	Nesting in trees distant from the colony edge had no effect on fledging success.	No advantage in the central part of colony
2 species/c olony (26 reed areas)	Purple Heron	southern France	nesting on trees or reedbeds	Thomas & Hafner 2000	Previously Grey Herons nested on trees (2 m) but recently most Grey Herons nested on reedbeds (0 m), and probably due to this nest site change Purple Herons decreased in population. Brood size was slightly higher when bred on reeds than trees.	Interspecific interaction in mixed-species heronry (by Grey Herons)
2 species/c olony (1 colony)	Little Egret	India	breeding timing and nest height	Hilaluddin et al. 2003	Cattle Egrets (early breeder) used higher trees (upper part of 10.7 m) for nesting than Little Egrets (late breeder) (upper part of 8.3 m). Tree species Ficus spp. were preferred.	Interspecific interaction in mixed-species heronry (by Cattle Egrets)?
		Florida in USA		Jenni 1969	Differences in vertical and horizontal placement of nests	
5 species/c olony (1 colony)	all species	Florida in USA	nest height and distance from the shoreline	Maxwell & Kale 1977	Differences in vertical and horizontal placement of nests. Louisiana Herons (2.2 m), Snowy Egrets (2.3 m), Cattle Egrets (2.2 m), Little Blue Herons (2.6 m), Great Egrets (2.8 m)	Species specific preference
		Atrantic Coast in northeastern USA		Burger 1978	Differences in vertical and horizontal placement of nests	Larger species nest higher than subordinate smaller species
5 species/c olony (1 colony)	all species	North Carolina in USA	height and other characteristics of each species nests in the colony	McCrimmon 1978	A fine vertical and horizontal separation in a colony. Great Egrets (4.4 m), Snowy Egrets (2.3 m), Cattle Egrets (2.3 m), Little Blue Herons (2.3 m), Louisiana Herons (2.0 m).	Species specific preference
single species/c olony (13 colonies)	Grey Heron	Northern Belgium	comparisons of breeding success and age of birds between edge and center of the colony	van Vessem & Draulans 1986	Pairs nesting in the center of the colony do not fledge more chicks than pairs nesting at the edge. The first-year breeding birds tend to occupy nests at the edge of a colony, but their proportion in the breeding population probably is too small to affect the results.	No advantage in the central part of colony
single? species/c olony (17 colonies)	Great Blue Heron	Ohio in USA		Carlson 1995	The tallest trees are used as nest-sites in any case.	No effect of trees (dead or live)
	Great Blue Heron	British Columbia in Canada	nest location from the colony center and chicks fledged or failed	Simpson et al. 1987	Nests that failed because of predation were nearer to the edge of the colony in 1978, but not in 1979.	Some advantage in the central part of colony

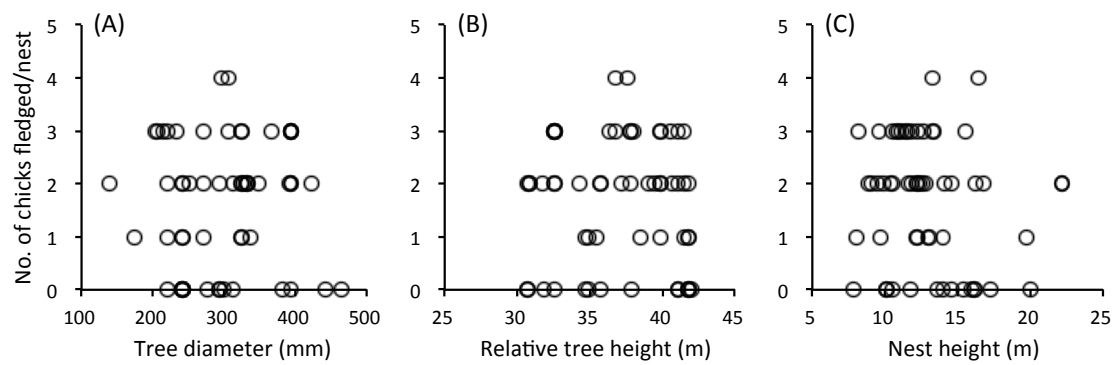




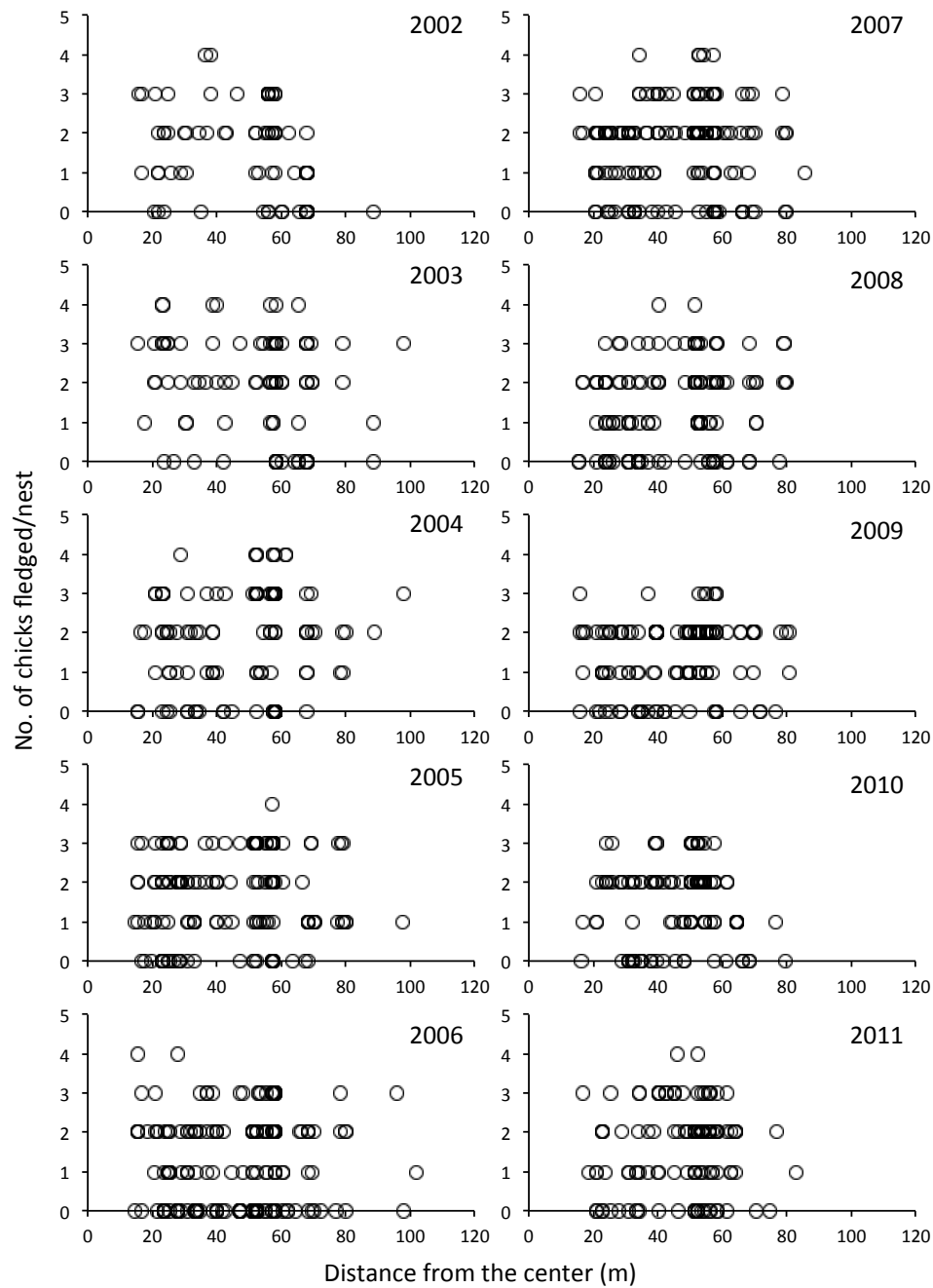
**Fig. 4-1.** Un-nested (dots) and nested (open squares or circles) trees by Grey Herons within the study colony area (surrounded with a fine line). (A) all tree species, (B) *Quercus serrata*, (C) *Carpinus tschonoskii* and *C. laxiflora*, (D) *Prunus jamasakura* and *P. spp.*, (E) *Pinus densiflora*, (F) *Acer mono*. Thick lines indicate the ridges of the hill. All trees with more than 50 mm in diameter at the breast height.



**Fig. 4-2.** Tree size distributions. (A) Tree diameter at the breast height (DBH) of all trees available (upper) and those nested by Grey Herons (lower) in the study colony. In the upper graph, trees less than 162 mm (the minimum diameter of nested trees) in DBH are shown in open bars. (B) Tree height from the ground of un-nested (upper) and nested (lower) trees more than 162 mm in DBH. (C) Relative tree height from the lowest altitude (132 m) in the colony area (i.e. tree height + altitude at the ground of each tree - 132) of un-nested and nested trees with more than 162 mm in DBH.



**Fig. 4-3.** Relationships between the nest site characteristics and the number of chicks fledged in Grey Herons. A, nested tree diameter at the breast height; B, nest height from the ground; C, relative nest site from the lowest altitude (132 m) of the colony area (i.e. nest height + altitude at the ground of each nested tree – 132).



**Fig. 4-4.** Relationships between the nest position in the colony and the number of chicks fledged in Grey Herons in 2002 to 2011. The nest position in the colony is presented as the distance from the center of the colony area (115 m north and 90 m east in Fig. 4-1).

## **5. Fidelity to the breeding colony and the long-term reproductive history**

### **5-1. Introduction**

Hérons and egrets are relatively large birds and have some peculiar life history features: they breed in colonies but usually feed solitarily, they migrate to a wide range of areas, and they usually live long (Kushlan and Hancock 2005). This life history involves seasonal migration between breeding sites and non-breeding wintering sites. The tendency to revisit the same breeding colony, and to use the same nests in the breeding season and the same foraging sites in the non-breeding season, is called site fidelity and has been documented in many birds and other animal species (Newton 2007). High site fidelity may be advantageous for migratory, long-lived birds if their breeding and foraging habitats are stable (Hamerstrom et al. 1973; Forsman et al. 2002). For example, past breeding experience increases the chance of breeding in the future, and familiarity with the environment allows birds to forage more efficiently (Newton and Marquiss 1982; Hoover 2003; Mittelhauser et al. 2012). However, these behavioral features are not useful in unpredictable environments. High fidelity also involves the costs of ectoparasitism (Møller 1989; Stanback and Rockwell 2003) or nest predation (Sonerud 1985; Hakkarainen et al. 2001). In addition to site fidelity, mate fidelity occurs in some bird species, where they tend to breed with the same mate in the breeding colony. Mate fidelity has the benefit of reducing the time spent in searching for a mate but has the cost of having to wait for a previous mate that might have died, particularly in situations with high annual mortality (Steenhof and Peterson 2009).

Site fidelity in herons and egrets has been reported to be weak in the case of movements from natal colonies to breeding colonies (e.g., Melvin et al. 1999), but has not been examined in other situations, such as the reuse of the same breeding colony, nest, and mate. This is because of the difficulty of continuously tracking individuals. To confirm fidelity, behavioral data on individually marked birds are needed. Individual discrimination of wild herons and egrets has been accomplished based on body color patterns and by artificially marking birds with dye of different colors for short-term observations of behavior, particularly in breeding nests (Fujioka and Yamagishi 1981; Fujioka 1989; Ramo 1993; Wei et al. 2005). To document survival and migration,

researchers have used banding (ringing) (Rydzewski 1956; Kahl 1963; Mead et al. 1979; Lekuona and Campos 1996; Melvin et al. 1999; Thomas et al. 1999; Campos et al. 2001; Fasola et al. 2002), radio-tracking (van Vesseem et al. 1984; Draulans and Vesseem 1985; van Vesseem and Draulans 1987b; Erwin et al. 1996), and satellite-tracking (Jourdain et al. 2008; van der Winden et al. 2010). However, traditional methods of banding using a small ring and tagging for radio- or satellite-tracking are not suitable for observing the breeding and foraging behavior of individual birds in the field. However, larger rings may be suitable for detailed and long-term observation of individual birds (Fernández-Cruz and Campos 1993).

Grey Herons (*Ardea cinerea* L.) live for 11–18 years (Lack 1949; Verheyen and LeGrelle 1952; Olsson 1958; North 1979; North and Morgan 1979), and their colonies are usually maintained over long periods of time (e.g., Marquiss 1989; Fernández-Cruz and Campos 1993), suggesting that site fidelity would be beneficial in this species. Mortality of adult Grey Herons is rather low at 28–30% per year (Olsson 1958; Mead et al. 1979), which allows for high mate fidelity. In this study, 69 banded Grey Herons were observed intensively for 9 years in a single-species heronry in suburban Tokyo. I estimated the degree of fidelity to the breeding colony, the nesting site in the colony, and the feeding site in the non-breeding period, and also examined mate fidelity by tracking individual long-term breeding histories in the colony.

## **5-2. Materials and methods**

Grey Herons were captured and marked in the colony at Tama Zoological Park in western Tokyo, Japan (35°38'N, 139°24'E), from July 2003 to August 2006. In this zoo (maximum altitude, 171 m), there are several woodlands and wild Grey Herons established a colony in 2000. The colony (usually 300 m in the major axis, 200 m in the minor axis) was in a small area of woodland consisting of *Quercus acutissima*, *Q. serrata*, *Carpinus tschonoskii*, *Prunus jamasakura*, and *Pinus densiflora*. The colony was a single-species heronry consisting of 111–218 nests during the study period (Chapter 3). Herons often foraged at the water sites in the roofless cages of zoo animals. Therefore, herons were captured with a large cage trap (2.0 m high, 6.5 m wide, 4.0 m long) set on the shores of a pond used for captive Red-crowned Cranes (*Grus japonensis*) and Oriental Storks (*Ciconia boyciana*). Smelts (*Hypomesus nipponensis*)

and loaches (*Misgurnus anguillicaudatus*) were used as bait. When a heron was observed entering a trap, the entrance of the trap was shut using a handle near the trap, and captured herons were immediately banded with a ring placed on the tibia (15 mm internal diameter, 25 mm length, 2.5 g weight). The ring was made of double plastic plates and each had a different combination of colors (Gravoply, Gravograph Co. Ltd., France). They were numbered by shaving the surface plate of the ring: black numerals on yellow (y) rings, white numerals on green (g) rings, and white numerals on red (r) rings. Permission to capture herons was received from the Bureau for the Environment of the Tokyo Metropolitan Government.

Marked herons were monitored in the colony from January 2004 to September 2012. When marked herons were located, their leg rings were observed using binoculars ( $\times 10$ ) and/or a spotting scope ( $\times 20$ -60, TSN-1, Kowa Co. Ltd., Japan). Their behavior (standing, foraging, nest building, incubation, or guarding) and location were recorded. If the birds were breeding, the number and body size (small, medium, or large) of chicks were also recorded. All nests used were numbered and plotted on a detailed colony map. The census intervals in the colony were 3–4 days in 2004–2008 and 7 days in 2009–2012. Plumage characteristics of first-year birds allowed them to be readily distinguished from older ones (Cook 1978a), and any bird over the age of 1 year was considered an adult. Only when copulation was observed were the sexes of marked birds identified.

Additional searches for marked birds were made outside of the colony on an irregular basis, but always at least once a week during the study period. Information on the resighting of marked birds was also gathered from several Japanese birders who were aware of the marking patterns of Grey Herons in the colony.

### 5-3. Results

During the survey, 69 birds were banded, 50 fledglings and 19 adults (Table 5-1). In total, 38 (76.0%) of the 50 marked fledglings were never resighted in the natal colony (patterns F1-F3 in Table 5-1), but 12 (24.0%) returned (F4-F13 in Table 5-1). Of the 12 returned birds, 4 (33.3%) began to breed at 2-years-old, 2 (16.7%) began to breed at 3-years-old, 1 (8.3%) began to breed at 4-years-old, and 5 (41.7%) never bred although two stayed until 3 and 7-years-old in the colony (Table 5-1). Nine years after fledging,

two birds were confirmed to be resident in the natal colony. Among the adults, 18 (94.7%) of 19 marked birds were resighted in the following breeding season, and most of them (15/18) bred in the natal colony. The birds tended to stay at the same breeding colony once they had returned. Over the 9 years, the 19 marked adults decreased in number yearly as follows: 18, 17, 14, 11, 9, 8, 7, and 4 (Table 5-1).

Figure 5-1 shows the nest sites of 20 birds breeding in the colony for at least 2 years. The pattern of nest site selection varied greatly among individuals. Site fidelity to the breeding nest was observed in some birds (g5, g7, g10, and g15 in males; g4, g52, and g56 in females), but was not observed in the other birds. Most pairs were identified by only one partner and four pairs consisted of birds that were both marked (Table 5-2). Two pairs remained completely in a pair bond at least 2 successive years before one of them was lost to the colony (g15 and g2, g55 and g56), and the pair g7 and g52 remained bonded except for 1 year and the pair g5 and g12 remained bonded except for a few second broods within the same year.

In total, 23 birds bred at least once; the age of 7 (30.4%) of these was known (Table 5-2). However, there was no effect of age on the number of chicks fledged. Two broods in the same breeding season were observed in 7 (9.0%) of 78 nests in which at least one parent was marked (Table 5-2). Successful nesting was achieved in 72 (87.8%) of 82 attempts and the number of chicks fledged ranged from one to four. The mean fledgling number was 1.85 (SD=1.04,  $N=82$ ) in all nests and 2.11 (SD=0.83,  $N=72$ ) in successful nests. The male g7 reproduced the most, producing 22 fledglings over the 9 years.

Figure 5-2 shows the history of the 23 birds that were resident in the colony for more than 2 years. Of these, 4 birds (all females) continued to stay at the breeding colony site even in the non-breeding period, but 19 (8 males, 3 females, 8 unsexed) left the colony from the late- and non-breeding seasons and were observed in outside locations.

The number of sites outside the colony where marked birds were observed totaled 176 for 15 marked birds; 1 (y22), 1 (g4), 6 (g5), 8 (g6), 2 (g7), 1 (g8), 7 (g10), 8 (g12), 2 (g34), 1 (g45), 133 (g54), 1 (g55), 1 (g56), 3 (r6), and 1 (r25). The locations where these marked birds were usually resighted were sites along the Tamagawa and Asakawa Rivers, near the colony (Fig. 5-3). Each bird appeared at almost the same site every year, suggesting a strong fidelity to foraging sites. The maximum distance that a marked fledgling (r25) was resighted was 1,580 km southwest of the colony (at Kume-jima



Island, the Ryukyus, south Japan; 26°21'N, 126°49'E), 54 days after release. Two fledglings (g34 and y22) that were marked but did not return to the colony were identified at other locations. One (g34) was resighted at Tamagawa River, 9 km northwest of the colony 3 years after release and the second bird (y22) was recovered as a carcass, 28 km northeast of the colony 5 years after release (Fig. 5-3; F2 and F3 in Table 5-1, respectively).

## **5-4. Discussion**

### **5-4-1. Life history**

Mortality could not be estimated in this study because of the small sample size of marked birds. Calculated mortality is usually higher in young birds than adults for Grey Herons: 55.9% in the first year, 46.9% in the second year, and 30.3% thereafter according to Mead et al. (1979); 69% in the first year and 31% in older birds according to Lack (1949); and 67% in the first year and 28% in older birds according to Olsson (1958). Similar trends have also been recorded in Great Blue Herons (71% in the first year and 29% in older birds; Owen, 1959), Great Egrets (76% vs. 26%; Kahl 1963), and Little Egrets (44.8–93.5% vs. 28.6%; Hafner et al. 1998).

The average number of Grey Heron fledglings per successful nest was reviewed by Kim and Koo (2009b) and was found to be 3.3–3.9 in Poland, 3.6 in Germany and Spain, 3.1 in Belgium, 2.9 in England, 2.3–2.9 in France, 2.6 in France and Spain, 2.3 in Spain, 2.2 in Spain, and 2.1 in Korea. In the colony studied in the present study, fledglings per successful nest also ranged from 1 to 4 with a mean of 2.1. Fernández-Cruz and Campos (1993) marked nestlings in a colony in western Spain with a color ring placed on the tibia or tarsus and performed a census from 1974 to 1981. The results indicated that the age at first breeding was 2 years and 11.6% fledglings returned to the natal colony as 2-year-olds, 5.6% as 3-year-olds and 3.1% as 4-year-olds. They also found that 1.4% of observed pairs raised two broods per year. The results of the present study are similar to the estimations of reproductive traits by Fernández-Cruz and Campos (1993): 24.0% of marked fledglings returned to the natal colonies, of which 33.3% began to breed as 2-year-olds, 16.7% began to breed as 3-year-olds, 8.3% began to breed as 4-year-olds, and 41.7% never bred. Two broods in the same breeding season

were observed in 7 (9.0%) of 78 nests. Watts (1995) stated that the age at first breeding is a relatively constant trait in herons and egrets, with reproduction starting at two or more years. In Black-crowned Night Herons, 1-year-old birds rarely breed (Custer and Davis 1982). However, 20% of Little Egret yearlings breed (Hafner et al., 1994). Fernández-Cruz and Campos (1993) recorded the age-related breeding success of Grey Herons. Pairs of four or more years laid more eggs than a pair of 2-year-old birds. This tendency was not observed clearly in the colony studied in the present study, although the sample size was too small to test this statistically.

#### **5-4-2. Dispersal and fidelity**

There are two main kinds of dispersal (Fasola et al. 2002). Natal dispersal is movement between the natal colony and the colony of first reproduction. Breeding dispersal is movement between previous and subsequent colonies where an individual attempts to breed, regardless of whether the attempt is successful or not. In contrast, migration is usually a movement between breeding and non-breeding sites. However, discriminating between these movement patterns is usually difficult in herons and egrets. There are records of indiscriminate dispersal/migration distances of 5–518 km and 3–280 km in young and adult Black-crowned Night Herons, respectively (Gill and Mewaldt 1979), 8–135 km and 0–32 km in young and adult Great Blue Herons, respectively (Gill and Mewaldt 1979), 12–4584 km in Great Blue Herons (Melvin et al. 1999), 16–3125 km in Great Egrets (Melvin et al. 1999), usually less than 160 km but up to 960 km in Little Blue Herons (Dusi 1967), 15–4115 km in Little Blue Herons (Melvin et al. 1999), from Spain to north Africa in Purple Herons (Jourdain et al. 2008), 4000 km in Purple Herons (van der Winden et al. 2010), 16–2829 km in Snowy Egrets (Gill and Mewaldt 1979; Melvin et al. 1999), 58–2328 km in Tricolored Herons (Melvin et al., 1999), from Spain to north Africa in Little Egrets (Bartolome et al. 1996) and across Europe and often to north Africa in Grey Herons (Rydzewski 1956; Campos et al. 2001). In the colony studied in the present study, 38 of 50 Grey Heron fledglings dispersed and 3 birds were resighted at 9 km, 28 km, and 1580 km. As observed in other herons and egrets, Grey Herons in Japan can also disperse over long distances.

Although long-distance dispersal is an important feature of bird life histories, birds also display site fidelity to breeding or overwintering sites (Paradis et al. 1998;

Mitterhauser et al. 2012). Birds tend to use the same breeding site once they have dispersed from the natal site (Paradis et al. 1998). In total, 6 of the 12 returned fledglings and 18 of the 19 adult Grey Herons remained in the colony for two or more years once they had bred or spent time there (Table 5-1). In addition to this high fidelity to the same colony, about half of the birds used the same nests successively, although others did change nest sites to breed (Fig. 5-1). The sex of a bird may not affect its tendency to use the same nest for successive years.

Grey Herons breed in colonies but usually feed solitarily. There are also communal roosts in the non-breeding season, which are usually formed on the tops of trees, probably for refuge from ground predators (Draulans and van Vessem 1986). The site in Tama Zoological Park is also used infrequently as a winter roost by Grey Herons, however most birds leave at the end of the breeding season (Fig. 5-2). Foraging individuals were often resighted in autumn and winter along the Tamagawa and Asakawa Rivers, where high site fidelity was apparent; the birds used the same feeding sites year after year (Fig. 5-3). The fact that some birds remained in the zoo area after breeding may be explained by usage of artificial foods supplied for zoo animals.

Hérons and egrets have a long lifespan and breed successively, and therefore mate fidelity is also expected. Although based on a small sample size (four pairs), mate fidelity was high in the Grey Herons in the study colony. In these pairs, nest fidelity was also confirmed (see Fig. 5-1). However, the mating systems of birds vary among and within species. In addition, molecular studies of paternity assurance have revealed extra-pair paternity in systems that, on the surface, appear to be monogamous (Griffith et al. 2002). However, extra-pair copulation has been rarely reported in Grey Herons (Milstein et al. 1970) and complete monogamy (proven based on genetic analyses) was confirmed in Brazilian natural breeding colonies of Great Egrets within the well-determined families (Miño et al. 2011). Ramo (1993) reported that 39 (12.9%) of 301 copulations observed in 31 pairs of Grey Herons were extra-pair copulations in a colony in southwest Spain, which may have been caused by the high density of birds in this particular colony (10.3–22.5 nests/tree) compared to the colonies recorded in previous studies (1.1–2.4 nests/tree). Extra-pair copulation has also been observed in Great Egrets (Wiese 1976; Krebs et al. 2004), Cattle Egrets (Fujioka & Yamagishi 1981), and Chinese Egrets (Wei et al. 2005). Behavioral observations of extra-pair copulations and genetic analyses of paternity assurance are required to determine how

effective mate fidelity is to the monogamous mating system of Grey Herons.

Table 5-1. Fates of individually marked 69 Grey Herons in the Tama Zoological Park (TZP) colony.

Pattern	No. of individuals		Years after marking											
	male	female	unknown	total	0	1	2	3	4	5	6	7	8	9
F1			36	36	f									
F2			1	1	f	-	-a							
F3			1	1	f	-	-	-	-	-b				
F4			2	2	f	○								
F5			1	1	f	-	○							
F6			1	1	f	○	○	○	○	○	○	○		
F7	1		1	1	f	-	○	○						
F8	1		1	2	f	-	●							
F9			1	1	f	-	●	●	●	●	●	○	○	○
F10			1	1	f	-	●	○	●	○	○	○	●	○
F11		1		1	f	○	○	●	○	○	○	○	○	○
F12		1	1	1	f	-	-	●						
F13		1	1	1	f	-	-	-	●	●				
A1		1	1	1	○									
A2		1	1	1	○	○								
A3		1	1	1	○	○	○	○	○					
A4	1	2		3	○	●	●	●	●	○	●	●	●	
A5	1	1		2	○	●	●	●	●	○	○			
A6	1			1	○	●	●	●	●	○	○			
A7	1			1	○	●	●	●	○	○	○			
A8			1	1	○	●	●	○	○	○				
A9	1		1	1	○	●	●	○	○	○	○	○		
A10			1	1	○	●	○	○	○	○	○	○		
A11	1		1	1	●	●	●	●	●	●	●	●	●	
A12		1	1	1	●	●	●	●	●	●	●	●	●	
A13	1		1	1	●	●	●	●	●	●	●	●	●	
A14		2		2	●	●	●	●	●	●	●	○	●	
A15		1	1	1	●	○	●	○	○	○	○	○	○	

f, individuals fledged in that year; ○, found but not confirmed to breed in TZP; ●, confirmed to breed in TZP; -, not found in TZP but alive.

a, This was resighted on 6 January and 4 February in 2006 in the Tamagawa River 9 km northwest from TZP after banded in 2004.

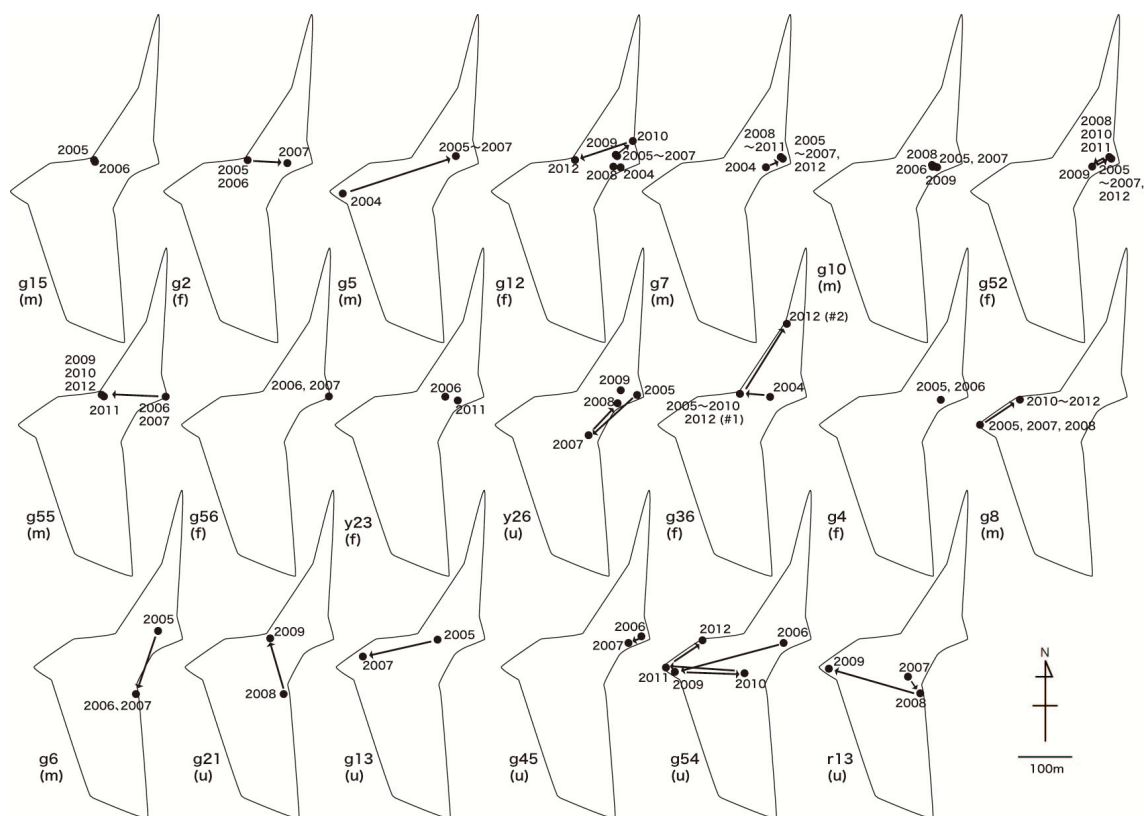
b, The carcass was found on 13 October 2008 at Saiko Lake, Toda, Saitama Prefecture, locating about 28 km southeast from TZP, after banded in 2003.

Table 5-2. Breeding histories (partner ID and fledgling number in each year) of individually marked Grey Herons in the Tama Zoological Park (TZP) colony. Marking was made for 2003–2006.

ID	Sex	Marked year	Year									
			2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
g15	male	2004	?	?	g2 (3)	g2 (3)						
g2	female	2004	?	?	g15 (3)	g15 (3)	um (2)					
g5	male	2004		um (3)	g12, um (3, 3)	g12, g12 (3, 3)	g12 (0)					
g12	female	2004		um (0)	g5, um (3, 1)	g5, g5 (3, 3)	g5, um (0, 3)	um (1)	um (3)	um (2)	?	um (1)
g7	male	2004		um (2)	um (3, 2)	g52 (2)	g52 (3)	g52 (2)	um (2)	g52 (2)	g52 (2)	g52 (2)
g10	male	2004		?	um (3)	um (2)	um (2)	um (2)	g52 (2)	?		
g52	female	2005			um (1)	g7 (2)	g7 (3)	g7 (2)	g10 (2)	g7 (2)	g7 (2)	g7 (2)
g55	male	2005			?	g56 (2)	g56 (3)	?	um (1)	um (2)	um (1)	um (2)
g56	female	2005			?	g55 (2)	g55 (3)					
y23	female	2003	f	?	?	um (0)	?	?	?	?	um (1)	?
y26	unknown	2003	f	–	um (2)	?	um (0)	um (0)	um (1)	?	?	?
g36	female	2004		um (0)	um (2)	um, um (3, 0)	um (unknown)	um (1)	um (2)	um (1)	?	um, um (1, 3)
g4	female	2004		?	um (2)	um (1)						
g8	male	2004		?	um (3)	um (3)	um (2)	um (3)	?	um (0)	um (4)	
g6	male	2004		?	um (1)	um (3)	um (3)					
g21	unknown	2004	f	f	–	–	–	um (2)	um (2)			
g19	unknown	2004	f	f	–	um (0)						
g13	unknown	2005			um (2)	?	um (3)	?	?			
g45	unknown	2005			?	um (1)	um (3)	?	?	?		
g54	unknown	2005			?	um (1)	?	?	um (1)	um (2)	um (2)	um (1)
r36	unknown	2005			f	–	–	um (1)				
r13	unknown	2005			f	–	um (2)	um (3)	um (1)			
r33	male	2006				f	–	um (0)				

ID, individual code; –, not found in TZP but alive; ?, found in TZP but not confirmed to breed; um, bred with unmarked individuals; f, individuals fledged in that year.

Number of fledglings in each nest are shown in parentheses (if bred two times, fledglings in the first and second broods are shown, respectively).



**Fig. 5-1.** The nest sites (closed circles) used in each year during 2004–2012 by individually marked Grey Herons in the Tama Zoological Park colony. The line indicates the boundary of the breeding colony. All 20 birds breeding for at least 2 years are shown with individual codes (m, male; f, female; u, unknown). For breeding success rates see Table 1. Where nest sites differ between the first and second broods in the same breeding season, they are marked with #1 and #2, respectively.







## **6. General discussion**

### **6-1. Findings from the data based on individual marking**

Our understanding of the dynamic and movable life styles of herons and egrets has been still limited due to difficulties in field observation. If we can take the behavioral and demographic data of individually discriminated birds in their habitats, they contribute greatly to reveal population dynamics, complex life histories, and individual interactions in the colony. In the past, therefore, many researchers have marked individual herons and egrets (Table 6-1).

Idiosyncratic color patterns on the bill, leg, lore, plume, and so on are useful for a short-term identification of individual birds. Color paint markings attached directly or using a paint gun from a short distance, without capture, are also used as temporal individual identification. Field studies of these methods revealed variation in chick growth of Little Egrets (Fujioka 1989), and frequency of extra-pair copulations in Cattle Egrets (Fujioka and Yamagishi 1981), Grey Herons (Ramo 1993), and Chinese Egrets (Wei et al. 2005).

Banding (ringing) is the traditional method of individual marking of birds and applied for herons and egrets from 1910s in Europe (Campos et al. 2001) and North America (Melvin et al. 1999). Accumulated data of recovered rings for a long time revealed their movement patterns. Grey Herons have been studied well in Europe on the basis of ringing recoveries of birds banded as nestlings. The dispersal from the natal colony keeps no steady direction of flight but the later the movements become directed, so that migration between their breeding and non-breeding seasons (Rydzewski 1956). Grey Herons ringed at the colonies in northern Europe usually recovered in southern or southwestern Europe or northern Africa (Rydzewski 1956). A total of 585 Grey Herons ringed at the outside and recovered in the Iberian Peninsula consisted of nearly all over Europe (Campos et al. 2001). In this area, post-breeding migration occurs mainly in September and October, pre-breeding migration in February and March (Lekuona and Campos 1996). In North America and Caribbean Islands, movements between banding and recovery places are mostly between north and south directions, with little exchange between eastern and western populations, in Great Egrets, Great Blue Herons, Snowy Egrets, Little Blue Herons, and Tricolored Herons (Melvin et al. 1999). Movements

between neighboring colonies are also cleared by recording banded birds. In Little Egrets in southern France, 75% of dispersing birds were coming from decreasing colonies and 72% joined to increasing colonies (Fasola et al. 2002). Thus, dispersal may depend on colony dynamics in a subregion.

Life history parameters can be estimated from the recovery of ringed birds. Ages were determined for 286 Grey Herons recovered in the Iberian Peninsula; 61.5% birds were 1-year-old, 14.0% 2-year-old, 5.9% 3-year-old, 5.9% 4-year-old, and others more than 4-year-old (Campos et al. 2001). Thus, first year birds are ready to move compared to older ones. According to Mead et al. (1979), average mortality for British-ringed Grey Herons is 55.9% in first year, 46.9% in second year, and thereafter 30.3% in 1955-1975. The mortality estimated from the band recovery record is 76% of the fledged Great Egrets that alive on July 1 during their first year and 26% for older birds per year (Kahl 1963). Life expectancy at fledging is 1.4 years, and at the start of the second year expectancy of further life is 3.3 years. The oldest reported bird reaches 16 years of age in Great Egrets, 18 years in Grey Herons, 21 years in Great Blue Herons, and 13 years in Black-crowned Night Herons (Kahl 1963). Intensive banding also reveals that nestling size rank affects subsequent breeding success of offspring in Little Egrets (Thomas et al. 1999). However, Cezilly (1997) stated that long-term data of individuals based on banding are still limited to estimate exact demographic parameters in herons and egrets.

Tracking of radio-tagged birds is rather recent method after a miniature long-life tag was made. This method enables to gather detailed movement patterns in a tracked area. For example, radio-tags were attached to breeding adult, non-breeding adult, and non-breeding first-year Grey Herons and traced their movements during the breeding season in Belgium (van Vesseem et al. 1984; van Vesseem and Draulans 1987b). Breeding birds explored a wide range of feeding area but became narrower and nearly territorial later in the breeding season, while non-breeders spent outside of colony further with seasons. In winter, the feeding patterns in time and space differed between first-year and older Grey Herons (Draulans and Vesseem 1985). The radio-tags with mortality sensors are available to estimate survival rates. Erwin et al. (1996) applied this method to Black-crowned Night-Heron and Snowy Egret chicks in Virginia colonies. Survival ranged from 80 to 100% before dispersal and 25 to 60% after 50 days after birds left the natal colony.

Tracking of a long flight is now possible to trace directly using a satellite-tracking system. This application shows that individual juvenile Purple Herons start migration to Africa in autumn at 40 km/h (Jourdain et al. 2008) and adult Purple Herons fly 4000 km within 5-7 days (van der Winden et al. 2010).

These individual-based observations are generally distinguished into two types of studies; (1) short-term but detailed observation of behavior in the nest or continuous location of individual birds, and (2) long-term but fragmented data collection to estimate movement distance and frequency, survival, and age structure, although they are not mutually exclusive. In my studies, I used some unique banding method that differing from the previous one. Previous rings used for individual identification are small and cannot be used for seeing the identification codes without recaptures. Instead, I used a rather large ring on which clearly visible numerals are drawn with different color combinations (see Figs. 2-1, 2-3). This type of rings were suitable to identify individual birds when observing from the distant places without disturbing the bird, and therefore I could obtain not only the detailed behavioral data, identifying individuals, but also the capture-resight data in a wide range of areas and for longtime.

## **6-2. Colony dynamics revealed in this study**

The dynamics of the Grey Heron colony is summarized in Fig. 6-1. After bred in the colony (Fig. 6-1a), fledglings disperse from the colony. Adults partly continue staying in the colony in winter but partly migrate to the neighboring wintering sites (Fig. 6-1b). In the next breeding season, some young birds return to the natal colony and most adults migrate from the wintering sites (Fig. 6-1c). In this time, some adults also immigrate to this colony from other colonies. Gathering of unfamiliar birds may cause an unstable state of colony members probably via social factors such as interference interactions for nesting sites, mates, and feeding sites. However, this unstable state may disappear owing to increase in breeding pairs in the colony (Fig. 6-1d).

Fledglings all dispersed from the colony and returned to the natal nest at the rate 24.0%. However, this rate was final value in 9 years monitoring; 8% of fledglings returned at 1-year-old, 12% returned at 2-year-old, 2% returned at 3-year-old, and 2% returned at 4-year-old. As known well in herons and egrets (Kushlan and Hancock 2005), fledglings of Grey Herons dispersed to southwest so far (1,580 km) in this study.

In contrast, most (94.7%) adults once arrived to the colony reused the previous colony. In the non-breeding period, they usually moved from the breeding colony to the different wintering sites. Such a wintering site of individual bird is rather fixed. This type of movement is called as seasonal migration. In the studied colony, however, several birds continued to stay in the breeding colony. Artificial feeding in the zoo may cause this phenomenon. In fact, they sometimes hunted fishes given to zoo animals. Inter-colonial movement is another important pathway to determine the colony members. However, it may be infrequent in this study because most adults continued to stay in the colony (i.e., they rarely immigrated to other colonies). The recent genetic analysis is useful to examine gene flows according to dispersal and immigration of birds. The sequence data of the mitochondrial D-loop region reveal no genetic structure among 16 breeding colonies of Reddish Egrets along the Texas Coast (Bates et al. 2009). Thus, individuals may mix among breeding colonies in the historical time scale, even though the genetic diversity in each colony was occasionally lost by reduced population size.

If the mortality is not so severe, the number of Grey Herons increases in the breeding colony in this way. My results clearly showed density-dependent effects on the breeding duration, the number of fledglings, and the breeding season length. The mean breeding duration (from building of the nest until fledging) of individual birds became longer as the number of birds in the colony. This may be related to the unstable state at the beginning of the breeding period, because social interactions are expected to increase as increasing the unfamiliar members in the colony.

Although the proportion of successful nests (with at least one fledgling) was not affected by the number of birds in the colony, the mean number of fledglings/successful nest decreased with the colony size. The factors affecting it were not examined in this study. Although predation is usually an important factor affecting fledging success and number, predation rarely occurred for 16 years in the studied colony locating in suburban Tokyo. Chick mortality of herons and egrets is due to not only starvation but also siblicide (Fujioka 1985; Inoue 1985; Mock 1987; Mock et al. 1987; Jakubas 2005). Siblicide is reported as a reason of death for 0% to 88% of Grey Heron chicks (Jakubas 2005; Stotskaja 1984). In this respect, further studies will be needed.

The increased number of colony members resulted in early starting of breeding at the colony level and a great variation in date starting individual breeding. Natural

selection favors adults whose nestlings are present when food is most available to the parents (Lack 1954; Butler 1993). If so, the reproductive success is expected to be higher on the average date than early or late reproduction. Seasonal timing of food availability is a strong stimulus for the initiation of nest attempts by herons and egrets (Kushlan 1986; Frederrick and Collopy 1989; Lopez-Ornat and Ramo 1992; Butler 1993; Kelly et al. 2007). In the San Francisco Bay area, Great Blue Herons and Snowy Egrets nest earlier in subregions dominated by freshwater wetlands (Kelly et al. 2007). This corresponds to early availability of seasonally flooded marshes, ephemeral creeks, and receding ponds after normal periods of winter rainfall. Great Blue Herons delayed breeding by the loss of available feeding habitats caused by severe flooding in the Mississippi River (Custer et al. 1996). In Poland, Grey Herons of inland colonies begin breeding later than those of coastal colonies because spring air temperatures are lower and ice cover is present on feeding sites longer in inland location (Jakubas 2011). Thus, accessibility of feeding sites (lack of ice cover) in spring is an important factor affecting the onset of breeding. However, in suburban Tokyo, winter temperatures are mild, rarely decreasing under 0°C. The effect of food availability on initiation of breeding will be examined in the future.

Moreover, nesting activity differs seasonally in a mixed-species heronry. For example, in the North Carolina coastal heronry, Great Egrets began nesting very early and followed by Snowy Egrets, Cattle Egrets, Louisiana Herons, and Little Blue Herons (McCrimmon 1978). This suggests that the degree of interspecific competition differs during the breeding season. However, the interspecific factors affecting the initiation of breeding are seemed not to fit to my result because the colony consist of single species.

### **6-3. Implications for management and conservation**

Recently, Grey Herons may increase in number in central Japan. At least 30 years ago, their colonies were rare in and around Tokyo, but recently several colonies seem to be established in suburban Tokyo (Table 6-2, Fig. 6-2). Although the causes are still unknown, their present state must be recorded and monitored in the future.

If we need management or conservation of this large heron in suburban Tokyo, appropriate spatial scale may be determined firstly. A comparison of landscape characteristics surrounding heron and egret colony sites with those surrounding

randomly selected, unoccupied sites reveals the primary importance of estuarine emergent wetland and open water within 1 km of colony sites in northern San Francisco Bay (Kelly et al. 2008). This suggests that the importance of local foraging opportunities near heronries. The landscape approach also point out that the reproductive success of the certain heronry is associated with variation in habitat extent at larger spatial scales, especially within 10 km of heronries. Thus, the colony site may be determined by the conditions of not only the colony site itself but also the wide-range of habitat. In France, Cattle Egrets, Squacco Herons, and Black-crowned Night Herons nest on sites surrounded by rice field, whereas Little Egrets' nest choice is not consistently related to availability of rice fields (Tourenq et al. 2004). The negative relationship between proportion of Little Egret nests within a colony and available rice-field surface area is especially noticeable at the 5-km scale (Tourenq et al. 2004). In this respect, the data is unavailable for Grey Herons in suburban Tokyo. Because this region includes several large rivers such as the Tamagawa and Arakawa Rivers and several estuaries along Tokyo Bay (Fig. 6-2), Grey Herons may use a wide range of feeding sites. In my study colony, at least  $10 \times 20 \text{ km}^2$  area was used for feeding sites (see Fig. 5-3). For conservation of colonial waterbirds, protection of breeding sites and preservation of large scaled feeding habitat are essential, and the appropriate spatial scale and long-term population monitoring are needed (Kushlan 1997; Hafner and Fasola 1997).

Another problem to manage and conserve herons and egrets is habitat changes in the colony site. Colonially breeding birds influence the habitats, particularly vegetation at colony site. One of the most important factors is an increased supply of nutrients into soil (Smith 1978; Ishida 1996; Mun 1997; Zolkos and Meissner 2008; Breuning-Madsen et al. 2010). In fact, the Grey Heron and Great Blue Heron colonies affect the colony site vegetation (Mun 1997; Shizu et al. 2009). In the Grey Heron colony at Oga Peninsula, northern Japan, the dropped feces, foods, dead-nestlings, and dead-adult birds are decomposed under the nest sites, and several large cedar trees died, by which the colony site shift toward neighboring new places year to year (Ogasawara et al. 1982). This suggests that it is difficult to maintain the colony for longtime when it is established in the fragmented small woods in the human-used lands. We need the methods to keep vegetation of such a small woodlot against the eutrophication caused by the colonial birds.

Interspecific interactions among ecological equivalents are one of important problems of expanded exotic animals. Herons and egrets can fly long distance and disperse widely by themselves. If dispersed to new habitat, the severe competition occurs with closely related native species. Among such examples, impact of Cattle Egrets on other species of herons and egrets is severe (Nunes et al. 2010). In southern France, declining nest success of Little Egrets in mixed colonies over the past three decades is explained possibly by exclusion from high-quality nest sites by Cattle Egrets (Dami et al. 2006). Cattle Egrets increased rapidly over the same time period and are known to be aggressive at the nest. In North America, Cattle Egrets also expanded, and their conflicts were more vigorous resulting that they had the highest brooding success in mixed-species colonies (Burger 1978a; Parkes et al. 2012). Cattle Egrets were not seen around the study colony at present, but we must pay attention to the distributional expansion of this egret in future.



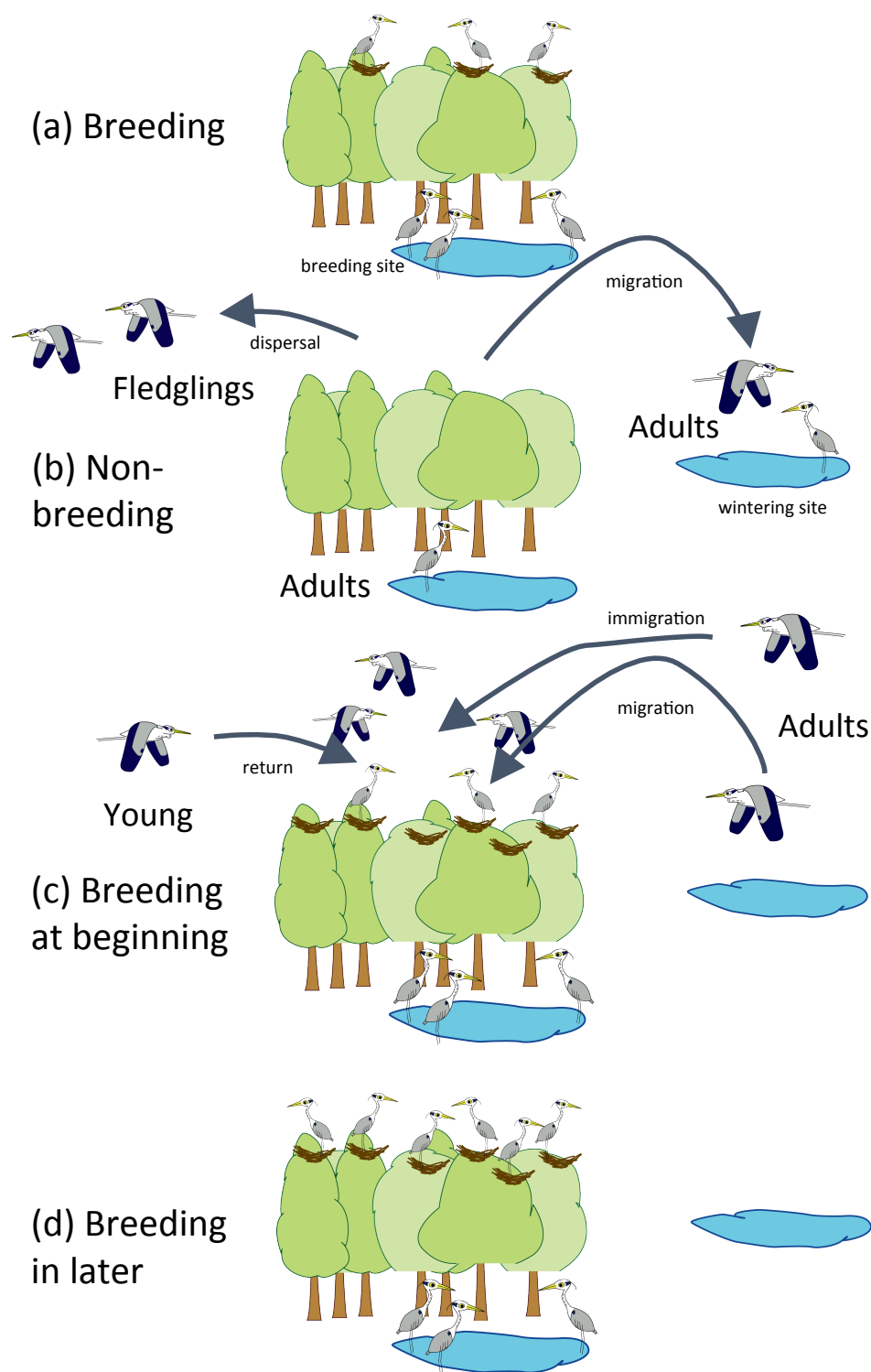
Table 6-1. Migration, survival, and other life history parameters based on individually-marked studies.

Species	Site	Year	Marking (recovered number of individuals)	Results	Reference
Black-crowned Night Heron	San Francisco Bay	1971-1977	Nestling banding and ring recovery (59)	Dispersal 5-518 km (young), 3-280 km (adult)	Gill & Mewaldt 1979
Black-crowned Night Heron	Virginia	about 100 days in each 1992, 1993	radio-tracking with mortality sensors (11, 20)	Survival rate; 89-92% before dispersal, 30-40% after 50 days from dispersal	Erwin et al. 1996
Black-crowned Night Heron			Nestling banding and ring recovery (141)	Mortality; 61% in first-year, 31% in older. The oldest 13 years old	Hickey 1952
Cattle Egret	Japan	34 days in 1978	Individual habits (10 pairs)	38 (29.2%) of 130 copulation are successful extra-pair copulations	Fujioka & Yamagishi 1981
Chinese Egret	China	37 days in 2003	Individual habits (11 pairs)	Higher extra-pair copulation	Wei et al. 2005
Great Blue Heron	North America	1914-1994	Nestling banding and ring recovery (216)	Dispersal 12-4584 km between north and south directions including Cuba, central and central America	Melvin et al. 1999
Great Blue Heron	San Francisco Bay	1971-1977	Nestling banding and ring recovery (11)	Dispersal 8-135 km (young), 0-32 km (adult)	Gill & Mewaldt 1979
Great Blue Heron			Nestling banding and ring recovery (349)	Mortality; 71% in first-year, 29% in older. The oldest 21 years old	Owen 1959
Great Egret	North America	1914-1994	Nestling banding and ring recovery (84)	Dispersal 16-3125 km between north and south directions including Cuba, central and central America	Melvin et al. 1999
Great Egret	North America	1935-1960	Nestling banding and ring recovery (178)	Mortality; 76% in first-year, 26% in older. The oldest 16 years old	Kahl 1963
Grey Heron	Belgium	58 days in 1982/83, 13 days in 1983/84	radio-tracking (7, 16)	In winter, the feeding patterns in time and space differed between first-year and older individuals	Draulans & van Vessem 1985
Grey Heron	Belgium	41 days in 1982	radio-tracking (5)	Breeding birds explored a wide range of feeding area but became narrower and nearly territorial later in the breeding season, while non-breeders spent outside of colony further with seasons.	Van Vessem et al. 1984, Draulans & van Vessem 1987
Grey Heron	Britain	1955-1975	Nestling banding and ring recovery (807)	First-year birds survive well in high winter temperatures. Maximum age 16 year-old	North 1979, North & Morgan 1979
Grey Heron	Britain	1955-1975	Nestling banding and ring recovery (807)	Mortality; 55.9% in first year, 46.9% in second year, and 30.3% thereafter	Mead et al. 1979
Grey Heron	Britain		Nestling banding and ring recovery (195)	Mortality; 69% in first-year, 31% in older. The oldest 16 years old	Lack 1949
Grey Heron	Europe	1910?-	Nestling banding and ring recovery (4187)	Dispersal and migration to southwest upto north Africa	Rydzewski 1956
Grey Heron	Iberian Peninsula	1910-1998	Nestling banding and ring recovery (585)	Recovery in the Iberian Peninsula from France (189), Germany (139), Sweden (75), Holland (53), Denmark (45), Switzerland (20), Russia (15), Poland (11), Great Britain (10), Czech Republic (10), Belgium (7), Norway (6), Finland (2), Hungary (1), Estonia (1), and Latvia (1)	Campos et al. 2001
Grey Heron	Spain	5 days in 1990, 14 days in 1991	Individual differences in color (15, 16 pairs)	39 (12.9%) of 301 copulations are extra-pair	Ramo 1993
Grey Heron	Spain	1966-1981	Nestling banding and resighting to breed (101 pairs)	Age at the first breeding was 2-year-old. Pairs of 4 or more years of ages laid more eggs than pairs of at least one 2 years old bird. 1.4% of observed pairs raised two broods per year. 11.6% fledglings returned to the natal colony in 2-year-old, 5.6% in 3-year-old, and 3.1% in 4-year-old.	Fernández-Cruz & Campos 1993
Grey Heron	Tokyo	2003-2012	Color banding (69)	12 (24%) of 50 marked fledglings returned to the natal colony. Age at the first breeding was 2-year-old (4 birds), 3-year-old (2), 4-year-old (1), and no bred (5). Fidelity of adults to colony, nest site, mate, and feeding site. Two broods per year in 7.7% breeding pairs. Maximum distance traced 1580 km southwest. No tendency to increase reproductive success with age. Maximum reproductive success, 22 fledglings/9 years.	This study
Grey Heron			Nestling banding and ring recovery (247)	Mortality; 78% in first-year. The oldest 11 years old	Verheyen & LeGrelle 1952
Grey Heron			Nestling banding and ring recovery (845)	Mortality; 67% in first-year, 28% in older. The oldest 18 years old	Olsson 1958
Little Blue Heron	North America	1926-1964	Nestling banding and ring recovery (218)	Travel to 960 km but usually less than 160 km (to Cuba and South America)	Dusi 1967
Little Blue Heron	North America	1914-1994	Nestling banding and ring recovery (63)	Dispersal 15-4115 km between north and south directions including Cuba, central and central America	Melvin et al. 1999
Little Egret	France	1987-1995	Nestling banding and ring recovery (253)	Survival rate 71.4% in adults, 6.5-55.2% in yearlings (variation is not affected winter temperatures). 20% of yearlings breed.	Hafner et al. 1998
Little Egret	France	1982-1996	Nestling banding and resighting (537)	Juveniles disperse more (usually >10 km) than adults (<10 km). 75% of dispersing birds were coming from decreasing colonies and 72% joined to increasing colonies in the 1800 km <sup>2</sup> breeding areas	Fasola et al. 2002
Little Egret	France	1982-1997	Nestling banding and resighting to breeding success (56)	Size hierarchy within a brood has long-term fitness consequences as number of fledglings.	Thomas et al. 1999
Little Egret	Japan	1986	Color-marked with a paint gun (20)	Desertion occurs frequently by the female parent and in a small brood	Fujioka 1989
Little Egret	Spain	1929-1993, 1988-1992	Nestling banding and ring recovery (217)	Dispersal in France, Spain, and north Africa	Bartolome et al. 1996

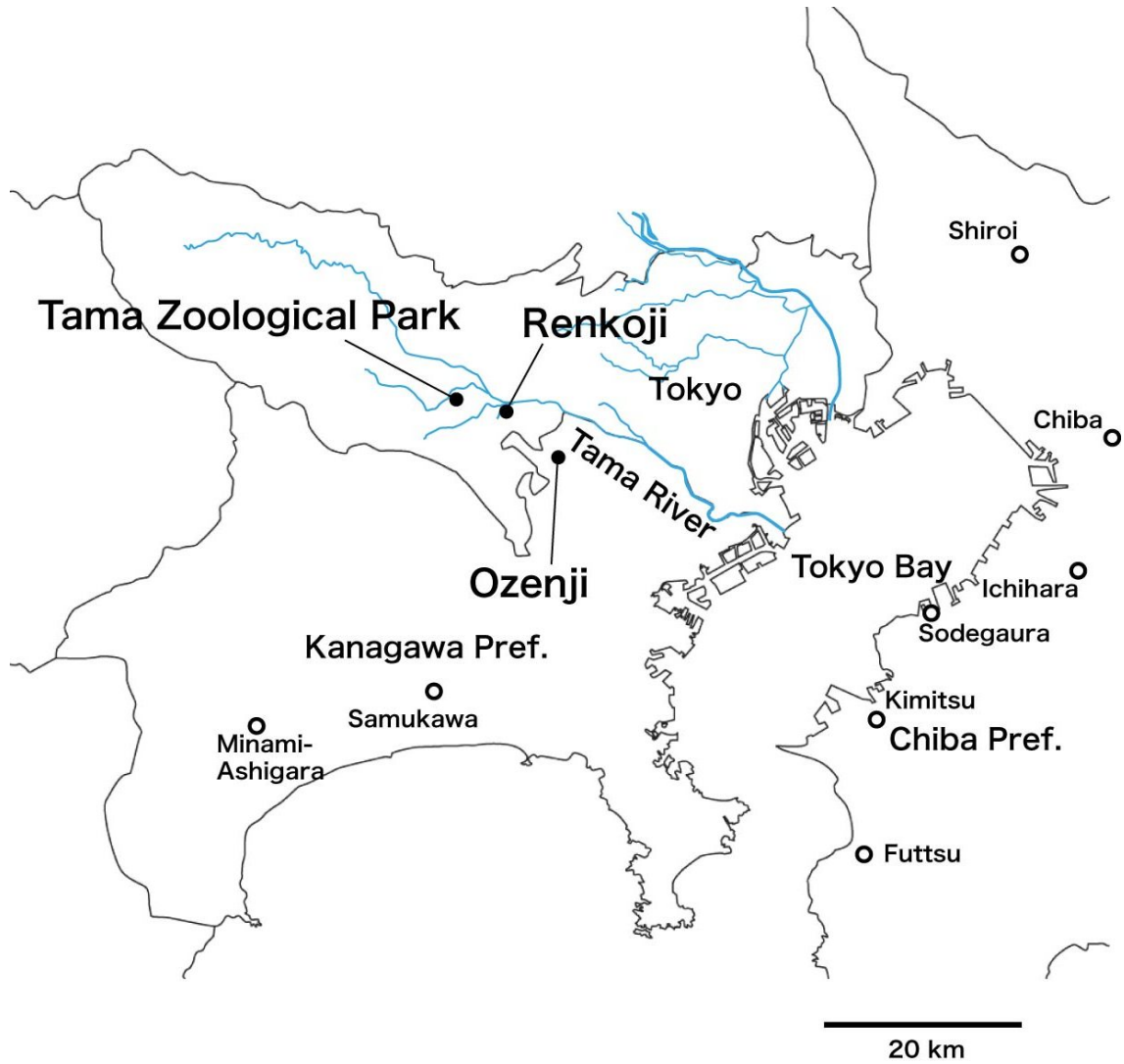
Purple Heron	Europe		Satellite transmitter (7)	Migrate into the Sahel of 4000 km per 5–7 days. One fly 5600 km non-stop	van der Winden et al. 2010
Purple Heron	France	July–Nov in 2004	Satellite transmitter to juveniles (4)	Migrated from Spain to Algeria, Morocco, and Mauritania in September at the flight speed 40 km/h.	Jourdain et al. 2008
Snowy Egret	North America	1914–1994	Nestling banding and ring recovery (111)	Dispersal 19–2829 km between north and south directions including Cuba, central and central America	Melvin et al. 1999
Snowy Egret	San Francisco Bay	1971–1977	Nestling banding and ring recovery (29)	Dispersal 16–209 km (young), 16–32 km (adult). Migration 566–2643 km (young), 248–418 km (adult)	Gill & Mewaldt 1979
Snowy Egret	Virginia	about 100 days in each 1992, 1993	radio-tracking with mortality sensors (22, 20)	Survival rate; 80–100% before dispersal, 25–60% after 50 days from dispersal	Erwin et al. 1996
Tricolored Heron	North America	1914–1994	Nestling banding and ring recovery (24)	Dispersal 58–2328 km between north and south directions including Cuba, central and central America	Melvin et al. 1999

Table 6-2. Known distribution of Grey Herons around Tokyo Bay.

Site	No. of Grey Herons	Colony	Period	References
Shiroi	?	mixed-species	1995–	Ueda (2003)
Chiba	7	mixed-species	at least 2006–	Ueda (2012)
Ichihara	84	single-species	at least 2006–	Ueda (2012)
Sodegaura	107	mixed-species	at least 2006–	Ueda (2012)
Kimitsu	46	single-species	at least 2006–	Ueda (2012)
Futtsu	807	mixed-species	at least 2006–	Ueda (2012)
Minami-Ashigara 1	10	mixed-species	at least 2004–	Kanagawa Chapter of Wild Bird Society of Japan (2004)
Minami-Ashigara 2	4–6	single-species	2003–	Kanagawa Chapter of Wild Bird Society of Japan (2004)
Samukawa	23–29	mixed-species	at least 2007–	Kanagawa Chapter of Wild Bird Society of Japan (2008)



**Fig. 6-1.** Population dynamics and individual life in the Grey Heron colony at suburban Tokyo. The colony state is indicated in time course of two years; the breeding (a) and non-breeding (b) periods in the first year, and the beginning (c) and mid/late (d) breeding period in the next year.



**Fig. 6-2.** Grey Heron colonies known around Tokyo Bay. Renkoji, Tama Zoological Park, and Ozenji are the colonies in this study. For the detailed information of colony finding and colony size, see Table 6-2.

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## 9. Appendixes

### 9-1. Publications

Shirai T (1999) Breeding biology of Grey Herons *Ardea cinerea* in the Tama River. Strix 17: 85-91 (In Japanese with English summary).

Shirai T (2013) Colony development and density-dependent processes in breeding Grey Herons. International Journal of Zoology 2013: 404065.

Shirai T (2013) Fidelity to the breeding colony and the long-term reproductive history of individually-marked wild Grey Herons. Journal of the Yamashina Institute for Ornithology 44: (in press).

### 9-2. Title and summary in Japanese

学位論文要旨（博士（理学））

アオサギの繁殖コロニーの長期変動と各個体の行動・繁殖履歴（英文）

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サギ類は、繁殖期になると、ある特定の場所に集合して繁殖コロニーを形成する。繁殖コロニーはよく目立ち、樹上に作られた繁殖巣を直接数えることができるため、コロニーサイズの年変化やある地域でのコロニーの離合集散過程などを追跡した研究が多い。しかし、コロニー動態を明らかにするためには、各個体の挙動を調査し、そこで生じる密度依存過程や個体の行動の変化から、コロニー全体をとらえなければならない。本研究では、各個体の行動や繁殖の履歴を通してコロニーの長期動態を明らかにする目的で、東京近郊に形成されたアオサギ単独の繁殖コロニーを、創成期から 16 年間にわたって観察し、コロニー内の密度依存過程、コロニー内での巣場所選択、コロニー構成員の移出入を調査した。

繁殖つがい数は創成期から徐々に増加し、飽和曲線を描いた。繁殖つがい数

の増加にともない、各つがいの造巢から巣立ちまでの期間が長くなり、一巢あたりの巣立ち雛数が減少する傾向があった。繁殖は、毎年、初春から夏にかけて見られた。繁殖つがい数が多いと、繁殖開始時期が早まり、また、営巣開始の早いつがいほど、造巢から孵化までの期間が長くなる傾向が認められた。つまり、繁殖期初期には、その年の新規繁殖個体や他のコロニーからの移住個体などとの相互作用が頻繁になり、育雛開始が遅延するのではないかと推定された。

コロニー内での巣場所選択に関しては、毎木調査を行い、樹種、胸高直径、樹高、相対的樹高（コロニー地域のもっとも低い地面から木の先端までの高さ）を営巣木と非営巣木で比較した。その結果、樹種については、ヤマザクラとコナラがよく利用されること、樹高自体ではなく、相対的樹高が高いほどよく営巣されることが明らかとなった。実際の巣は樹高の 83%の位置にかけられていた。しかし、野外で見られた巣の垂直的、水平的位置と各巣の巣立ち雛数の間には統計学的に有意な関係は認められなかった。

9年間については、総計 50 個体の巣立ち直後の幼鳥と 19 個体の成鳥に足環を装着して個体識別を行い、観察を継続した。幼鳥については、12 個体が出生コロニーに帰ってきた。そのうち、4 個体は 2 歳で、2 個体は 3 歳で、1 個体は 4 歳で初めて繁殖を行った。5 個体はコロニー内にいたが繁殖はしなかった。これら 12 個体のうち 9 年後にもまだ 2 個体がコロニー内で見られた。成鳥はほとんど（19 個体のうち 18 個体）が、翌年以降も引き続き繁殖コロニー内に戻った。同一コロニー内で繰り返し繁殖した場合、同じ巣場所で繁殖することもあれば、違う巣場所で繁殖することもあった。雌雄とも個体識別された 4 つがいの繁殖履歴を見ると、どちらかがいなくなるまでつがい相手をかえない傾向が認められた。毎年、非繁殖期（秋から冬）になると、繁殖コロニーでは見られなくなる個体が多い。そうした個体は、近辺の川沿いの決まった場所で毎年目撃される傾向があり、繁殖コロニーと非繁殖期の採餌場の移動を毎年繰り返していることが示唆された。巣立ち雛は長距離移動を行うことが知られているが、今回も、幼鳥に足環を付けてから 54 日後に、久米島で確認された個体があった。

アオサギは、大型で長寿である。巣立ち後は出生コロニーから分散するが、成鳥は繁殖コロニーに対して固執する傾向がある。狭い範囲に密集して営巣するため、毎年、繁殖期初期には不安定な状態が生み出され、繁殖成功度への密度依存性が顕在化すると考えられる。