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Authors: Mashiko, Miyuki, and Toquenaga, Yukihiko

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Site Fidelity in Lineages of Mixed-species Heron Colonies

Miyuki Mashiko[1,2,*] and Yukihiko Toquenaga[1]

[1]Graduate School of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Tennoudai, Tsukuba, Ibaraki, 305-8572, Japan

[2]Current address: National Institute for Land and Infrastructure Management, Ministry of Land, Infrastructure, Transport and Tourism, 1 Asahi, Tsukuba, Ibaraki, 305-0804, Japan

[*]Corresponding author; E-mail: mashiko@pe.ies.life.tsukuba.ac.jp

Abstract.—As heron and egret colonies are sometimes abandoned due to human activity and subsequently newly established at nearby locations, colony locations *per se* cannot represent colony fates. Here, "colony lineages" were traced by connecting short-distance location shifts between colony sites in consecutive years to quantify the site fidelity of heron colonies themselves rather than the breeding-site fidelity of individuals. Site fidelity of 61 colony lineages recorded from 1963 to 2013 in and around Ibaraki Prefecture, Japan, was evaluated by persistence periods with survival analysis and shapes of historical trajectories by applying the correlated random walk analysis. While 36% (n = 22) of colony lineages did not show site fidelity and lasted only 1 year or indicated untangled shapes of historical trajectories, 64% (n = 39) of colony lineages exhibited site fidelity by reusing the same locations for multiple years or by staying within a small area with entangled shapes of historical trajectories. Even though suitable breeding sites were abundant in the study area and site fidelity of colony members was low, a high rate of site fidelity in colony lineages may be achieved when a few faithful pioneer herons and egrets are followed by many others.
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Key words.—Ardeidae, colony lineage, correlated random walk, egret, heron, site fidelity, trajectory.

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Breeding-site fidelity is common to most bird species that form colonial breeding sites (Cézilly *et al.* 2000; Bried *et al.* 2003). Colonial herons and egrets (Ardeidae) can form colonies on trees, bushes, reeds and the ground in inland areas, and their colonies often persist at the same locations for many years (Kushlan and Hancock 2005). However, some heron colonies exist for only one or at most a few years, and others shift to neighboring locations (Bancroft *et al.* 1988; Kelly *et al.* 2007). Such colony abandonment and relocation are sometimes caused by human disturbance because the noise and unpleasant odors of heron colonies can be disagreeable and annoying for residents when they are located near residential areas (Hafner 2000; Telfair *et al.* 2000; Parkes *et al.* 2012).

Solving such conflicts between human residents and avian breeding colonies requires knowledge of how these colonies are formed and persist at specific locations. Research on species distribution and habitat selection may provide insights into the development of appropriate ecological approaches for tackling these problems (Parkes *et al.* 2012), but research has conventionally focused on the philopatry or site fidelity of individuals within persisting colonies (Atwood and Massey 1987; Aebischer 1995; Vergara *et al.* 2006). However, avian colonies are often formed with individuals that are not highly philopatric. For example, the frequency with which individual herons and egrets return to their natal or previous breeding locations was 55% at most (Fernández-Cruz and Campos 1993; Melvin *et al.* 1999; Fasola *et al.* 2002). These colonies were annual, or only formed during the breeding season within a year. Thus, colonies with site fidelity are reformed with different members annually at exactly the same locations. Moreover, colonies can be relocated to nearby sites when human beings force the birds to evacuate former colony sites by completely destroying nesting resources. For such colonies, the site fidelity of colonies themselves rather than the breeding-site fidelity of individuals can be used to solve conflicts between human residents and colonial avian species.

As colonies are relocated due to human activity and other causes, colony locations *per se* cannot represent colony fates. Therefore, "colony lineages" can be traced by connect-

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ing multiple colony sites for each colony history (Garden 1958). Colony abandonment is often followed by the establishment of a new colony at a nearby location, and such new sites should be considered descendants of the abandoned colonies rather than new colonies (Mashiko and Toquenaga 2013). Site fidelity of moving colonies should be defined based on the frequency of relocation, persisting period of each colony site, and the shapes of the trajectories of relocation events.

Our objectives were to quantify the site fidelity of heron colony lineages based on their historical trajectory, or the consecutive movement path of colony sites within a lineage. We analyzed 51 years of colony data for the northern Kanto Plain, Japan. Since the breeding and foraging habitats are homogeneously distributed (Carrasco *et al.* 2014, 2015) and human disturbance occurs frequently in the area, we hypothesized that colony lineages with site fidelity should be characterized by: 1) not one-year but rather multiple-year persistence periods; and 2) not untangled but rather entangled shapes of historical trajectories.

METHODS

Study Area

This study focused on 11,865 km^2 in Japan in a region that included the Ibaraki Prefecture and bordered on the regions of Fukushima, Tochigi, Saitama and Chiba Prefectures in the northeastern part of the Kanto Plain, Japan (35° 53′ N to 36° 54′ N, 139° 41′ E to 140° 49′ E; Fig. 1). The north is mountainous and not suitable habitat for herons and egrets. The remainder of the region is flat lowland with large areas along rivers used for rice production and lotus fields scattered near Lake Kasumigaura. The flooded fields and irrigation ditches support large numbers of foraging herons and egrets (Lane and Fujioka 1998). Breeding habitat was homogeneously distributed here; when we gridded the entire study area into 915-m x 915-m cells, 94.5% of the cells contained at least one pixel (45.7 m x 45.7 m) of trees or bamboo, primarily moso bamboo (*Phyllostachys pubescens*), Simon bamboo (*Pleioblastus simonii*) or dwarf bamboo (*P. chino*), thickets that are potential breeding sites for herons and egrets (Carrasco *et al.* 2014, 2015; Fig. 2). Residential areas were also scattered throughout the lowland, and human disturbance occurs frequently where heron and egret colonies are located adjacent to residential areas (Fig. 2).

Every year, the herons and egrets breed mainly in mixed-species colonies from March to August: Grey Heron (*Ardea cinerea*) arrives first in March; Great Egret (*A. alba*), Little Egret (*Egretta garzetta*) and Black-crowned Night-Heron (*Nycticorax nycticorax*) arrive in April; Intermediate Egret (*A. intermedia*) arrives in late April; and finally, Cattle Egret (*Bubulcus ibis*) arrives by early May. Colony size varied considerably, from approximately four to over 3,000 individuals (Environmental Agency of Japan 1994; Mashiko and Toquenaga 2013). Intermediate and Cattle egrets are summer migrant species, but the other four species are a mixture of residents and migrants in the area, and some individuals winter in this area. Until the early 1990s, some colony sites were also used for roosting by wintering Great and Little egrets from September to February (Anzai 1990); however, since 1995, all colony sites have been used only for breeding by the six species, and all colonies become vacant by October.

Colony Data

Colony sites in the study area from 1963 through 2013 were included. The most intensive surveys were conducted from 1999 to 2013 (annual number of colony sites = 22.0 ± 1.1) during which we obtained colony location data from region-wide aerial and ground-based searches. Aerial censuses were conducted from 1999 to 2000 using aircraft (Fujioka *et al.* 2001) and from 2002 to 2013 with aerial photography using a radio-controlled paraglider (Mashiko and Toquenaga 2013). For ground-based searches, colony sites were found by checking the places in which colonies had been located in previous years, and all colony sites were surveyed at least once in a breeding season. When a colony was abandoned, searches were made to determine whether other colonies had formed nearby. From 1983 to 1998 (annual number of colony sites = 17.5 ± 0.9), we obtained colony location data from ground-based searches (Koshida 2007). We obtained colony location data from local literature and personal communications with local amateur avian observers before 1983 (annual number of colony sites = 3.3 ± 0.5). We also complemented the data with literature and interviews from 1983 and later to minimize the number of colony sites not detected.

Our focus was on colony lineages, and we needed as much documented history for each colony as possible over a long period. Thus, we included all known colony sites since 1963 even though some colonies prior to 1999 may have been undetected. Preliminary examination showed that the results of analyses excluding data prior to 1999 did not differ from those using the entire dataset.

Confirmation of Colony Lineages

To determine colony lineages, first we documented the year and location of establishment, persistence, and abandonment of each constituent colony site. A colony site was deemed abandoned when it was confirmed that no breeding activities were conducted in the following year at the location of the previous year's colony site. A colony site was deemed newly es-

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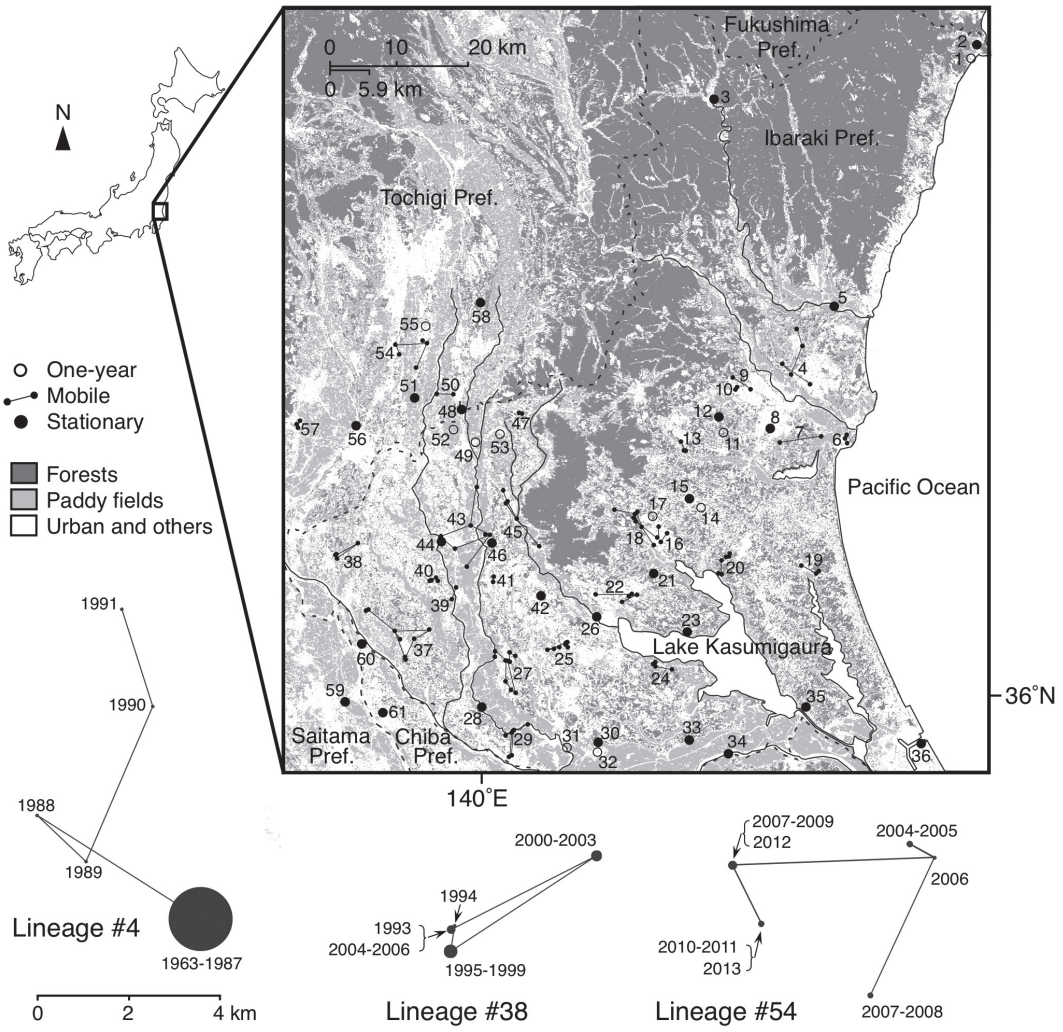


Figure 1. Map showing the location of 61 colony lineages in the study area around Ibaraki Prefecture, Japan, from 1963 to 2013. Broken lines represent prefectural boundaries, and continuous lines represent the main rivers in the study area. Enlarged figures of mobile lineages (no. 4, 38, and 54) showing different shapes of trajectories are included below the map. The diameters of the circles reflect the persistence period of each colony site. Pref. = Prefecture.

tablished when breeding activities were confirmed at a location where there had been no colony in the previous year. When we could not determine the existence of a colony at a specific site in one year (year t), we first confirmed its presence in previous years ($t - k$, $0 < k$) as well as in the subsequent year ($t + 1$). If the site's presence could be confirmed both before and after year t, it was considered present in year $t - i$ as well where $0 \leq i \leq k$. Conversely, even if the colony was confirmed both before and after the year t, when we were able to positively confirm that a colony site did not exist in year t, we treated the colony that lasted until $t - k$ and the colony established in $t + 1$ as separate. To determine the persistence period for each colony site, the number of years from the first establishment at a location was counted.

We evaluated colonies based on lineage, rather than the observed colony sites themselves, to account for short-distance location shifts. When abandonment and new establishment occurred in neighboring locations in successive years, the new site was assumed to be a descendant of the abandoned one. This is supported by the behavior of heron and egret individuals at the beginning of their breeding season when they choose their colony site: if a site has become unsuitable for nesting through the natural death of vegetation or human-induced disturbances, herons and egrets first circle above the location of the colony site it had used in the previous year. They sometimes fly away, but at other times they stay on trees nearby and, finally, this nearby location becomes a new colony site (M. Mashiko and Y. Toquenaga, pers. obs.; Fig. 2). To determine a reason-

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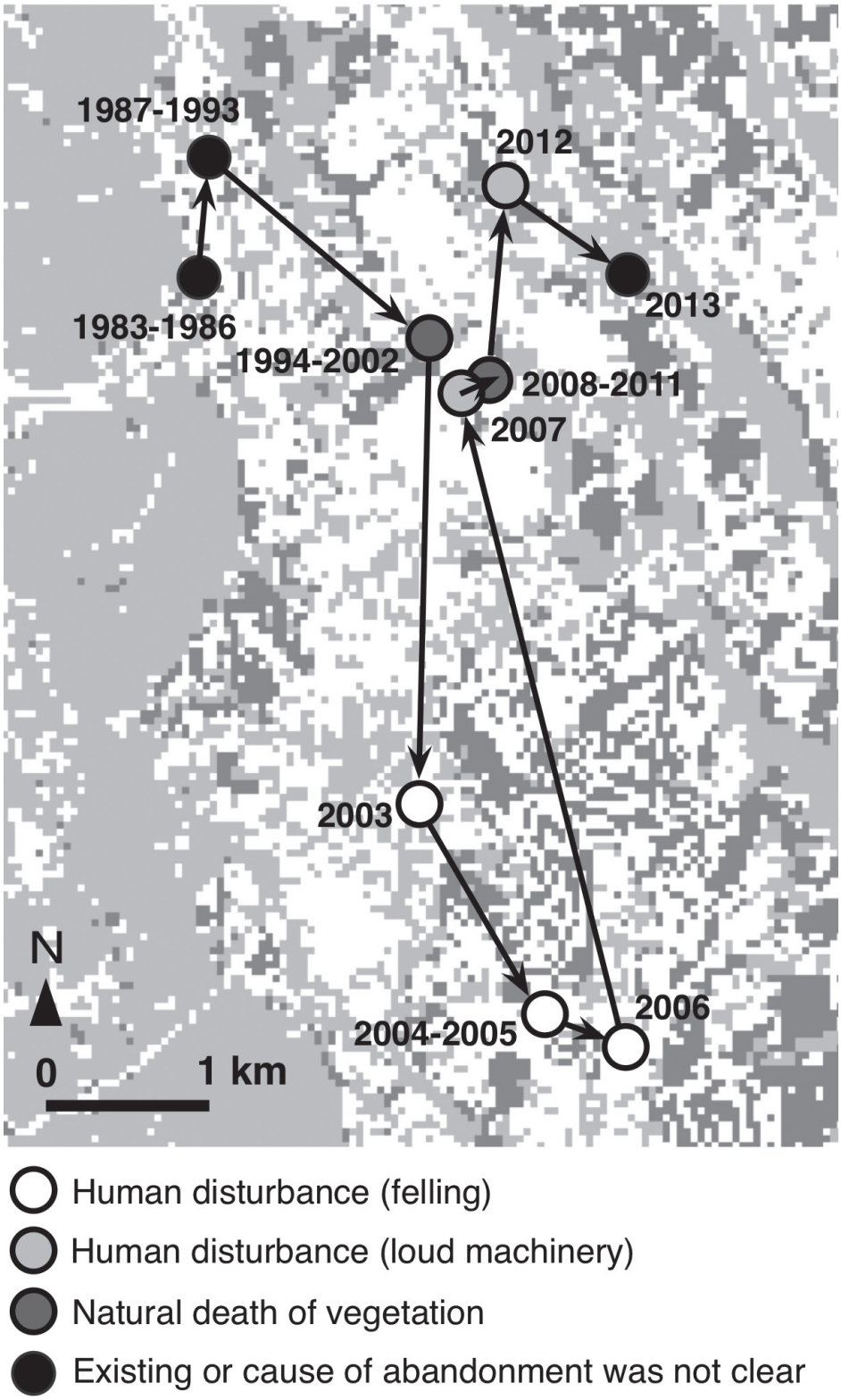


Figure 2. Enlarged map showing trajectory of lineage no. 27 with its observed causes of abandonment of constituent colony sites.

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able maximum distance for colony-site shifts included within a single lineage, we calculated mean nearest-neighbor distance from the center of observed colony sites (11.85 ± 1.76 km; 1999-2013), and it was assumed that each colony had a circular domain within which foraging herons and egrets belonged to the colony. The radius of the domain of attraction was set to be half the average nearest-neighbor distance (5.93 km; Mashiko and Toquenaga 2013). Since our focus was site fidelity at the colony level, we defined colony lineages regardless of whether the colony site at year t was composed of the same or different birds at year $t - 1$.

To detect which lineages exhibited site fidelity, we first focused on the persistence periods for lineages and classified them into two categories: "one-year" and "multiple-year". For multiple-year lineages, which may indicate site fidelity, we focused on the number of colony sites that the lineage had used and classified them into two categories: "mobile", which includes at least one location shift, and "stationary". To determine how many lineages in these two categories exhibited site fidelity, we performed the following analyses.

Measuring Site Fidelity of Colony Lineages

For stationary lineages, being stationary alone did not indicate site fidelity. For instance, when we compared site fidelity of a stationary lineage that persisted for 2 years with a mobile lineage that included two colony sites that existed for only 1 year and that persisted for 3 years, it could not simply be determined that the stationary lineage that persisted for 2 years exhibited site fidelity. To examine whether stationary lineages exhibited site fidelity, we compared persistence periods for sites of stationary lineages with those for sites of mobile lineages. Persistence periods for sites of mobile lineages were used as the null expectations for this comparison because if the persistence periods of stationary lineages were shorter than the average of those of mobile lineages, it would be difficult to assert that stationary lineages exhibited site fidelity. Since the datasets for persistence periods contained censored data (an abandonment event of a colony site was not observed before the end of our study period), non-parametric survival curves were estimated for each category with the Kaplan-Meier method in the survival analysis (Kleinbaum 1996). Differences between the curves were evaluated with the log-rank test.

To investigate whether the mobile lineages exhibited site fidelity, we examined colony trajectories (i.e., the consecutive movement path of colony sites within a lineage) by applying a correlated random walk method (Kareiva and Shigesada 1983) at the colony level. Since the shapes of trajectories are considerably different among lineages even if those lineages are composed of the same number of colony sites and movements (e.g., lineages #4 and #38 in Fig. 1), we considered a mobile lineage to exhibit site fidelity if the trajectory remained within a small area (entangled), and to not exhibit site fidelity if the trajectory was increasingly distant (untangled) or intermediate between entangled and untangled (border). To clarify which trajectories were entangled and which were untangled, we developed an index of the distance between a focal point and the last site of a trajectory (DFL), and compared those values to the observed and expected trajectories. DFL is inspired by net squared displacement, which is widely used for analyzing the movement patterns of mammals (Bergman *et al.* 2000) and insects (Brouwers and Newton 2010), as well as growth in plants (Cain 1990).

We calculated the DFL of observed trajectories. The focal point was a location at which the weighted sum of the distances from all given colony sites in a trajectory were minimized. We obtained this point using the *zsummin* function in the statistical program R package *orloca* (Fernandez-Palacin and Munoz-Marquez 2012), which deals with the Fermat-Weber location problem. Weighting was based on the persistence period of each colony site. For each observed trajectory, we constructed 100 expected trajectories by choosing a length and turning the angle randomly from all segments of all mobile trajectories as many times as the length of persistence period of the observed trajectory ($n = 517$, length: ranged from 0 to 5,908.6 m (482.7 ± 53.5 m), turning angle: ranged from −177° to 167.5° (0 ± 1.9°)). When a sampled length or turning angle forced the movement into a body of water or mountainous region (gray regions in Fig. 3), we sampled another length or turning angle so as to construct expected trajectories within a geographical range where colonies could be formed (white regions in Fig. 3). Finally, we compared the observed DFL

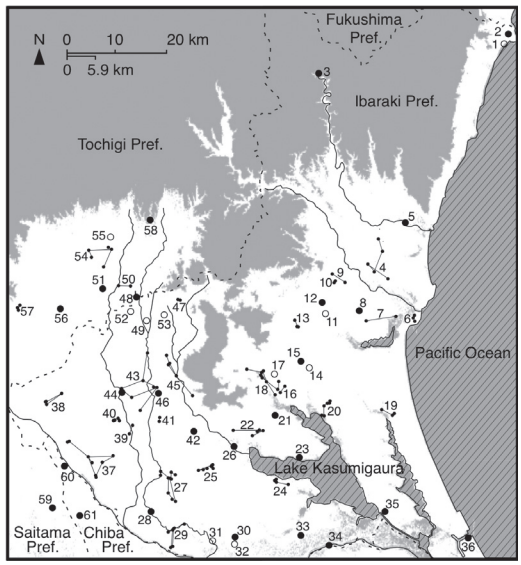


Figure 3. Map showing a geographical range where heron colonies could be formed. For constructing expected trajectories of mobile lineages, white areas indicating lowlands with an altitude of 0 m to 100 m, where heron colonies could be formed in trees and bamboo thickets, were used but gray areas indicating mountainous regions (> 100 m) or deep bodies of water were not used. Pref. = Prefecture.

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with the mean DFL of randomized trajectories to examine the entanglement of observed trajectories. We identified entangled and untangled trajectories when the DFL of the observed trajectory was respectively smaller and larger than the 95% confidence limits of those of the randomized trajectories. Trajectories that fell within the 95% confidence limit were classified as border.

Some colony lineages may have multiple trajectories: when a lineage contained more than one colony site in the same year, the trajectory diverged into different paths (e.g., lineage #54 in Fig. 1). Similarly, originally unique trajectories could be joined when colony sites from two trajectories were abandoned in the same year and, in the following year, a single colony site was newly established in a location near both the abandoned sites. However, even if a lineage contained more than one colony site in the same year, we used the larger, major colony site to make a single trajectory so as to avoid making too many trajectories when reliable data for the colony sizes of those sites were available (Mashiko and Toquenaga 2013). We examined the entanglement for all trajectories using DFL, but judgment of entanglement of multi-trajectory lineages was made for each colony lineage rather than each trajectory: the lineage was categorized as untangled, border, or entangled when the judgment of all trajectories was the same, and it was deemed border when the judgment differed among trajectories. All statistical analyses were conducted with statistical program R (R Development Core Team 2013). Where appropriate, we report mean ± SE.

RESULTS

During the 51-year period from 1963 to 2013, a minimum of 163 colony sites were used for at least one breeding season in the study area (Fig. 1). This included seven colony sites that were re-established at exactly the same location after their abandonment. The recorded 163 colony sites were categorized into 61 lineages. While 10 out of 61 lineages (16.4%) existed for only 1 year (open circles in Fig. 1), the remaining 51 lineages persisted for more than 1 year (Fig. 4A). These 51 multi-year lineages were composed of 26 mobile and 25 stationary lineages (Fig. 4B). Mobile lineages were composed of 127 colony sites. Stationary lineages were composed of 26 colony sites because one lineage had two colony sites within a 5.93-km

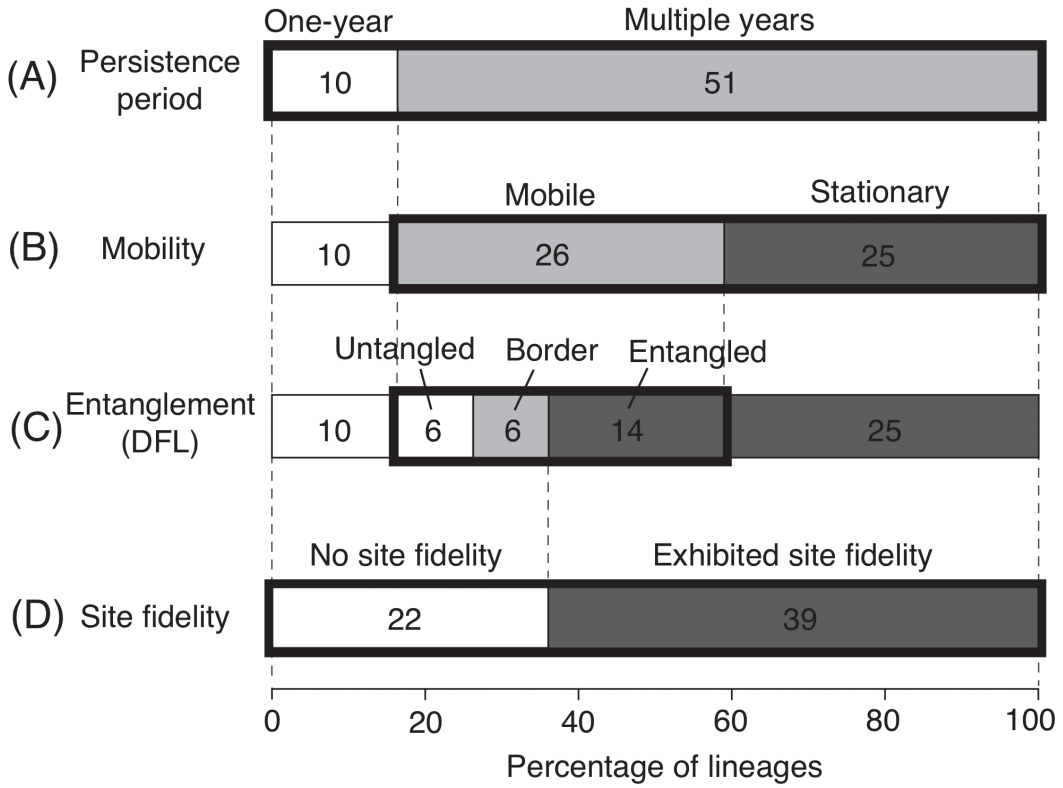


Figure 4. Summary of the classification of 61 lineages. Values represent the number of lineages. White, light gray and dark gray sections represent no site fidelity, border, and site fidelity, respectively.

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radius in the same year. Survival curves differed between colony sites of stationary lineages and null expectations: persistence periods of colony sites in stationary lineages were much longer than those in mobile lineages ($\chi^2 = 14.4$, $P < 0.001$; Fig. 5). Thus, the stationary lineages exhibited site fidelity by reusing the same site for many years.

The 26 mobile lineages were composed of 39 trajectories because five out of 26 lineages had multiple trajectories. The number of colony site shifts in a lineage ranged from one to nine (3.1 ± 0.29). Results of entanglement of trajectories evaluated based on DFL revealed that six lineages were above the line of equality for observed and expected DFL, six were border, and 14 were below (Fig. 6). Hence, four lineages were untangled, but 14 lineages (53.8%) were entangled (Fig. 4C). When those results were combined with one-year and stationary lineages, 22 lineages (36.1%) did not exhibit site fidelity, but 39 lineages (63.9%) did (Fig. 4D).

DISCUSSION

Lineages of heron and egret colonies demonstrated that these species had a preference for reusing the same or nearby sites as in previous years even though breeding sites are widely available throughout the study area. One possible explanation of the mechanism behind site fidelity is that herons and egrets have fidelity to foraging sites as well as to colony sites (Yamada 1994), and thus subsequently select certain locations as colony sites. Food availability, measured as the area of potential foraging habitat around the colony, has often been thought to be the most important factor affecting the location and size of a heron colony (Fasola and Barbieri 1978; Gibbs 1991). However, variables related to foraging sites did not have a major impact on locations and sizes of colonies in our study area (Fujioka *et al.* 2001; Tohyama 2005; Carrasco *et al.* 2014, 2017). Thus, the site fidelity of colony lineages is not merely caused by individuals' preferences for foraging habitats.

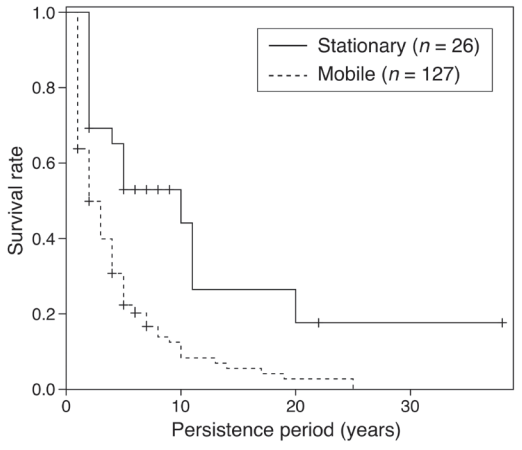


Figure 5. Survival curves of the persistence period of the colony sites using the Kaplan-Meier estimate. The broken line represents colony sites that constituted mobile lineages ($n = 127$), and the solid line represents those that constituted stationary colony lineages ($n = 26$). Vertical bars represent censored observations.

The frequency of return to natal or previous breeding locations has been well studied in colonial seabirds (Atwood and Massey 1987; Spendelow *et al.* 1995), but only three studies have assessed it in herons and egrets. Fernandez-Cruz and Campos (1993) banded Grey Heron fledglings ($n = 319$) at a colony in Spain over 5 years, with an 11.6% return to the colony the following year, 5.6% return after 3 years, and 3.1% return after 4 years. Melvin *et al.* (1999) measured natal site fidelity in the USA from a dataset spanning from 1914 to 1994 with 16.2% for Great Blue Herons (*A. herodias*), 23.8% for Great Egrets, 18.0% for Snowy Egrets (*E. thula*), 7.9% for Little Blue Herons (*E. caerulea*) and 12.5% for Tricolored Herons (*E. tricolor*). Fasola *et al.* (2002) investigated the dispersal rate of Little Egrets in colonies in the Camargue in southern France. They marked 6,618 chicks and 504 adults over 16 years and found an average estimated dispersal rate among colonies of 45%; in other words, 55% of individuals seemed to exhibit natal- or breeding-site fidelity. These low average individual site fidelities seemingly contradict our results showing that nearly two thirds of heron colony lineages exhibited site fidelity.

A high degree of site fidelity at the colony level may occur when a few faithful individuals return to a colony site and many others follow them. Generally, frequency of breeding-site fidelity is higher in males than in females

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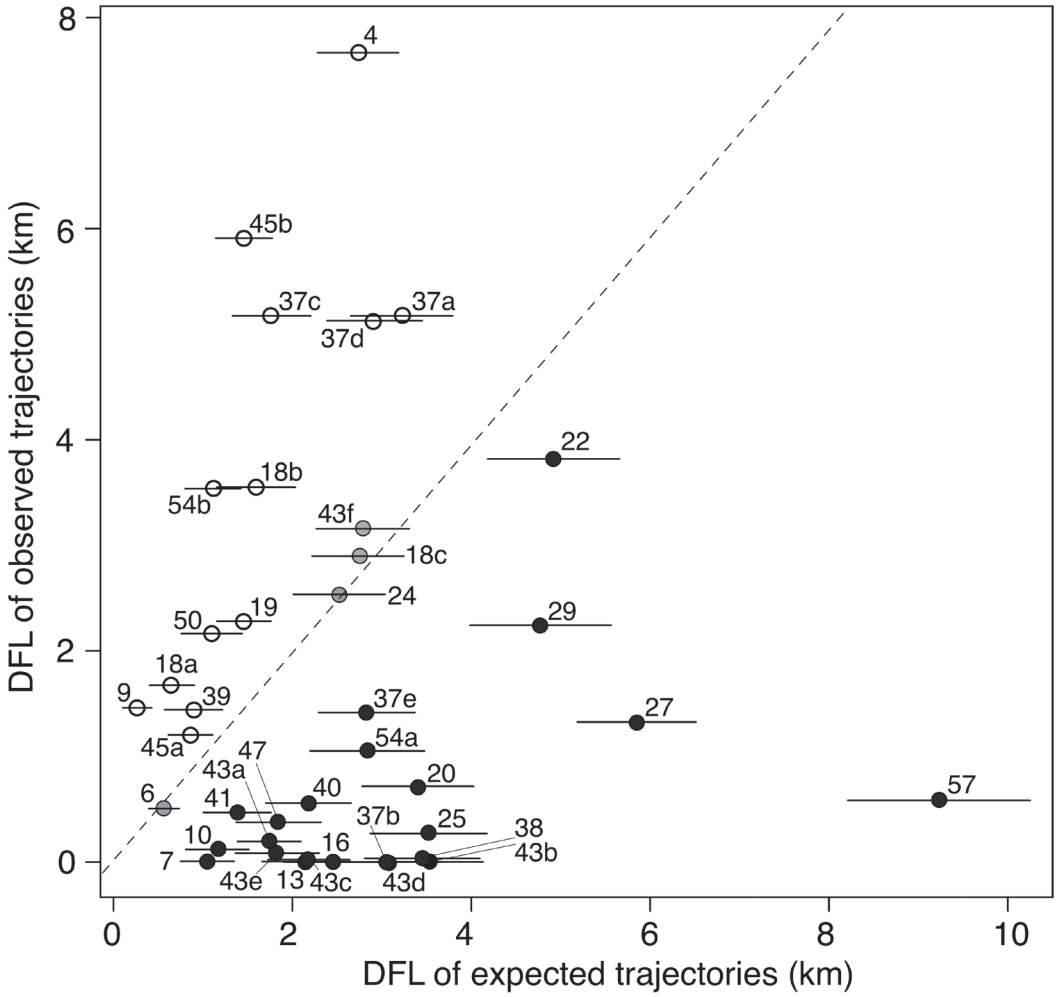


Figure 6. Comparison of observed and expected trajectories by distance between focal point and last colony site (DFL) of 26 mobile lineages. Each circle represents a trajectory. ID of the lineage and trajectory corresponds to Figure 1. Letters represent multiple trajectories in a lineage: lineage #18, 37, 43, 45 and 54 had 3, 5, 6, 2 and 2 trajectories, respectively. The broken line represents the line of equality. Trajectories were categorized into untangled (open), entangled (filled), and border (gray). Each circle with a line represents the exact value for observed trajectory and mean with a 95% confidence interval for the expected trajectory.

among bird species (Greenwood 1980; Shields 1982), the rate of nest- or colony-site fidelity is higher in adults than in juveniles (Haymes and Blokpoel 1978; Aebischer 1995), and the experience of breeding success at a colony site could also enhance fidelity to that location (Vergara *et al.* 2006). In our case, a proportion of male, adult or resident herons and egrets may have been familiar with colony locations. Those individuals may have exhibited colony-site fidelity and taken the initiative in the colony site selection at the beginning of every breeding season.

While other nomadic individuals, such as females, juveniles, dispersive adults and migrant species, may not exhibit fidelity to a specific colony site, they may be cued by the presence and abundance of conspecifics or hetero-specifics when choosing where to settle and thus contribute to a high degree of site fidelity at the colony level. This mechanism is expected to operate broadly in the breeding-habitat patch choice of social animals like colonial birds (Forbes and Kaiser 1994; Toquenaga *et al.* 1995; Serrano *et al.* 2003). Herons and egrets also refer to the presence of other spe-

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cies as a source of information for choosing their colony sites (Belzer and Lombardi 1989). Site fidelity or dispersal of individuals may be influenced by the status of their colonies, as with allee effects of colony size in colony site selection of individuals (Serrano *et al.* 2005).

Conversely, about one third of colony lineages did not exhibit site fidelity. There is a positive correlation between an individual's reproductive success and its subsequent nest- or colony-site fidelity (Vergara *et al.* 2006), and first-year breeders or immature birds rely on the reproductive successes of nesting adults to assess their own chances of breeding successfully in a given patch and to make settling decisions (Danchin *et al.* 1998; Schjørring *et al.* 1999; Calabuig *et al.* 2008). Heron and egret individuals that had bred at single-year colonies may be less likely to recruit follower individuals because they may have suffered lowered reproductive success, due to any number of factors including human disturbances, and moved to different colonies the following year.

Site fidelity was observed in more than half of mobile lineages, and it could have originated from a few faithful pioneer individuals with many others following them. Even when heron colonies shift their locations to alternative sites, mobile colony lineages tend to stay within a small area rather than moving far away unless some unsuitable condition, such as human disturbances, overrides the ecological advantages of site fidelity. For mobile colony lineages with an entangled trajectory, management techniques should be developed to retain colonies at locations where conflict with neighboring humans can be minimized. A historical perspective of colony lineages is necessary so as not to become trapped in a vicious circle of conflict, and the application of random walk models by considering the trajectories of mobile bird colony lineages as movement paths of an individual looking for suitable locations is useful for examining the site fidelity of gregarious animals at the colony level.

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