



Which combination of release techniques and ages minimizes post-release dispersal during Oriental Stork reintroduction?

¿Qué combinación de técnicas de liberación y edades minimizan la dispersión posterior a la liberación durante la reintroducción de la Cigüeña oriental?

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ABSTRACT. Many reintroduction attempts have encountered difficulties with long-distance dispersal of the released animals. In previous studies, release techniques and ages of the released individuals have been tested separately to examine their influence on post-release dispersal, with varied results. Dispersal patterns may be determined by a combination of release techniques and individual characteristics (age or rearing history). To reintroduce the Oriental Stork (*Ciconia boyciana*) to Japan, we released 1–7-year-old birds using soft and hard release techniques. The effects of different combinations of release techniques and ages or rearing histories on Oriental Stork dispersal distance and area within the first year after release were documented using global positioning system tracking data. Following soft and hard releases, some 1-year-old released birds became widely dispersed. However, all 1–3-year-old birds stayed in close proximity to the release sites. Therefore, hard-release techniques may be less problematic for Oriental Stork reintroduction if 1–3-year-old birds are selected for release. Soft-released first-year birds that had larger core areas and longer dispersal distances were not transported and trained, had only family members as their cage mates, and were reared by foster parents until fledging. Therefore, rearing histories could be an important factor in determining dispersal area and distance. To prevent the long-distance dispersal of species with the same ecological characteristics as the Oriental Stork (carnivorous, territorial, unattracted to conspecifics), we suggest hard-releasing 1–3-year-old birds.

RESUMEN. Muchos intentos de reintroducción han encontrado dificultades con la dispersión a larga distancia de los animales liberados. En estudios anteriores, las técnicas de liberación y las edades de los individuos liberados se han probado por separado para examinar su influencia en la dispersión posterior a la liberación, con resultados variados. Los patrones de dispersión pueden estar determinados por una combinación de técnicas de liberación y características individuales (edad o historial de cría). Para reintroducir la Cigüeña oriental (*Ciconia boyciana*) en Japón, liberamos aves de entre 1 y 7 años utilizando técnicas de liberación blandas y duras. Se documentaron los efectos de las distintas combinaciones de técnicas de suelta y edades o historias de cría sobre la distancia y el área de dispersión de la Cigüeña oriental durante el primer año tras la suelta, utilizando datos de seguimiento del sistema de posicionamiento global. Tras las sueltas blandas y duras, algunas aves liberadas de 1 año se dispersaron ampliamente. Sin embargo, todas las aves de 1 a 3 años permanecieron cerca de los lugares de liberación. Por lo tanto, las técnicas de suelta forzada pueden ser menos problemáticas para la reintroducción de la Cigüeña oriental si se seleccionan aves de 1 a 3 años para la suelta. Las aves del primer año liberadas en condiciones blandas, con zonas núcleo más amplias y distancias de dispersión más largas, no fueron transportadas ni adiestradas, sólo tuvieron como compañeros de jaula a miembros de su familia y fueron criadas por padres adoptivos hasta volantones. Por lo tanto, las historias de cría podrían ser un factor importante a la hora de determinar el área y la distancia de dispersión. Para evitar la dispersión a larga distancia de especies con las mismas características ecológicas que la Cigüeña oriental (carnívoras, territoriales, que no se sienten atraídas por congéneres), sugerimos liberar con dureza aves de 1 a 3 años de edad.

Key Words: *Ciconia boyciana*; dispersal distance; reintroduction; release age; release technique

INTRODUCTION

Concerns about biodiversity loss have been increasing in recent years (Ceballos et al. 2015; International Union for the Conservation of Nature: <https://www.iucnredlist.org/>). Reintroductions are attempts to introduce species to parts of their historical ranges where they were extirpated, to reestablish disappeared populations (IUCN/SSC 2013). The number of published examples in which reintroductions have been used as a conservation tool has increased rapidly since the late 1990s (Seddon et al. 2007). Reintroductions have been highlighted as a potential solution to species loss due to anthropogenic-induced climate change (Armstrong and Seddon 2008, Polak and Saltz 2011, Morandini and Ferrer 2017). However, the success rate of these attempts has not been high (Morris et al. 2021). Difficulties have often been encountered with long-distance dispersal by

released animals, which causes reduced growth or unfavorable composition in the reintroduced population during the early establishment phase (Armstrong and Seddon 2008, Richardson et al. 2015b, Berger-Tal et al. 2020). High prevalence and incidence of long-distance dispersal across taxa are suggested to be a significant problem that urgently needs to be addressed (Bilby and Moseby 2024). Dispersal of the released individuals is chiefly dependent on three factors: stress or confusion from unsuitable release procedures and environmental changes, a lack of conspecifics at the release sites, and exploratory behavior to find more suitable habitats and breeding sites (Stamps and Swaisgood 2007, Richardson et al. 2015b, Berger-Tal et al. 2020). If conservation practitioners and researchers do not address these factors, prolonged and long-distance dispersal can occur with released individuals (Stamps and Swaisgood 2007).

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Release techniques and individual characteristics are important factors in preventing long-distance dispersal (IUCN/SSC 2013). Hard and soft release techniques have primarily been used for reintroductions. The hard release technique involves animal release immediately after transportation to the release site, whereas soft release allows the animal to acclimatize to the release site's environment before release. A soft release could also include the provision of resources such as food, shelter, or refugia to the target individuals. Soft releases offer ample opportunities for released individuals to adapt to unfamiliar environments and reduce stress caused by release procedures, environmental changes, and access to food and other resources in the new sites (Stamps and Swaisgood 2007). Furthermore, they are predicted to enhance social cohesion, especially in cases in which multiple birds were housed in the same enclosure (Horwich 2001). In contrast, hard releases can cause greater dispersal, notably in birds that are released into unfamiliar environments without acclimatization (Nagata and Yamagishi 2016). Although soft releases seem to be a better technique than hard releases, a phylogenetic meta-analytical approach indicated that both techniques had similar effects with respect to birds (Resende et al. 2021).

Extensive research has focused on age as a significant factor influencing post-release movement in various species (van Heezik et al. 2009). In territorial birds, adult individuals tend to establish exclusive territories, whereas juveniles disperse over longer distances than adults, primarily driven by their exploratory behavior (Krüger et al. 2014, Miller et al. 2017). In Common Terns (*Sterna hirundo*) and House Sparrows (*Passer domesticus*), older birds exhibit higher tolerance to stress and confusion resulting from environmental changes than do their younger counterparts (Heidinger et al. 2008, Lendvai et al. 2015). Therefore, releasing older birds is expected to mitigate dispersal. The origin of individuals, whether they are wild or captive-bred animals, has also been discussed as a factor influencing the post-release movement of released individuals (Crates et al. 2023). The perception of stressors can vary considerably between wild and captive-bred individuals (Jones and Merton 2012). Richardson et al. (2015a) emphasized the advantages of soft release for birds, particularly when dealing with captive-bred individuals. Similarly, Jones and Merton (2012) recommended that captive-reared individuals undergo soft release with support, whereas wild-caught individuals should be released immediately.

Various studies have independently examined release techniques and age to prevent post-release dispersal, yielding diverse levels of effectiveness (Clarke et al. 2002, van Heezik et al. 2009, Mitchell et al. 2011, Bradley et al. 2012, Hardouin et al. 2014). However, the optimal release strategy varies among taxa. Therefore, conducting releases in an experimental way can help to identify the optimal strategy. We hypothesized that if release techniques and appropriate age selection are not implemented for captive-bred territorial birds, the released individuals disperse over greater distances. Specifically, the hypothesis suggests that younger birds subjected to hard release are susceptible to various dispersal factors. Both hard and soft releases of older birds could result in their vulnerability due to the lack of conspecifics. Furthermore, soft release of younger birds could induce exploratory behavior. Therefore, we assumed that long-distance dispersal is likely in younger birds subjected to hard release. Understanding post-

release site fidelity in reintroduced individuals is crucial for effective reintroduction management strategies (Berger-Tal and Saltz 2014). Even if the dispersal distance is small, a large home range can still hinder reintroduction success. Variation in post-release behavior may stem from simplified captive environments compared to those in the wild (Crates et al. 2023). However, the specific rearing procedures that influence post-release movement remain unclear.

The Oriental Stork (*Ciconia boyciana*) is classified as an endangered bird species (BirdLife International 2018). In Japan, the wild breeding population of the Oriental Stork was declared extinct in 1971 due to a substantial decline caused by factors such as overhunting, habitat loss, pollution, and inbreeding within the remaining population (Ezaki et al. 2013). To address this issue, we imported > 60 birds as founders between the 1960s and 2000s from Chinese zoos and natural habitats in Russia (Matsumoto 2020). In 2005 and onwards, captive-bred birds (1–7 years old) were released into Hyogo Park of the Oriental White Stork (HPOWS) as part of efforts to restore the former species range. Both soft and hard release techniques were employed, and some birds were equipped with satellite transmitters before release. Our study aimed to assess the effects of various release techniques, ages, and rearing histories on the dispersal area and distance of released Oriental Storks in Japan. Minimizing post-release dispersal is crucial for the advancement of reintroduction biology (Armstrong and Seddon 2008). The results obtained by evaluating different release methods provide valuable insights for enhancing release protocols and contribute to the formulation of effective conservation strategies.

METHODS

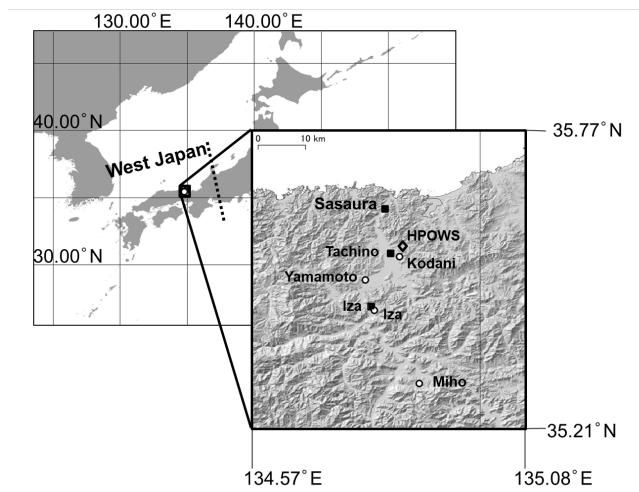
Subject birds

The Oriental Stork source population originated from migratory birds that breed in the Russian Far East and migrate to southeastern China for overwintering (Shimazaki et al. 2004, Fan et al. 2020). Oriental Storks are long-lived species that attain maturity at a minimum age of two years (Ohsako et al. 2012). We released individuals based on pedigree diversity through captive breeding at HPOWS and zoos. Most of the released or fledged Oriental Stork individuals were marked with color bands to facilitate individual identification. We focused on 18 subject birds (10 males and 8 females) that were captive-reared at HPOWS (Appendix 1). The sex of birds was determined through DNA analysis of blood samples (HPOWS, *unpublished data*).

Release site and year

The release sites were located within the breeding area that was previously inhabited by the Oriental Stork population (Fig. 1; Hyogo Prefectural Board of Education and Hyogo Park of the Oriental White Stork 2014). Hunting of wild Oriental Storks is currently prohibited by law, “stork-friendly farming” has been implemented (farming that does not rely on chemical fertilizers and pesticides), and artificial nest poles have been installed around the release site. The site is predominantly characterized by paddy fields, with secondary forests in the surrounding landscape. To minimize the potential risk of accidents for released storks, e.g., collisions with artificial structures due to disorientation caused by rapid environmental changes or lack of familiarity with the wild, we deliberately selected an open area with few artificial

Fig. 1. Map of Oriental Stork release sites. Open circle = soft release site, filled square = hard release site, open diamond = Hyogo Park of the Oriental White Stork (HPOWS), dotted line = division of western and eastern Japan.



structures and little pedestrian traffic. To mitigate the risk of storks being attacked by conspecific species, we selected areas located outside the territories of such species. To facilitate the acclimatization of storks during soft releases, we selected paddy biotopes > 1 ha, providing year-round feeding grounds. The timing of release during the day was selected when the weather was not too stormy.

The release sites were all within a 40 km radius. We soft-released 11 birds between 2006 and 2018 (one male and one female in 2006 and 2007, three males and one female in 2013, one female in 2017, and two males in 2018; Appendix 1). The birds left the enclosure within the first few days after opening the roof net. We hard-released seven birds (one male and two females in 2006, two males and one female in 2007, and one female in 2018).

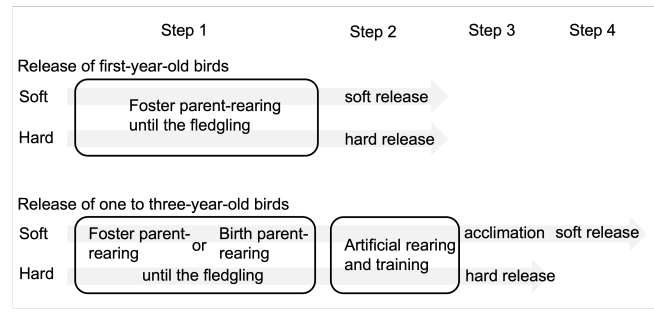
Release techniques and ages

Over five years following the experimental release in 2005, the reintroduction plan was designed to test four release methods: (1) soft release of first-year birds, (2) soft release of one- to three-year-old birds, (3) hard release of one- to three-year-old birds, and (4) captive females held in an open-roofed cage to allow them to breed with males living in the wild to release the fledglings. Although the first three methods were effectively implemented, the fourth method was executed only once because of an unexpected attack on the released female by a wild male on the release day. After the release techniques and ages had been decided, individuals were selected for the reintroduction plan. Details of release techniques, ages, and bird selection are included in Appendix 2.

Soft release of first-year birds

We followed a specified release process (Fig. 2). The initial step involved foster parent-rearing to the fledgling stage. We transferred two eggs from the captive-bred parent birds in HPOWS to the foster parent birds in the enclosure for soft release

Fig. 2. General steps followed for Oriental Stork releases.



approximately 25–29 days after laying. The second step consisted of the soft release phase. After determining that the fledglings were flight-ready, the roof nets were opened, allowing the fledglings to exit freely. Throughout the first month, the roof remained open, and food was provided to support their transition.

Hard release of first-year birds

We predominantly subjected first-year birds to soft release. However, we also included one bird (214; Appendix 1) that underwent a hard release during its first year to compare its dispersal patterns with those of the soft-released individuals. The initial step for this bird was the same as in the soft release method used for first-year birds. The second step involved a hard release procedure. We placed the stork in a wooden transport box measuring 930 × 430 × 1050 mm. The bird was then transported by car to the designated release site, where it was released individually into the open field.

Soft release of one- to three-year-old birds

The first step involved a similar process to the soft release of first-year birds, with the exception that some birds were reared by their birth parents. The second step consisted of artificial rearing and training. After completing the initial step, the birds were transferred to individual cages, shared cages with multiple birds, or a training cage. Throughout this second step, the birds underwent multiple transfers between individual or shared cages and the training cage. Over a period of approximately 300–650 days, the birds were trained together with other birds to develop their flight ability, conspecific response, and foraging skills. The specific protocols followed during the training phase are outlined in Appendix 2. The third step involved acclimation. The birds were relocated to an enclosure designed to acclimate to the external environment, where they resided for at least three months after training. The fourth step encompassed the soft release. During this stage, we opened the roof nets of the enclosure, allowing the birds to exit freely. Supplementary feeding was provided if birds returned to the enclosure within the first month.

Hard release of one- to three-year-old birds

The first and second steps of the hard release process for one- to three-year-old birds were identical to the corresponding steps in the soft release method. The training was conducted for approximately 100–500 days. The third step involved the hard release of individuals. After training, the birds were reared in individual cages for some days and then hard released. The protocol followed was the same as that used for the hard release of first-year birds.

Transmitter attachment

To attach transmitters, all focal birds were captured by two staff members. We captured the birds by hand or used a fishing net with a diameter of approximately 60 cm. Storks were selected for transmitter attachment to minimize any negative effects. Transmitters were attached at least seven days before the birds were released to determine whether there were any problems with the transmitter or the individual. We used a solar-powered GPS Argos transmitter (Solar Argos/GPS 70 g PTT, Microwave Telemetry, Columbia, Maryland, USA). The size of the device was $9.70 \times 3.84 \times 2.49$ cm, the length of the antenna was 17.78 cm, and the mass was 70 g. The total weight was 90 g, including the attachment, which was approximately $\leq 3\%$ of the body mass (3700–5550 g) of the subject birds. The transmitter was attached using a custom harness made of tubular Teflon ribbon (width 19 mm, mass 17.8 g). Details of the transmitter attachment protocol are included in Appendices 2 and 3.

Positioning interval and duration

The devices acquired six global positioning system locations per day at 1-h ($N = 8$ transmitters) or 3-h ($N = 10$ transmitters) intervals and transmitted the locations via Argos every three days. Positions were recorded between 06:00 and 18:00 local time with a 12-h off-duty cycle. We used only five positions per day, derived from both transmitters at different intervals. We calculated the straight-line distance between two locations using QGIS Desktop 3.10.1 (QGIS Development Team 2019). Erroneous locations were filtered based on the maximum flight speed of 112 km/h of the related Black Stork (*Ciconia nigra*; Chevallier et al. 2010).

Classification of subject birds

Our subject Oriental Storks fitted with transmitters were classified into two groups according to age (first-year-olds = younger; one- to three-year-olds = older), and two based on rearing methods. Therefore, four combinations of release techniques and ages were used: S0 = soft release of first-year-olds (five males, two females), H0 = hard release of first-year-olds (one female), S1-3 = soft release of one- to three-year-olds (two males, two females), and H1-3 = hard release of one- to three-year-old birds (three males, three females).

Dispersal area and distance

We used a 25% kernel density estimate (KDE) and a 50% minimum convex polygon (MCP) to calculate the core area after release. An MCP of 50% has often been used in previous research on the home range of storks (Zurell et al. 2018, Xu et al. 2021). However, not only core areas, but those connecting core areas, have often been included with the MCP. To identify accurately the core areas frequently used by released birds, we employed both the MCP and KDE. Although a KDE of 50% is commonly used to measure the core area (Laver and Kelly 2008), we selected a KDE of 25% because a KDE of 50% included too many areas uninhabitable by storks, such as the ocean. We defined the dispersal distance as the straight-line distance from the release site to the center of gravity for the core area. When an individual had several core areas, the distance between the release site and the center of the core area containing the largest number of positions was used as the dispersal distance, and the sum of each core area size was used as the core area size. We computed a KDE of 25% and an MCP of 50% for each individual distribution as

the core area using the statistical analysis software R version 3.6.2 (R Core Team 2019) and the package adehabitatHR version 0.4.16 (Calenge 2006).

Statistical analysis

The kernel density estimate was only used in the statistical analysis for dispersal because the core areas of released stork occurrence were fitted more accurately by the KDE than the MCP (Appendices 4–8). To determine the factors affecting core area size and dispersal distance, we used a generalized linear mixed model with gamma distribution and a log-link function, in which the explanatory variable candidates were: release technique (hard or soft release), age at release (first-year or one- to three-year-old birds), and sex. Individual identity was included as a random effect. Model selection was performed using the Akaike information criterion (AIC). The model with the smallest AIC was selected as the simplest, best-fitting model. Because the captive rearing history and release age were correlated, we analyzed the effects of captive rearing history on core area size or dispersal distance separately from the preceding analyses. Captive rearing history focused on the number of transfers between cages and training days, the maximum number of individuals reared together, and the number of released birds raised by foster parents or birth parents. To compare the effect of the birds' rearing parents (birth or foster parents), we conducted a Mann-Whitney U-test. Statistical analyses were performed using R version 3.6.2 (R Core Team 2019) and the packages lme4 version 1.1.23 (Bates et al. 2015), MuMIn version 1.43.17 (Bartoń 2020), and car version 3.0.7 (Fox and Weisberg 2018).

RESULTS

Factors affecting core area size and dispersal distance

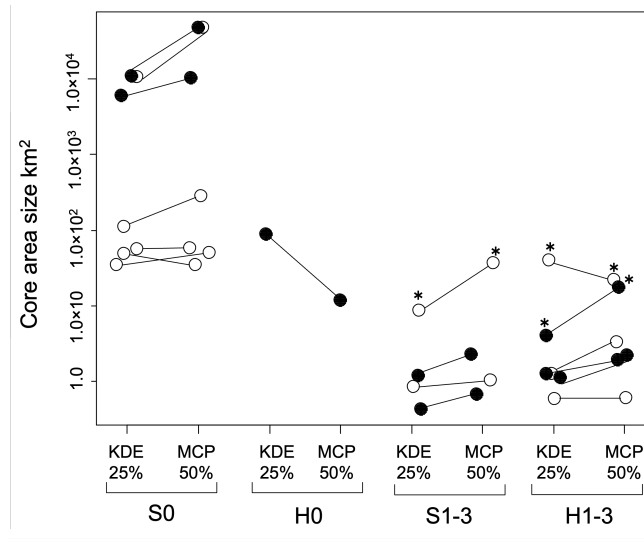
In terms of the core area size, the AIC identified the full model as the best fitting, in which only the effect of release age was significant (Table 1). The model indicated that the core area size was smaller for birds released as one- to three-year-olds than for birds released in their first year (Fig. 3). For both KDE and MCP, S0 was divided into two groups, which were larger than those for H0, S1-3, and H1-3 (Fig. 3).

Table 1. Summary of model selection results for factors affecting the core area size of reintroduced Oriental Storks in Japan. Explanatory variables in the model include the release technique (soft and hard), release age (first-year and 1–3-year-old birds), and sex (male and female).

Rank	Model	Δ AIC	Akaike weight	Log likelihood
1	Release age*** + Method + Sex	0.00	0.993	89.012
2	Release age*** + Method***	9.89	0.007	83.068
3	Release age***	18.84	0.000	77.592
4	Release age*** + Sex	20.77	0.000	77.626
5	Null	25.53	0.000	73.249
6	Sex	27.83	0.000	73.096
7	Method + Sex	32.72	0.000	71.654
8	Method***	33.81	0.000	70.104

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 3. Core area sizes of released Oriental Storks. S0 = soft release, first-year bird; H0 = hard release, first-year bird; S1-3 = soft release, 1–3-year-old bird; H1-3 = hard release, 1–3-year-old bird; KDE = kernel density estimate; MCP = minimum convex polygon; filled circle = female; open circle = male. Points joined by a line are the same individual bird. Asterisk indicates a breeding individual.



In terms of dispersal distance, the AIC also identified the full model as the best-fitting model, in which only the effect of release age was significant (Table 2). The model indicated that dispersal distance was shorter for birds released as one- to three-year-olds than for birds in their first year (Fig. 4). For both KDE and MCP, the dispersal distance of S0 varied substantially among individuals (Fig. 4). However, the dispersal distance of S1-3 and H1-3 were relatively short, and their individual variation was relatively low.

Three of the eighteen subject birds started breeding during the study period, including one individual from the S1-3 (ID:391) and two individuals from the H1-3 groups (ID:384 and ID:389). Their core areas were relatively small (Fig. 3), and their dispersal distances were relatively short (Fig. 4).

Correlations between rearing history and core area size or dispersal distance

We found marginally significant ($P = 0.05\text{--}0.1$) negative correlations between core area size and the number of transfers between cages ($r = -0.44$, $P = 0.06$), the maximum number of individuals living together ($r = -0.45$, $P = 0.06$), and the number of training days ($r = -0.42$, $P = 0.09$; Fig. 5). Core area size tended to be smaller in released birds raised by birth parents than by foster parents (Mann-Whitney U-test, $Z = 1.68$, $P = 0.09$).

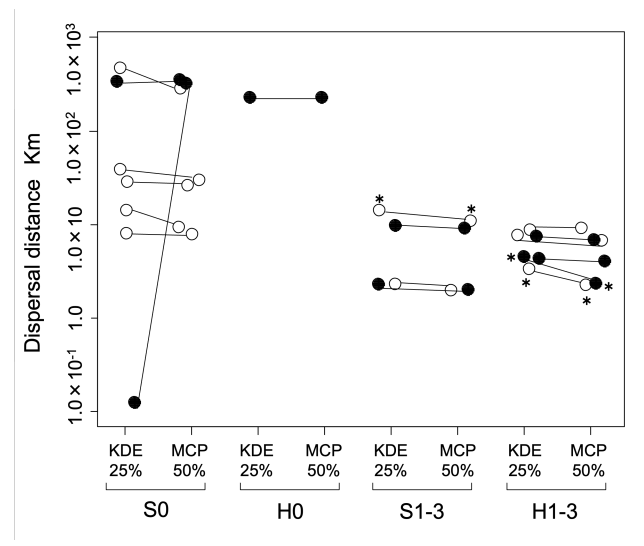
Dispersal distance was negatively correlated with the maximum number of individuals living together ($r = -0.47$, $P = 0.05$; Fig. 6). We also found a marginally significant negative correlation between dispersal distance and the number of transfers between cages ($r = -0.46$, $P = 0.06$), but dispersal distance and the number

Table 2. Summary of model selection results for factors affecting dispersal distance of reintroduced Oriental Storks in Japan. Explanatory variables in the model include the release technique (soft and hard), release age (first-year and 1–3-year-old birds), and sex (male and female).

Rank	Model	Δ AIC	Akaike weight	Log likelihood
1	Release age* + Method + Sex	0.00	0.429	92.898
2	Null	0.64	0.311	89.578
3	Release age*** + Sex***	2.97	0.097	90.415
4	Release age***	3.93	0.060	88.934
5	Method*** + Sex***	5.33	0.030	89.233
6	Method***	5.54	0.027	88.126
7	Sex***	5.57	0.026	88.114
8	Release age* + Method	6.15	0.020	88.824

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 4. Dispersal distances of released Oriental Storks. S0 = soft release, first-year bird; H0 = hard release, first-year bird; S1-3 = soft release, 1–3-year-old bird; H1-3 = hard release, 1–3-year-old bird; KDE = kernel density estimate; MCP = minimum convex polygon; filled circle = female; open circle = male. Points joined by a line are the same individual bird. Asterisk indicates a breeding individual.

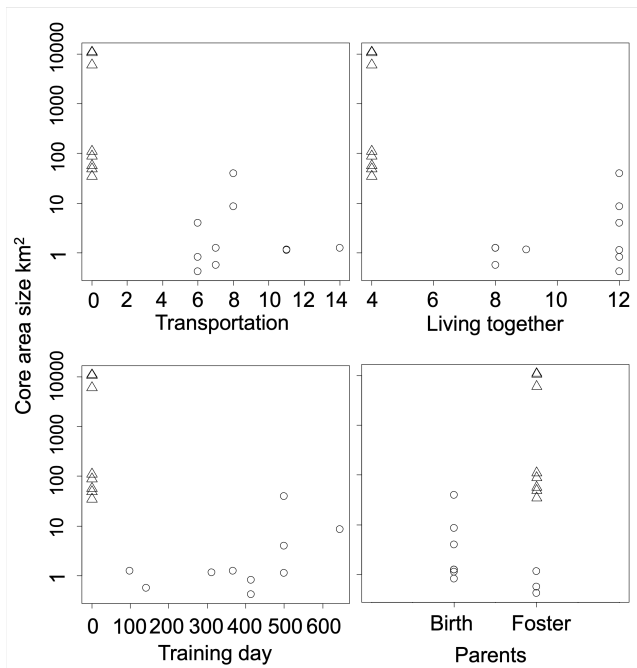


of training days were uncorrelated ($r = -0.32$, $P = 0.36$). Dispersal distance was smaller for released birds raised by birth parents than by foster parents ($Z = 2.04$, $P = 0.04$).

DISCUSSION

We assumed that long-distance dispersal and large dispersal area of post-release Oriental Storks are more likely to occur in H0 than in the other three groups. However, we found that the core area sizes and dispersal distances were not clearly greater in H0 than in the other groups. Therefore, our hypothesis was only partially supported.

Fig. 5. Relationship between core area size and rearing history. Transportation is the number transfers between cages. Living together is the maximum number of individuals reared together. Training day is the number of training days. Parents indicates whether the released bird was raised by foster parents or birth parents. Triangle = first-year bird, circle = 1–3-year-old bird.



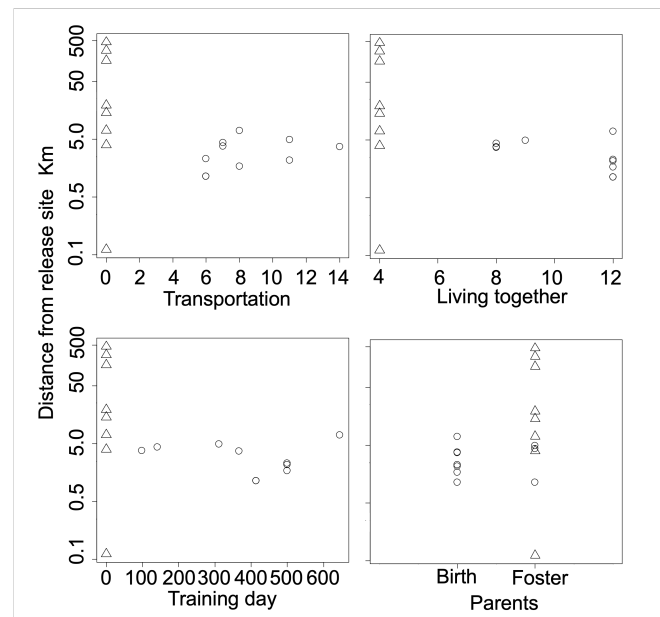
Effects of release age

The statistical models indicated that release age was the most influential factor. In another carnivorous, territorial bird species, the Barn Owl (*Tyto alba javanica*), wild juveniles were observed to disperse farther from the release site than were older individuals. This behavior was attributed to the juveniles' inexperience in hunting live prey and searching for suitable areas with abundant prey (Saufi et al. 2020). In contrast, a study of dispersal rates in soft-released Kokako (*Callaeas wilsoni*) showed no significant differences between adults and subadults at 7 days post-release (Bradley et al. 2012). Reintroduced Kokako are attracted to the playback of conspecific songs (Molles 2008). In species in which conspecific attraction plays a crucial role, variation in dispersal between younger and older individuals may be smaller because younger birds prioritize proximity to conspecifics over finding better feeding sites or establishing their own territories through dispersal. Therefore, selecting older individuals, preferably older than fledglings, for release could be an effective strategy to prevent long-distance dispersal in species that are relatively unattracted to conspecifics or are territorial breeders, such as Barn Owls and Oriental Storks.

Effects of release technique

A dispersal study of wild Barn Owls using five combinations of release techniques and ages, i.e., hard-released adults, hard-released juveniles, soft-released juveniles, soft-released adults, and

Fig. 6. Relationship between distance from the release site and rearing history. Transportation is the number transfers between cages. Living together is the maximum number of individuals reared together. Training day is the number of training days. Parents indicates whether the released bird was raised by foster parents or birth parents. Triangle = first-year bird, circle = 1–3-year-old bird.



soft-released hand-reared fledglings, only identified soft-released adults in the study area for > 30 days, indicating that the other release methods were ineffective (Saufi et al. 2020). Another study of adult, captive-reared, territorial Burrowing Owls (*Athene cucularia hypugaea*) released in pairs concluded that soft-released birds were more likely to stay at the release site, for up to two weeks after release, than were hard-released birds (Mitchell et al. 2011). In both Barn Owls and Burrowing Owls, individuals that remained closer to the release site had either bred or formed bonded pairs during the pre-release acclimation period. In some cases in our study, both male and female Oriental Storks were released simultaneously; however, the 3-month pre-release acclimation period may have been too short for pair bonding. A study of a similar species with comparable life history traits, captive-reared Crested Ibis (*Nipponia nippon*) adults, examined trip distances up to six months after release and found that soft-released birds remained closer to the release site compared to hard-released ones (Nagata and Yamagishi 2016). Notably, Crested Ibis is a colonial breeder (Wingfield et al. 2000), whereas Oriental Stork is a solitary nesting species. These findings suggest that soft release may be more effective when birds are released in pairs or are susceptible to conspecific attraction.

Effects of release sex

We did not detect any sex differences in dispersal area and distance, possibly due to the different ages of the study birds. However, in a study of reintroduced Crested Ibis, adult birds showed sex differences in dispersal (Nagata and Yamagishi 2016).

First-year females had longer mean dispersal distances (189.16 km²) than males (112.73 km²), similar to the natal dispersal pattern of White Storks (Chernetsov et al. 2006). In contrast, among one- to three-year-old birds, males had longer mean dispersal distances (7.22 km²) than females (5.68 km²).

Effects of rearing history

Captive rearing methods appeared to influence the breeding behavior of Crested Ibis post-reintroduction (Okahisa et al. 2022). Therefore, examining rearing method characteristics that affect post-release dispersal behavior is crucial. We found that individuals that were neither transported nor trained had only cage mates as their family (i.e., foster parents and two juveniles), were reared by foster parents until fledging, and had larger core areas and longer dispersal distances. Their rearing histories corresponded to those of soft-released first-year birds. Therefore, rearing histories can be an important factor in determining dispersal area and distance. However, we could not distinguish between release age and rearing method to determine which factor contributed more to dispersal. Therefore, future research is needed to investigate the relative contributions of these factors to dispersal.

Comparison with the wild population

Wild Oriental Stork juveniles, 4–21 days after fledging, exhibit individual variation in their MCP 50% home range (0.29–6.7 km²; Xu et al. 2021). Similarly, the core area of storks released in their first year varied significantly among individuals (ranging from 34 to 11,000 km²). Although substantial individual differences in the core areas are characteristic of this species, the differences were more pronounced in released captive-reared birds compared to their wild counterparts. This result might be attributed to the extended tracking period of the study birds.

The founders of Japanese-reintroduced Oriental Storks migrate from the breeding areas of the Russian Far East to southwest China along the coast from late July to late October. They then stay in wintering areas until late March (Shimazaki et al. 2004, Fan et al. 2020). Interestingly, we found that some first-year birds had core areas far to the west of the release site during the wintering period. Although these birds may exhibit similar migration behavior to the founders, further studies are needed to understand the relationship due to our relatively small sample size.

Effects of artificial feeding

Many reintroduced individuals depended on food intended for captive birds in the open cages of HPOWS. Three S0, four S1-3, and two H1-3 birds established their core areas to include HPOWS despite the small area (Appendices 5–8). Thus, food stealing could influence core area size and dispersal distance. HPOWS identified and recorded the occurrence of reintroduced individuals in open cages during the feeding of captive individuals. The dispersal areas and distances of one- to three-year-old birds were small and less variable, but their occurrence in open cages varied greatly from 0 to 86%. The occurrence of first-year birds in the open cage varied considerably depending on dispersal distance: 0% for the three long-dispersed birds, and 0–65% for the seven short-dispersed birds, varying on an individual basis. Therefore, feeding dependency in the open cage did not influence the dispersal of released storks.

Effects of bird density

Density-dependent effects also determine dispersal behavior (Matthysen 2005). Variations in the dispersal area and distance of the released first-year birds have been increasing annually, possibly related to the population size around the release site (Deguchi et al. 2022). The daily average number of occurrences of reintroduced birds in the open cage may be an indicator of the population density around the release area (11.6 birds in 2013, 9.39 birds in 2017, and 9.33 birds in 2018). The dispersal area and distance of released first-year-old birds in those years varied substantially among individuals released in the same year (area and distance, respectively: 34.58–11,002.42 km² and 0.13–474.03 km in 2013, 6017.11 km² and 338.85 km in 2017, 56.30–110.05 km² and 28.70–228.51 km in 2018). Therefore, density dependence may not have affected the dispersal of first-year birds. This intraspecific variation needs to be studied further in the future.

CONCLUSION

Based on our findings, we conclude that one- to three-year-old Oriental Storks had smaller and less variable dispersal areas and distances than did first-year birds. Hard-release techniques may be less problematic for Oriental Stork reintroduction if one- to three-year-old birds are selected for release. To prevent long-distance dispersal in species with similar ecological characteristics, such as being carnivorous, territorial, and unattracted to conspecifics, hard release of one- to three-year-old birds is recommended. However, our study was limited by a small sample size, and we emphasize the need for further research on other species with similar or different ecological traits to develop effective strategies for preventing long-distance dispersal in reintroduction efforts.

Author Contributions:

R. K. and T. D. conceived the ideas and designed the methodology; M. F. and Y. O. collected the data; R. K. analyzed the data; R. K. and T. D. led the writing. All authors contributed data and contributed to the writing and editing.

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Data Availability:

All data analyzed during this study are available from the corresponding author on reasonable request.

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Appendix 1. Detailed information on subject birds of the Oriental Stork released in Japan. M and F refer to the male and female, respectively. Age refers to the age in years of age at release. No. refers to the number of GPS positions during the first year.

ID	Sex	Age	Positioning Interval	Positioning Time zone	Release Date [†]	Release Site	Release Technique	Body mass (g)	No.
381	M	2	3h	6:00-18:00	2006/9/24	Koudani ¹	Soft	4750	1293
382	F	2	3h	6:00-18:00	2006/9/24	Koudani ¹	Soft	4100	1210
391	M	3	3h	6:00-18:00	2007/9/23	Yamamoto ²	Soft	5450	1202
399	F	2	3h	6:00-18:00	2007/9/23	Yamamoto ²	Soft	4800	1156
477	M	0	1h	6:00-18:00	2013/6/13	Iza ³	Soft	4950	1754
476	M	0	1h	6:00-18:00	2013/6/22	Iza ³	Soft	4900	1764
481	M	0	1h	6:00-18:00	2013/7/25	Miho ⁴	Soft	4600	1811
480	F	0	1h	6:00-18:00	2013/7/19	Miho ⁴	Soft	3700	1801
179	F	0	1h	6:00-18:00	2017/8/4	Miho ⁴	Soft	3800	1713
212	M	0	1h	6:00-18:00	2018/10/3	Miho ⁴	Soft	4700	1809
213	M	0	1h	6:00-18:00	2018/10/3	Miho ⁴	Soft	4800	1812
363	F	3	3h	6:00-18:00	2006/9/23	Tatino ⁵	Hard	4650	1439
384	F	2	3h	6:00-18:00	2006/9/23	Tatino ⁵	Hard	3800	1175
389	M	2	3h	6:00-18:00	2006/9/23	Tatino ⁵	Hard	5400	1139
403	F	2	3h	6:00-18:00	2007/9/22	Sasaura ⁶	Hard	4850	1487
405	M	1	3h	6:00-18:00	2007/9/22	Sasaura ⁶	Hard	5550	1105
408	M	1	3h	6:00-18:00	2007/9/22	Sasaura ⁶	Hard	5550	1307
214	F	0	1h	5:00-19:00	2018/9/27	Iza ²⁷	Hard	4250	1825

[†]In the soft release, because some individuals do not leave their cages for several days even after the roof is opened, there are individuals whose release date differs from their actual release date.

¹35°31'56.2"N 134°50'50.1"E

²35°29'17.8"N 134°46'57.2"E
³35°25'50.3"N 134°47'58.3"E
⁴35°17'32.1"N 134°53'04.8"E
⁵35°32'18.8"N 134°49'49.5"E
⁶35°37'21.8"N 134°49'11.2"E
⁷35°26'15.5"N 134°47'36.5"E

Appendix 2. Details of Methods (release techniques, ages, bird selection, and transmitter attachment) and Result (distribution of core areas).

METHODS

Release techniques and ages

Soft release of first-year birds

Egg-fostering was accepted in all cases. The frequency and amount of food provided were regulated according to the food requirements of the chicks, and 800–3,900 g of Japanese horse mackerel (*Trachurus japonicus*) and loach (*Misgurnus anguillicaudatus*) were provisioned in plastic tubs in each enclosure one to four times per day (Matsumoto et al. 2017). When they were soft-released, the foster parents had their flight feathers cut or were equipped with wing brails to prevent them from leaving the enclosure (Matsumoto et al. 2017).

Hard release of first-year birds

We transferred the first-year birds from captive-bred parents to Hyogo Park of the Oriental White Stork (HPOWS) to foster parents in this park, similar to the soft-released first-year-old birds.

Soft release of one- to three-year-old birds

The frequency and amount of food provided during the fledgling period were maintained similar to those during the release of the first-year birds. For the second step, the choice of the cage was determined by the availability of cages and the release plan. In the individual cage, approximately 500–600 g of living or thawed horse mackerel, rainbow trout (*Oncorhynchus mykiss*), crucian carp (*Carassius* spp.), and loach were provided in plastic tubs once or twice daily. After the first step, the timing of the transfer of cages was prior to the next breeding season for parents of subject bird, approximately half a year after the birth of subject birds from October to November. In the shared and training cage, the same prey species and feeding frequency as those in the individual cages were provided, with the food amount being calculated as 650 g multiplied by the number of birds in the cages. For the third step, the size and environment in the enclosure were the same as those used for the soft release of the first-year-old storks. The feeding frequency, amount, and prey species were the same as those when multiple birds were reared in the shared and training cage. We soft-released the birds when it was easy for them to find prey animals because of rice reaping in paddy fields.

Selection of birds for release

Release of first-year birds

To prevent pedigree bias in the reintroduced wild population, the release of birds from a different pedigree group at the release site each year was crucial.

Release of more than one-year-old birds

Four steps, including training, were undertaken to select birds for release. In the first step, suitable individuals were selected considering the kin bias and sex ratio of the reintroduced population. Individuals with unsuitable pedigree, history, age, and physical defects were omitted for future reproduction of all captive storks, comprising approximately 100 birds.

In the second step, individuals that passed the first step, comprising approximately 20 birds, were evaluated for the behavior necessary for survival in the wild, such as flight, walking, foraging, reproduction, and sociality. These individuals were then selected for further training. Juveniles were not considered in their reproductive behavior.

The 9–26 birds that were selected had three types of training, namely flight, foraging, and socialization, including interaction with different individuals, in a training cage. The cages contained wetlands and streams.

For the training, two to twelve individuals were reared together in a training cage. For flight ability assessment, obstacles were set up at four different heights (195, 145, 120, and 90 cm), and the flight time, frequency, and obstacle avoidance were recorded. Storks with incomplete flight ability were not selected for release. For the conspecific response, birds from different families and sexes were trained to live together in the same cages, and their responses to threats and attacks, cooperative behavior, and reproductive behavior were evaluated. The birds were observed for 6–7 h per day for a total of 40–50 h per bird to select the candidates. If it became difficult for individuals to live with other individuals in the cage, such as those that attacked other individuals or became extremely weak, we immediately stopped training and excluded them from the candidates. To promote foraging ability, we released live fish into a stream during one of two feeding events per day. All the individuals caught fish by themselves.

Transmitter attachment

The custom harness to attach the transmitter consisted of a neck loop and a body loop underneath the wings and in front of the legs (Appendix 3). We first attached Teflon ribbons that were 90 and 50 cm long (width 19 mm, mass 17.8 g) to the front and rear ends of the transmitter, respectively. A neck loop with a diameter of 15 cm was then constructed. The neck loop was placed over the head and neck of the bird. The transmitter sat at the back of the bird and was held in place while the body loop was constructed. We adjusted the body loop to avoid being too tight when we attached the front and rear ends of the Teflon ribbons using thread or an aluminum tube with a length of 18 mm, a short diameter of 3.5 mm, a long diameter of 7.2 mm, and a mass of approximately 1 g. The negative effects of harness attachment, abrasion, and drag caused by the harness not fitting the bird's body shape (Cappelle et al. 2011, Lameris et

al. 2018) were addressed by adjusting the length of the front and back ribbons. Long-term harness tracking reduces the survival and reproduction of birds (Lameris and Kleyheeg 2017, Lameris et al. 2018). However, because it is difficult to carry out long-term monitoring using visual observation for highly mobile storks, transmitter attachment using harnesses was chosen.

RESULTS

Distribution of core areas

Three soft-released first-year-old birds (179, 480, and 481; Appendix 4) had a relatively large core area far and close to the release site, based on both the kernel density estimate (KDE) and minimum convex polygon (MCP). The other four birds (212, 213, 476, and 477; Appendix 5) had small core areas close to the release site. For the KDE, bird 179 had two core areas, one each in the Chugoku and Kyushu regions (Appendix 4). Bird 480 had three core areas, with one in the Kinki region and two in the Kyushu region. Furthermore, bird 481 had two core areas, that is, one each in the Kinki and Kyushu regions. For the MCP, birds 179, 480, and 481 had one core area from Kyushu to Chugoku. For the KDE, bird 212 had two core areas, while the other three birds only had one core area (Appendix 5). For the MCP, birds 212, 213, 476, and 477 had one core area. Birds 212 and 213 acclimatized together during the pre-release period. Birds 212 and 213, based on both the KDE and MCP, had a core area at the same location.

The hard-released first-year-old bird 214, based on both the KDE and MCP, had a core area in the Shikoku region far from the release site (Appendix 6).

Soft-released one- to three-year-old birds, based on both the KDE and MCP, had core areas close to the release sites (Appendix 7). For the KDE, birds 381, 382, and 399 had one core area, and bird 391 had two core areas. However, for the MCP, all individuals had one core area. Birds 381 and 382 acclimatized together during the pre-release period. Birds 381 and 382, based on both the KDE and MCP, had overlapping core areas.

All hard-released one- to three-year-old birds, based on both the KDE and MCP, had core areas close to the release site (Appendix 8) and one core area.

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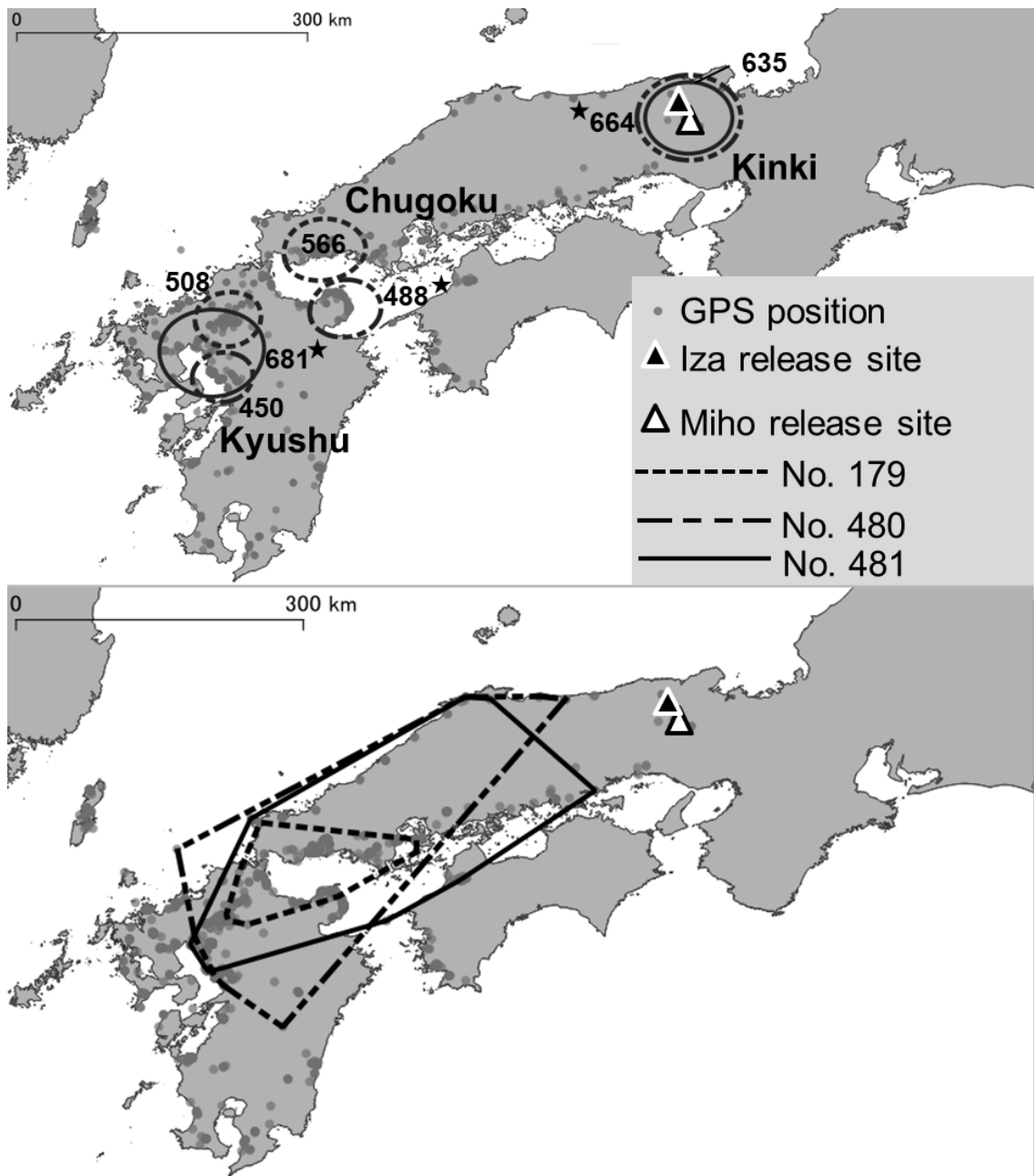
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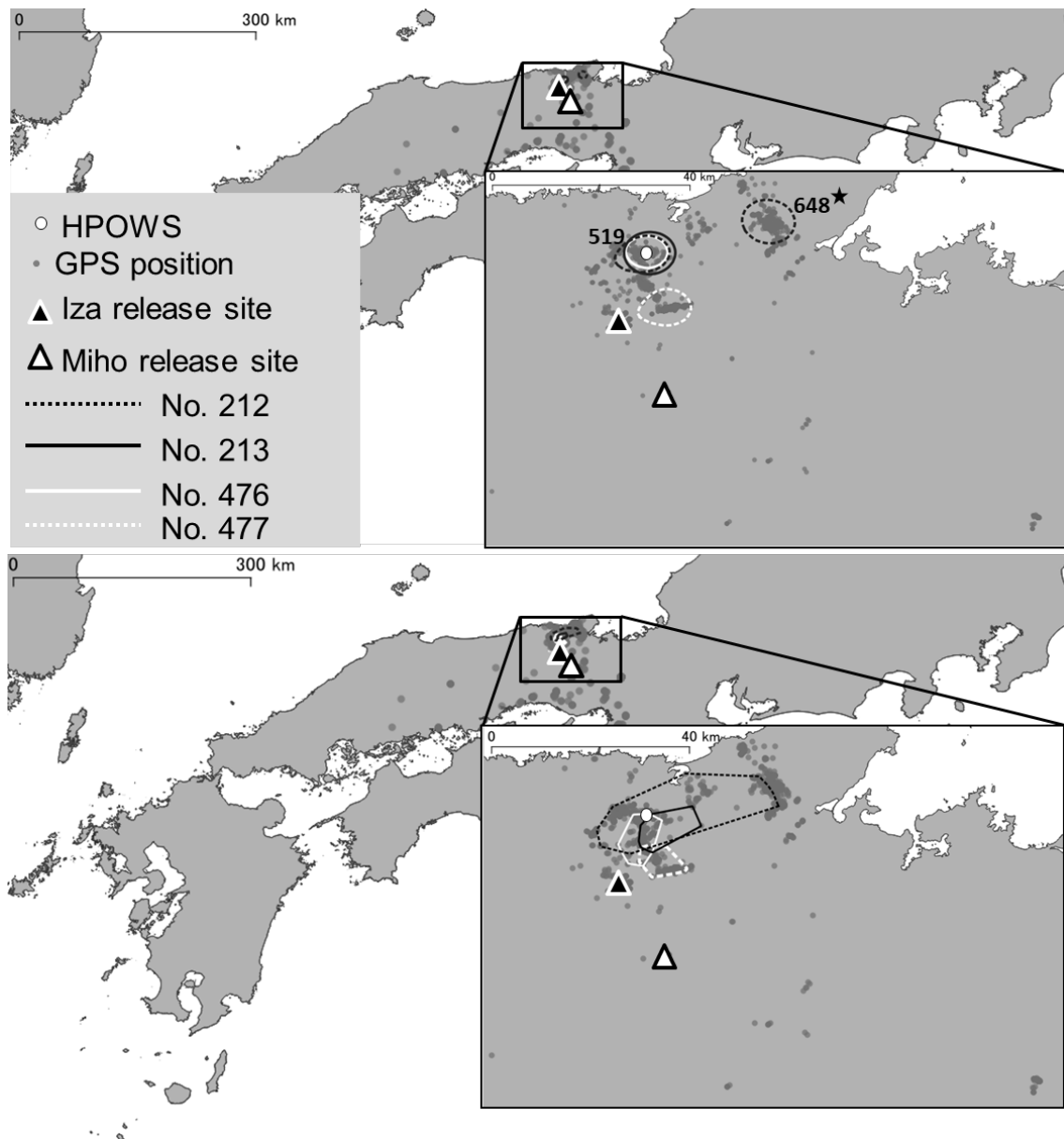
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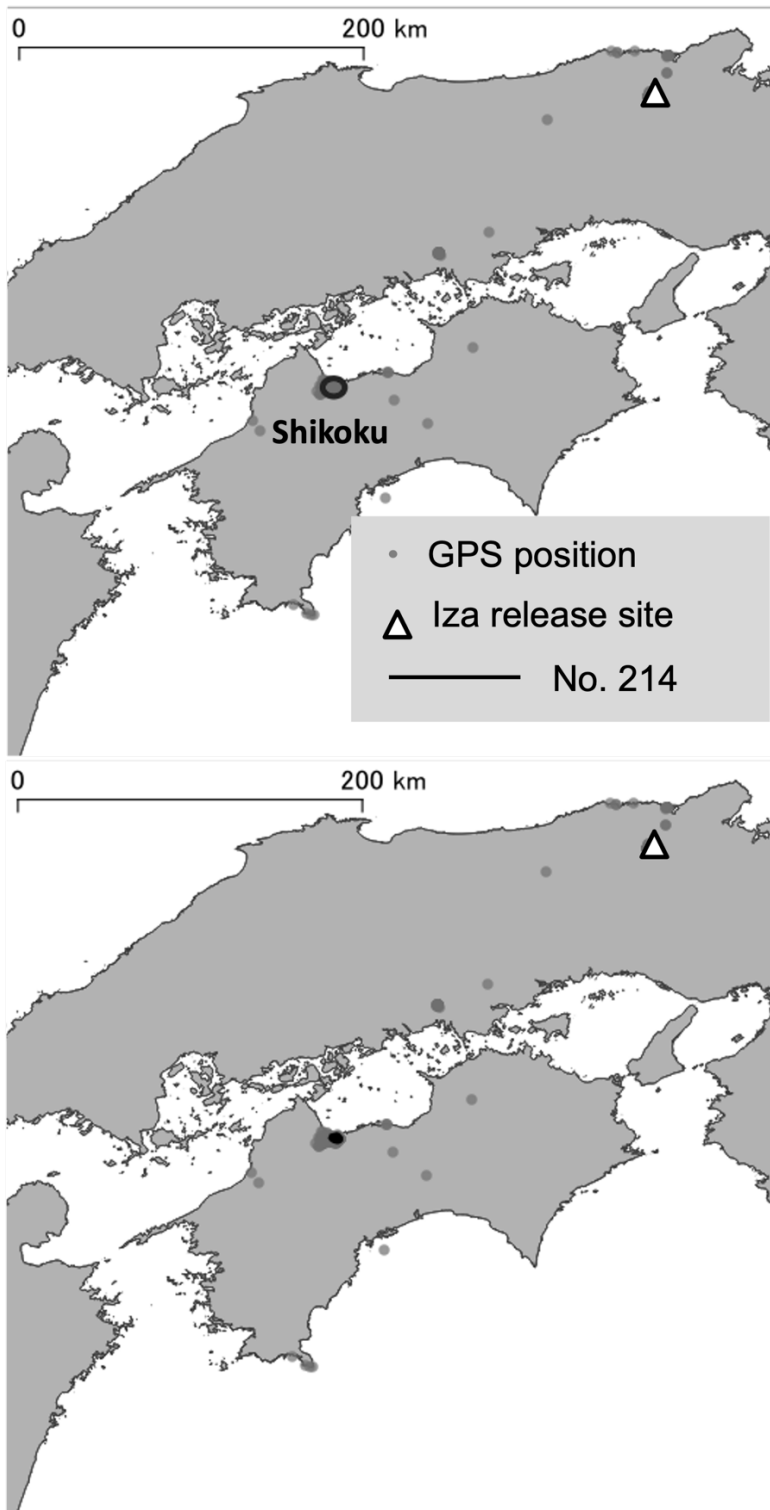
Appendix 3. We first attached Teflon ribbons that were 90 and 50 cm long (width 19 mm, mass 17.8 g) to the front and rear ends of the transmitter, respectively. A neck loop with a diameter of 15 cm was then constructed. The neck loop was placed over the head and neck of the bird. The transmitter sat at the back of the bird and was held in place while the body loop was constructed.



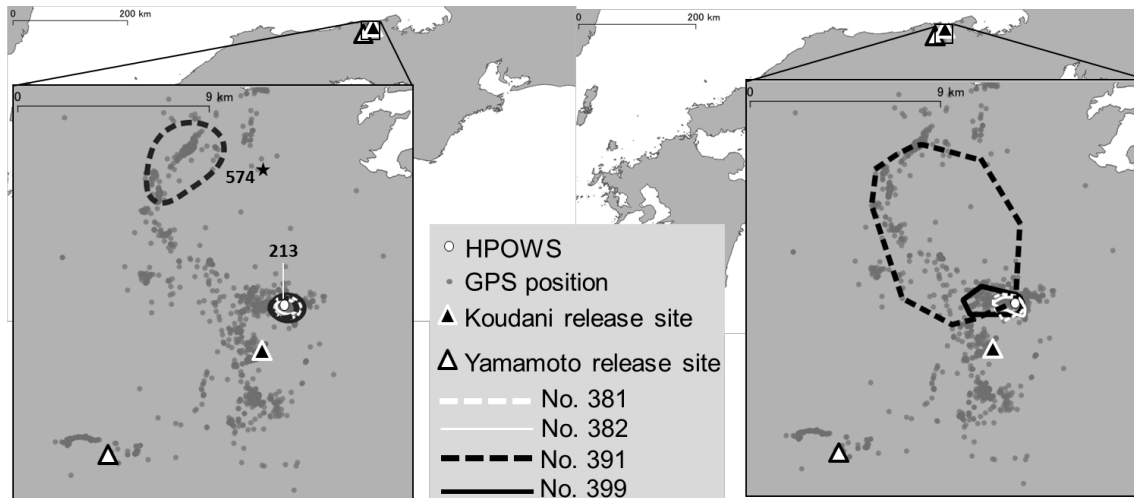
Appendix 4. Core areas [25% kernel density estimates (upper) and 50% minimum convex polygon (low)] for soft-released first-year-old birds ($n = 3$) that dispersed relatively far from the release site. Outline colors for the release site symbols correspond to the colors of the core area for the birds released. When the birds had multiple core areas, the number of positions included in the core area was indicated. The core area with the star-attached number was used for measuring the dispersal distance.



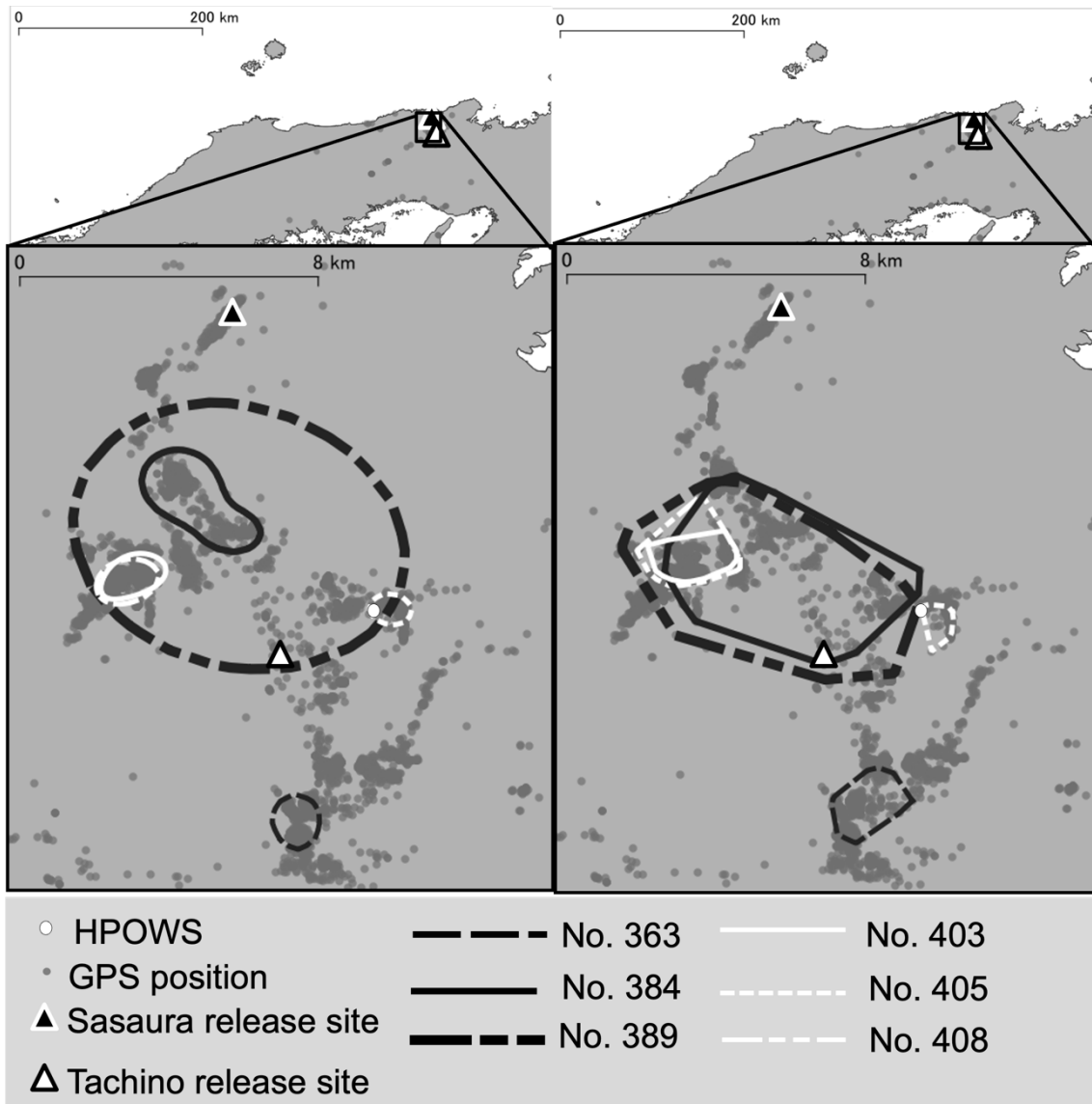
Appendix 5. Core areas [25% kernel density estimates (upper) and 50% minimum convex polygon (low)] for soft-released first-year-old birds ($n = 4$) that dispersed slightly from the release site. Outline colors of the release site symbols correspond to the colors of the core area for the birds released. When the birds had multiple core areas, the number of positions included in the core area was indicated. The core area with the star-attached number was used for measuring the dispersal distance.



Appendix 6. Core areas [25% kernel density estimates (upper) and 50% minimum convex polygon (low)] for hard-released first-year-old birds ($n = 1$). Outline colors of the release site symbols correspond to the colors of the core area of the birds released.



Appendix 7. Core areas [25% kernel density estimates (left) and 50% minimum convex polygon (right)] for soft-released one- to three-year-old birds ($n = 4$). Outline colors of the release site symbols correspond to the colors of the core area of the released birds. When the birds had multiple core areas, the number of positions included in the core area was indicated. The core area with the star-attached number was used for measuring the dispersal distance.



Appendix 8. Core areas [25% kernel density estimates (left) and 50% minimum convex polygon (right)] for hard-released one- to three-year-old birds ($n = 6$). Outline colors of the release site symbols correspond to the colors of the core area for the birds released.