Title Page

Title:

Examining the genetic influences of migratory status on island colonisation by naturally and recently established populations of a bird species

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Abstract:

Seasonal migration influences long-distance dispersal and population establishment, which are the two important steps for successful island colonisation. Migratory behaviour facilitates the long-distance dispersal of individuals through frequent appearance outside a species' normal range, while sedentary behaviour may lead to dispersal by post-fledgling flocks whose accidental immigration provide sufficient propagules for population establishment. We assessed the relative contributions of migratory and sedentary populations to island colonisation, by performing population genetics analyses on four recently and naturally established island populations of the Bull-headed Shrike (*Lanius bucephlaus*). Analyses using 15 microsatellite loci inferred colonisation by flocks of immigrants from possibly sedentary populations for all the islands studied. On one island, we found a correlation between wing length and the genetic probability of assignment to a migratory population, indicating a genetic contribution by migratory immigrants. Yet migratory immigrants to this island were inferred to be only two over eight years of sampling. We imply that sedentary populations were successful island colonists because more immigrants can be provided through their post-fledgling dispersal than through solitary migration. This is the first attempt to examine, using population genetics, influence of migratory behaviour on island colonisation thereby, bridging the gap between population ecology and island biogeography.

Keywords:

Bull-headed Shrike, long-distance dispersal and establishment, island biogeography, migratory behaviour, population genetics, vagrancy

Introduction:

Long-distance dispersal over an ocean barrier and subsequent population establishment (long-distance dispersal and establishment, LDDE) is regarded as an important aspect of island biogeography, facilitating the development of biotas on remote islands [1–3]. For successful LDDE, two steps — successful long-distance dispersal and successful population establishment — are crucial [4]. Traits for higher dispersal abilities facilitate long-distance dispersal [5], and thus these traits, in theory, can generate higher propagule pressure (composite measures incorporating both the number of individuals in a single simultaneous arrival event and the frequency of arrival events). Larger founding populations are less susceptible to population,

genetic and environmental stochasticity and guarantee higher genetic diversity [6], which leads to successful population establishment. One such trait is seasonal migration [7]. Vagrancy, or the appearance of species outside their normal ranges, occurs more frequently in long-distance migratory species or populations than in less migratory species or populations [8,9]. Species regularly undertaking long migrations are exposed more frequently to, and are more susceptible to, weather disturbances that may carry individuals away as vagrants [8–10]. In fact, migratory species are predicted to have had greater opportunities to expand their ranges, and colonise new areas than non-migratory species, as inferred by several comparative phylogenetic and macroevolutionary studies [10–12].

However, the relationship between seasonal migration and population establishment remains unexamined at the population-level, because of a lack of studies of natural LDDE events [10,13]. In macroevolutionary studies, extinction of populations cannot be considered [14], and the migratory status of species can change throughout their evolutionary histories [15]. The contribution of sedentary species on LDDE may have been underestimated by these aspects in macroevolutionary studies. In fact, some traits related to high migratory tendencies may adversely hinder population establishment. As many long-distance migrants migrate solitarily driven by genetic programming [9,16], vagrants of such species provide only a small propagule size. Conversely, in sedentary or less migratory species, post-fledgling movements away from natal areas in search of suitable territory are sometimes associated with flock formation, and the rare vagrancy of such flocks can provide a relatively large number of potential population founders [8]. Multiple colonisation events by large flocks (orders of hundreds) have been inferred in short-distance migratory species [17]. Migration under genetic control may also urge individuals to move on, even if they become vagrants [18]. Since contradictory effects of migratory behaviour on LDDE are possible, there is a need to consider the influence of migratory behaviour on LDDE, by investigating the composition of migratory and sedentary immigrants in a recently established population. However, no such investigation has been conducted in previous studies of newly and naturally established populations [19–22].

Here, we introduce a system in which the Bull-headed Shrike (*Lanius Bucephalus*), a medium-sized passerine, has naturally colonised five remote Japanese islands over a period of 50 years (figure 1). These five islands are located 200–500 km beyond the previously normal breeding range of the species, well beyond the normal dispersal range of many other medium-sized passerine species [23], suggesting that colonisation was accomplished via long-distance dispersal. The Bull-headed Shrike is partially migratory (it is a summer visitor to Hokkaido and northern Honshu) but it is principally sedentary on the rest of the main islands of Japan

(southern Honshu, Shikoku, Kyushu) [24,25]. Movements of flocks consisting of several dozen post-fledgling juveniles in sedentary populations are known [26,27], and these may provide high propagule pressure for colonisation. Migratory shrikes are typically nocturnal, solitary migrants (figure S1) (Hara pers. obs., [9]), indicating that their migration is genetically programmed as in other obligate partial migrants [16]. Ringing recoveries have shown that migratory Bull-headed Shrikes winter in southern Honshu and Kyushu [28], and they also reach the Ryukyu Archipelago (Japan's southwestern most islands) [29,30]. Therefore, from a geographical perspective, both sedentary and migratory shrike populations are capable of colonising these islands. Replicates of new island shrike populations provide us with a rare opportunity to examine the relative importance of sedentary and migratory mainland populations for population establishment.

We performed population genetics analyses of Bull-headed Shrikes on the main islands of the Japanese Archipelago and on several remote islands. Genetic diversity indices were compared between mainland and insular populations to infer the degree of bottleneck or immigration on each island. Moreover, effective population sizes of putative founders were estimated for the island populations. The results allowed us to examine whether insular populations are the result of immigration involving the simultaneous arrivals of large numbers of individuals from possibly sedentary populations or only a few solo migratory individuals. A mainland region that has a higher genetic affinity with each insular population was explored by several approaches. The possible source population type (sedentary or migratory) can be inferred for the island populations. We detected frequent immigration from the main islands of the Japanese Archipelago on Minami-Daito Island (MDT) in these analyses. Individuals of migratory avian populations tend to have longer wings than sedentary populations of the same species [20,31]. Therefore, we assessed the possible genetic contribution of migratory immigrants by studying whether there was an association between wing length and genetic assignment probabilities of individuals belonging to a migratory or a sedentary population. Finally, we discuss the possible impacts of immigrants with different migratory ecologies on the new island populations.

Methods:

Study system and field procedure

The first observations of breeding attempts by Bull-headed Shrikes on various remote Japanese islands are as follows: 1) On MDT and Kita-Daito Island (KDT), in the Daito Islands, in 1972–

1974 [32], 2) On Chichi-jima (CCJ), in Ogasawara Islands, in 1987–1988 [33], 3) On Nakano-shima, in the Tokara Islands, in 1989 [34], and 4) On Kikai-jima (KKJ), in the Amami Islands, in 2012 [35]. Both KKJ and Nakanoshima lie within the Ryukyu Archipelago where the shrike is a winter visitor. Tropical cyclones (Typhoons) usually pass Japan on a track from the southwest towards the northeast during autumn when migratory and post-fledgling movements occur [36]. North winds in the western part of a cyclone can potentially carry birds away from their normal range to remote islands. CCJ is not only the furthest island from the Japanese mainland, but also to the south-southeast thus few cyclones track there from the mainland.

We collected blood samples from shrikes from several populations on mainland Japan and from four out of five remote islands (MDT, KDT, CCJ and KKJ) (figure 1, table S1). Samples were stored in 99.5% ethanol. Field sampling was conducted time-intensively and locally both for insular and many of the mainland populations during the breeding period (n = 58 on Osaka in 1989, n = 35 on Hokkaido in 1997 and 1998, n = 18 on CCJ in 1998, n = 4 on KDT in 2008, n = 5 on KKJ in 2013 and 2015, n = 25 on Nagano in 2019, see below for MDT). We used mist nets and spring net traps to capture shrikes for blood sampling. Tissue and blood samples from Kyushu (n = 14) and the Kanto region (n = 18) were collected regionally throughout multiple years. While most samples were collected during site-specific breeding seasons, some were collected during pre-breeding seasons when sedentary shrikes occupy breeding territories [27]. The shrike population in Hokkaido is migratory, whereas in the regions of Honshu (Kanto, Nagano, Osaka) and Kyushu the shrike populations are sedentary breeders. On MDT, we collected samples from multiple breeding seasons, from 1998 (n = 23) and annually from 2002 to 2008 (n = 295 in total). On MDT, we also recorded the age, sex, and morphometric traits of each individual, including natural wing length and tarsus length measured using a digital caliper with a precision of 0.02 mm. We used data collected in 1998 as representative of the earlier genetic structure of the MDT population for calculating genetic diversity indices and inferring the genetic structure, whereas data collected from 2002 to 2008 were used for analysis of temporal genetic change and for inferring an association between genetics and wing morphology.

Laboratory procedure and calculation of genetic diversity indices

DNA extraction of samples was performed using either Qiagen Blood & Tissue Kit (Qiagen) or Dr.GenTLE (TaKaRa), following the manufacturers' protocols. The genotype of each of the samples was determined at 15 microsatellite loci. Because each population may include a

different proportion of closely related individuals, results from some of the following genetic analyses may be biased [37]. Therefore, we also prepared a dataset (hereafter, dataset without relatedness) in which relatedness of individuals was controlled for each population using COLONY v.2.0.6.6 [38]. We used the dataset without relatedness in the following analyses unless stated. Information on primers used, the experimental and genotyping protocols and preparation of the subset of the data are described in the supplementary material and table S2.

Null allele frequencies were estimated for each locus for each population by using CERVUS v. 3.0.7 [39]. Tests for linkage disequilibrium were conducted using GENEPOP v. 4.7 [40,41]. Because there were 105 multiple comparisons among loci, the critical value α was adjusted to 0.00048 using the Bonferroni correction. We compared heterozygosity and allelic richness among populations separately, by constructing two linear mixed regression models, using lmerTest packages in R [42]. In each model, we included population as an explanatory variable and locus identity as a random factor. Allelic richness was calculated under the rarefaction method using HP rare [43,44]. Heterozygosity was calculated for each locus for each population using INEST v. 2.2 [45]. We did not conduct Bonferroni correction in these models (see the supplementary material for details). A test for heterozygosity excess associated with a genetic bottleneck under the two-phase model [46] was also conducted for each population in INEST v. 2.2. Pairwise Fst between pairs of populations was calculated with 95% confidence intervals, accounting for the presence of null alleles using FreeNA [47]. Differences in mean Fst values were compared between each set of inter-mainland-island comparisons for each island (e.g., between Fst for Kanto-MDT and that for Hokkaido-MDT). Significance levels were calculated by using two-sided permutation tests with 10,000 resampling. Scripts and data are available at Dryad [48].

Spatial genetic structure

The genetic structure of the mainland and insular Bull-headed Shrike populations was inferred by several methods. We conducted STRUCTURE analysis [49,50] through the R package strataG [51]. This analysis was based on the ‘Admixture model’ assuming correlated allele frequencies among populations, with 10 replicates of 100,000 cycles of burnin and 500,000 cycles of Markov chain Monte Carlo. The number of genetic clusters, K, was tested from 1 to 10. The Evanno method was used to infer the best value of K by ΔK values from the results [52]. We combined all 10 replicates into one output by using CLUMPP [53], and the results were shown across several K values including the best K. Discriminant analysis of principal components (DAPC) [54], implemented in the R package adegenet v. 1.2.1 [55], was also

conducted because it is able to assess genetic structure within a complex population structure, which was suspected based on the STRUCTURE analysis. We performed 1,000 replicates of cross-validation to determine the number of principal components with the lowest mean squared error to be retained in the DAPC analysis. After cross-validation, 35 principal components were retained in the DAPC and the first and the second discriminant functions were used for plotting.

We also assessed the genetic affinity of each insular population to each mainland population by means of model comparisons of population histories, using DIY-ABC v2.0 [56]. We performed model comparisons separately for each island. In each set of comparisons, we prepared five competing models in which the ancestral island population split from one of the five mainland populations at t2, and it colonised the island at t1 years before sampling with an effective population size, N_{island}. The time parameter t1 was fixed according to the observations of first breeding attempts by Bull-headed Shrikes on each island. The five mainland populations were assumed to have simultaneously split from one ancestral population at t3 (t3 > t2). We assumed that the effective population size $N_{mainland}$ was shared among all populations except those on remote islands. We also assumed generation time to be one year as more than half of breeding individuals were yearlings on MDT (Matsui, pers. obs.), perhaps indicating short life expectancy on islands. We prepared 10,000,000 simulated datasets and compared relative posterior probabilities using logistic regression estimates for the first 100,000 simulated datasets to decide the best model. Posterior estimates for parameters were calculated under the best models. Confidence in scenario choice was evaluated by using the ratio of posterior probabilities, which was calculated for the best model relative to the second-best. Scenario choice was confident when the ratio of posterior probabilities exceeded 3.16 [57]. Details for DIY-ABC analyses are described in the supplementary material and table S3 for priors. Scripts and data are available at Dryad [48].

Detecting migratory immigrants on Minami Daito Island

We used the original dataset without controlling for relatedness in the analyses below. An effect of being assigned to the Hokkaido (migratory) population on wing length was examined. We first constructed a base linear regression model, wing length ~ tarsus + sex + measurer, to explain variation in wing length. We performed DAPC with a dataset including samples from MDT collected in 1998 and all the mainland populations, and genetic assignment probabilities to each population were calculated for the unique individuals collected in 1998 (n = 23) and 2002–2008 (n = 284) on MDT. Our final linear regression model was wing length ~ tarsus + sex

+ measurer + Hokkaido + Kanto + Nagano + Kyushu + MDT (in 1998), where site names indicate assignment probabilities to the respective sites. Tarsus length was converted to a value between 0 and 1 for a better comparison of its effect with other variables. The assignment probabilities to Osaka were excluded to avoid strong correlations with assignment probabilities to the other sites since many individuals were assigned to the Osaka population. Details of model construction and DAPC are provided in the supplementary material. Scripts and data are available at Dryad [48].

We also examined the temporal change in the genetic structure on MDT by conducting a Mantel test on samples collected in different years using ape v. 5.3 [58], for pairwise Fst and Cavalli-Sforza and Edwards' genetic distance Dc [59] calculated for samples collected in different years, by using FreeNA [47]. We conducted calculations by retaining individuals recaptured in different years. Scripts are available at [48].

Results:

Genetic diversity indices

In total, 495 individuals were genotyped for 15 microsatellite loci; only 0.78% of the dataset was missing data. After conducting sib-ship assignment analysis, 85 individuals were removed from the dataset without relatedness. This dataset included 171 individuals from five mainland and four island populations (representatives for MDT were those collected in 1998). There was no evidence of linkage equilibrium after Bonferroni correction for multiple comparisons. Null allele frequencies exceeded 0.2 across many mainland and insular populations for one locus (Llu102). Therefore, Llu102 was excluded in all the DIY-ABC analyses (see table S4 for details of null alleles). Heterozygosity was significantly lower for insular populations (with the exception of MDT) than those for mainland regions in the linear mixed regression model (figure 2a, table S5). Low levels of allelic richness were also supported for CCJ ($p < 0.01$) and marginally for KKJ ($p = 0.08$) in our linear mixed regression model, while the allelic richness of MDT and KDT did not differ from those for mainland regions ($p = 0.22$ and 0.28, respectively) (figure 2b, table S5). The low heterozygosity of KDT may be attributed to the small sample size.

A model including an inbreeding coefficient performed better than one without it only in the Kyushu population based on the deviance information criterion 2 values (table S6), while 95% credibility intervals for inbreeding coefficients included 0 for all the populations, indicating that inbreeding was not statistically supported in any population. Population bottlenecks were statistically supported only for CCJ ($p = 0.007$) and KKJ ($p = 0.025$) by

heterozygosity excess.

Genetic differentiation and spatial genetic structure

Genetic differentiation of insular populations was supported by Fst, STRUCTURE analysis and DAPC, but the degree of genetic differentiation differed among populations (figure 2c, 3a-b). Differentiation of insular populations from the mainland populations was statistically supported by Fst for most of the pairs. Differentiation was not supported between Kyushu and KKJ, nor between KDT and all of the mainland populations (figure S2). The degree of genetic differentiation of CCJ from the mainland regions was higher than that of KKJ and MDT (p = 0.0061 for KKJ and 0.0078 for MDT, 10,000 permutations, α = 0.017 after Bonferroni correction). The degree of differentiation of each island also varied depending on which mainland populations were used for a comparison; pronounced differentiation of CCJ from Kyushu, genetic similarity of KKJ to Kyushu, and genetic similarity of MDT to Kanto were inferred (10,000 two-tailed bootstrap, α = 0.005 after Bonferroni correction).

In the Bayesian clustering approach by the STRUCTURE analysis, the genetic differentiation of CCJ was supported (the highest ΔK values occurred at K = 4) (figure 3a, figure S3). However, one individual from CCJ, whose 36.4–48.5 % (K = 4 and 5, respectively) of group membership, was assigned to clusters found outside CCJ, suggests the possibility of post-differentiation gene flow from the mainland. Slight genetic distinctiveness on MDT appeared when K = 4 or a larger value was considered, yet genetic clusters were shared with the mainland populations, possibly indicating a high level of gene flow from the mainland. The genetic distinctiveness of KKJ and KDT populations was inconclusive, probably due to the small sample sizes [60].

CCJ population was discriminated from the rest of populations by the first discriminant function, while MDT, KDT, and KKJ populations were discriminated from mainland populations by the second discriminant function (figure 3b). A larger number of individuals from MDT were located towards the mainland population cluster than CCJ and KKJ, indicating a higher rate of immigration and gene flow from the mainland on MDT. Based on these discriminant functions, there was a slight trend indicating that eastern or northern populations (Hokkaido and Kanto) were placed towards the second quadrant, while western populations (Osaka and Kyushu) were placed towards the fourth quadrant of the plane. Therefore, the CCJ and MDT/KDT populations were inferred to be genetically closer to the eastern mainland populations, and the KKJ population was placed closer to the western mainland populations.

Based on scenario comparisons by DIY-ABC, the best models did not perform significantly better than the second-best model for CCJ and MDT (table 1). Therefore, scenarios suggesting that CCJ and MDT have higher genetic affinities with Osaka and Kanto, respectively, were not supported statistically. For KKJ, the ratio of posterior probabilities exceeded 3.16, supporting that assumption that KKJ population split from the Kyushu population. Estimates for the effective population size when colonisation occurred (N_{island}) for CCJ and KKJ were confidently higher than ten (modes were 18.6 and 19.1, respectively), and were similar to the number of pairs observed during field surveys of the populations. N_{island} for the MDT population was estimated to be apparently large compared with estimates from other islands and data from field surveys. Relatively high credibility intervals of N_{island} for KKJ maybe related to the recent colonisation and/or the small sample size.

Detecting migratory immigrants on Minami-Daito Island

A linear regression model was constructed to explore the association of genetic assignment probabilities to a migratory population (Hokkaido) and wing morphology. There was a significant positive correlation between the assignment probabilities to the Hokkaido population and wing length, even after controlling for the effect of assignment probabilities to the other mainland populations or to the MDT population in 1998 (estimate = 2.18 ± 0.96, p = 0.02, figure 4, table S7). Thus, a genetic contribution from a migratory population to the MDT population was inferred. The effects of being assigned to the other populations were not statistically supported (table S7), suggesting that wing length may not differ between insular individuals and putative immigrants from sedentary mainland populations. Meanwhile, only two out of 307 individuals (figure S4) were possible migratory immigrants (or their recent descendants) exceeding 50% of assignment probability to Hokkaido according to [19]. The Mantel test supported the temporal change of genetic structure on MDT over eight years of sampling based on the Cavalli-Sforza and Edwards' genetic distance (R = 0.568, p = 0.04) while the support was marginal based on Fst (R = 0.474, p = 0.074) (figure S5). No change in heterozygosity or allelic richness was observed throughout the study years on MDT (figure S6, table S8).

Discussion:

Integrating multiple genetic analyses of recently and naturally established insular populations of the Bull-headed Shrike indicate that sedentary immigrants have made greater contributions to

island colonisation than migratory immigrants. Our interpretations are based on results showing that the island populations shared greater genetic affinities with sedentary populations (figure 2, 3, table 1), and that island immigrants consisted of flocks of individuals (figure 2, table 1), which were most likely of sedentary birds undergoing post-fledgling dispersal [26,27] rather than solitarily migrating birds (Hara, pers. obs., [9]).

We inferred higher genetic affinities of the MDT and KKJ populations to the Kanto and Kyushu populations, respectively, although the affinities of the CCJ population remained inconclusive. The estimated effective population sizes (N_{island}) for CCJ and KKJ were roughly consistent with the sizes observed during field surveys, suggesting that these island populations genetically comprise mainly founder individuals [20]. Moreover, low heterozygosity, allelic richness, and genetic differentiation from the mainland, due to a genetic bottleneck, were detected on CCJ and KKJ within ten years of colonisation. This is in accordance with the results of both theoretical [61–63] and empirical studies (e.g., [20,64]) under conditions without recurrent immigration. Together, most of the immigrants on CCJ and KKJ could have been limited to founding flocks consisting of from one to several dozen individuals, as N_{island} inferred. If there is any recurrent immigrant on CCJ, then it might involve solo migratory immigrants. Gene flow from the mainland was indicated in only one of our sample individuals in the STRUCTURE analysis; no large influence on the entire genetic structure (which was the expectation if several individuals immigrated [65]) was detected. The MDT population was characterized by a larger estimate of N_{island} than the number of observed pairs, a low level of genetic differentiation from the mainland, and the maintenance of high genetic diversity. These results were consistent with the previous studies in which repeated immigration or a large number of multiple immigrants on isolated populations was inferred [17,19,64,65]. Genetic contributions of migratory individuals to immigration events were at least detected as a positive association between wing length and genetic assignment probabilities but inferred to be small relative to the population size.

Vagrancy, or the displacement of individuals, can occur either during post-fledgling dispersal by sedentary populations or during seasonal migration by migratory populations. The latter frequently results in long-distance movements assisted by tropical cyclones [8,9]. An individual Bull-headed Shrike, sighted flying over the Pacific Ocean, was observed 500 km south of the Japanese mainland at N29° E135° [66]. Strong north-westerly winds associated with an autumn typhoon presumably pushed the bird off course from its mainland migratory route [66]. There may be many independent incidents of solo migrating individuals such as this bird, being displaced far out into the Pacific Ocean, some of which may reach remote islands.

Although the vagrancy of sedentary shrikes is probably far less frequent, if and when it does occur, flocks of many non-related individuals may travel together as they drift off course [26,27], making them more likely successful colonists than migratory shrikes. Therefore, the number of individuals involved in immigration (*i.e.*, propagule pressure) is considerably more important for successful LDDE than a high dispersive trait *per se*. This has been suggested in theory [6] and by experiment [67], but remained untested in nature [10]. Our results provide the first evidence highlighting the relative importance of propagule pressure in a natural system.

Local and altitudinal short-distance movements are recognized within the sedentary populations of the Japanese mainland (southern Honshu, Shikoku and Kyushu), even though they are essentially "sedentary" [24,26]. The ecology of these movements (such as distance they move or whether movement is obligate or facultative) is not well understood. However, given that flock formation triggers flock movements [9], such movements may be limited to post-fledging juveniles since flock formation has only been reported in sedentary populations [26,27]. Our results indicate that island colonisation in the Bull-headed Shrike is influenced mostly by movements made by essentially non-migratory populations.

A relatively large contribution of sedentary rather than migratory individuals to LDDE by the Bull-headed Shrike agrees with previous implications that migratory species are less favoured for population establishment than are sedentary species [18,68]. However, as we detected the genetic contribution of migratory individuals to the MDI population, this was probably not due to genetically programmed migration which inhibits settling down by seasonal migrants [18]. The migratory behaviour of this species may be flexible in terms of island settlement due to its relatively short-distance nature, which was reflected in a high degree of gene flow between sedentary and migratory populations.

Evaluation of genetic analyses

Different levels of genetic differentiation of the island populations may be related to genetic drift after colonisation. Unsupported genetic differentiation of the KKJ population from the possible source area (Kyushu) may reflect a relatively large number of founder individuals without experiencing subsequent genetic drift [17,21]. The KKJ population was established by the most recent colonisation event (sample collection was within five years of colonisation), thus it is relevant that no subsequent genetic drift has occurred on this island yet. In contrast, the CCJ population became highly genetically differentiated within ten years, which may have blurred the genetic relationship between this island and the mainland regions. This pattern can

be called isolation by colonisation, where a genetic bottleneck following colonisation leads to considerable genetic differentiation [69].

A high rate of immigration from the mainland to MDT was unexpected given the geographically isolated nature of the island. Though a high genetic affinity of the MDT population in 1998 to the Kanto population was inferred, the origins of the founder populations remain uncertain due to the inference that recurrent immigration has occurred. Few migratory immigrants detected on MDT may have caused the temporal change in the population genetic structure, since repeated but low levels of immigration can rapidly change the genetic structure of an insular population [65]. We believe this to be less likely because assignment to the Osaka population was more frequent during a period from 2002 to 2008 (but see below). The origin of the KDT population remains unknown due to the small sample size. However, from its position on the DAPC plane, a metapopulation structure involving KDT and MDT is possible. Uncovering the metapopulation structure between these two islands may provide further information on how the MDT population has been maintained.

Migratory and sedentary populations could not be readily discriminated using our microsatellite marker set. We should not ignore the possible low discrimination power of our marker set and the low coverage of mainland populations, which may not correctly assign individuals to genetic clusters or sufficiently infer genetic structure. However, our results do not contradict previous reports indicating that only low levels of genetic differentiation may be observed between migratory and non-migratory populations [70,71]. Furthermore, high levels of differentiation based on wing morphology have also been reported in relation to migratory behaviour [70,72]. Wing length is under polygenic control and highly heritable [73], so the positive correlation between wing morphology and genetic affinity with migratory population is plausible. Meanwhile, as has been reported in previous studies, the evolution of shorter wings is frequently associated with colonisation due to directional selection (e.g., [20,65]). The genetic contributions of migratory populations may perhaps be underestimated due to the *in situ* evolution of shorter wings on MDT. Further investigation including greater coverage of the mainland region, high-throughput sequencing, and fitness data of insular birds, will decouple the effects of migratory immigrants and the directional evolution of wing morphology in insular populations.

Conclusion

Recently established populations of animals founded by natural colonisation (non-human-

assisted) may reflect the ecologically realistic genetic structure of the early stage of population colonisation [19,21]. This study was of a rare system in which a species including both migratory and sedentary populations colonised multiple remote islands 200–600 km from their normal breeding areas, within only several decades. Surprisingly, sedentary individuals were shown to contribute more to island colonisation than vagrancy-prone migratory individuals. This was probably because of the potentially different number of individuals involved in the different ecological movements during which drifting to islands occurs. To our knowledge, this is the first attempt to examine the influences of migratory behaviour on population colonisation at the population-level and to bridge a gap between population ecology and island biogeography, namely long-distance dispersal and establishment. Further investigation of this system guarantees a deeper understanding of the effects of migratory behaviour on the distributions of organisms.

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Tables

Table 1 Summary of the best models and parameter estimates for the origins and demographic parameters of insular populations under the best model, inferred by approximate Bayesian computation approach. Each parameter is shown as effective population size or generation time (in year). Numbers within brackets indicate 95% credibility intervals. P_R corresponds to the ratio of posterior probabilities.

	Priors	Posteriors						Field survey	
	t_1 (time since colonisation)	Best model (relative posterior probabilities)	P_R	N_{island}	t_2	$N_{mainland}$	t_3	No. pairs	ref
Chichi-jima	10	Osaka (0.28)	1.04	18.6 [14.6, 303]	48.9 [24.3, 949]	167,000 [41,100, 283,000]	1,180 [319, 4,770]	< 35	Takagi pers. obs.
Kikai-jima	5	Kyushu (0.51)	3.19	19.1 [14.3, 1,003]	57.7 [26.1, 958]	218,000 [44,900, 286,000]	744 [253, 4,680]	> 13	[74]
Minami-Daito Island	25	Kanto (0.43)	1.81	392 [206, 1,610]	200 [46. 3, 968]	193,000 [36,600, 281,000]	1,310 [322, 4,770]	> 80	[32]

Figure captions

Figure 1 The range of the Bull-headed Shrike and the location of sampling sites for this study. Land colours correspond to different origins of the populations: summer migrants (yellow), residents (sedentary, green), winter visitors (blue), and residents due to recent colonisation (red, the numbers within squares correspond to the colonisation sequence). Insets correspond to squares with the same numbers. Sampling sites on the mainland are denoted by circles (intensive local sampling) and squares (regional sampling). Black solid and hatched arrows correspond to possible immigration events by sedentary and migratory individuals, inferred from the present study. Abbreviations for island populations are as follows: Chichi-jima = CCJ, Kikai-jima = KKJ, Minami-Daito Island = MDT, and Kita-Daito Island = KDT.

Figure 2 Comparisons of genetic diversity indices across five mainland and four insular populations, including (a) heterozygosity, (b) allelic richness, and (c) pairwise Fst. Mean values with 95% confidence intervals across 15 loci were indicated. Results of permutation tests were only indicated for pairwise Fst within each category of island-mainland comparisons (comparisons with $p < 0.005$ were indicated with asterisks). Abbreviations for populations are as follows: Hokkaido = HK, Kanto = KT, Nagano = NG, Osaka = OS, Kyushu = KY, others refer to figure 1.

Figure 3 Results of genetic clustering for the mainland and insular individuals, inferred by the (a) STRUCTURE and (b) discriminant analysis of principal components (DAPC). (a) Genetic assignment of individuals to each number of genetic cluster K, ranging from $K = 2$ to 5, is shown. Each bar indicates an individual, and the height of different colours shows the assignment probabilities to each corresponding genetic cluster. (b) A scatterplot shows the first two discriminant functions of the DAPC. Different colours represent different prior information on populations. Inertia ellipses are drawn for individuals (dots) from the same prior populations. In an inset, eigenvalues are shown for each discriminant function.

Figure 4 An effect of assignment probability to Hokkaido (Pr(Hokkaido) inferred by the DAPC) on the natural wing length of the Bull-headed Shrike on Minami-Daito Island, while the effects of the other variables were accounted for in a linear regression model. The relationship was shown separately for males and females with 95% confidence intervals.

Figures

Figure 1

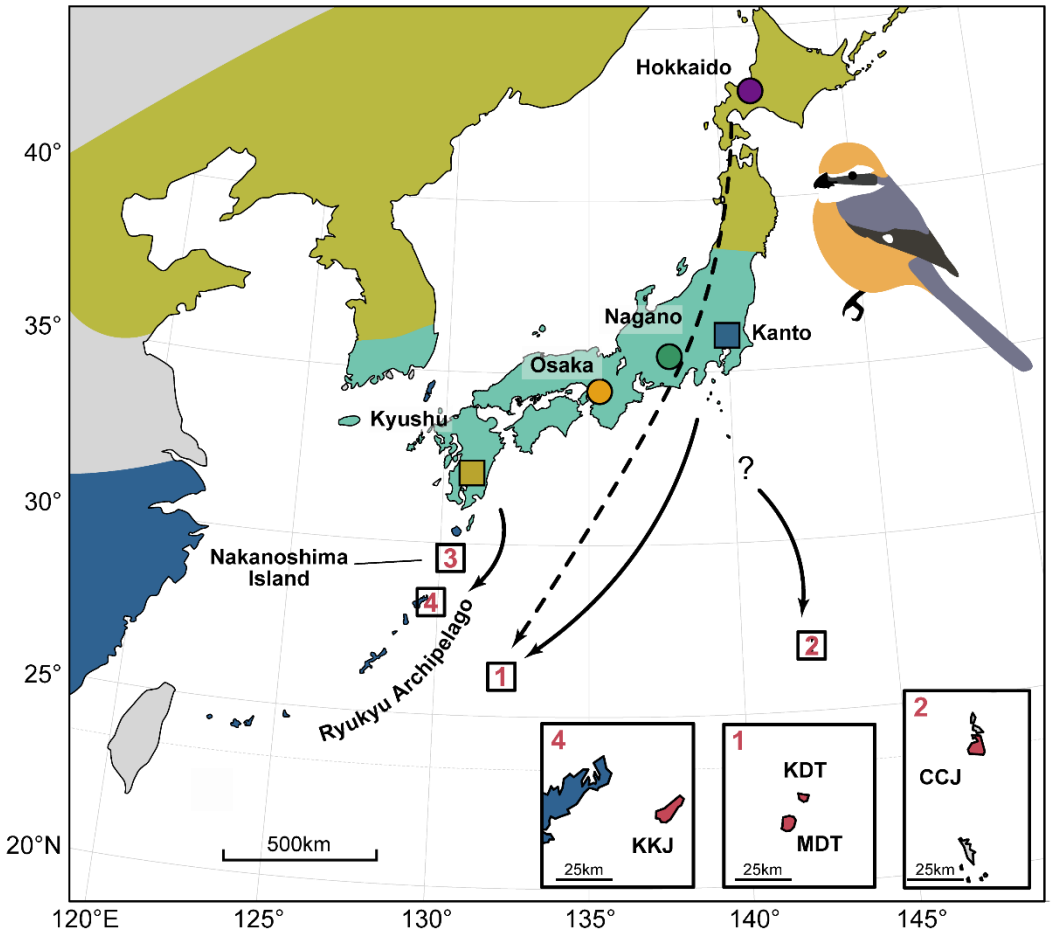


Figure 2

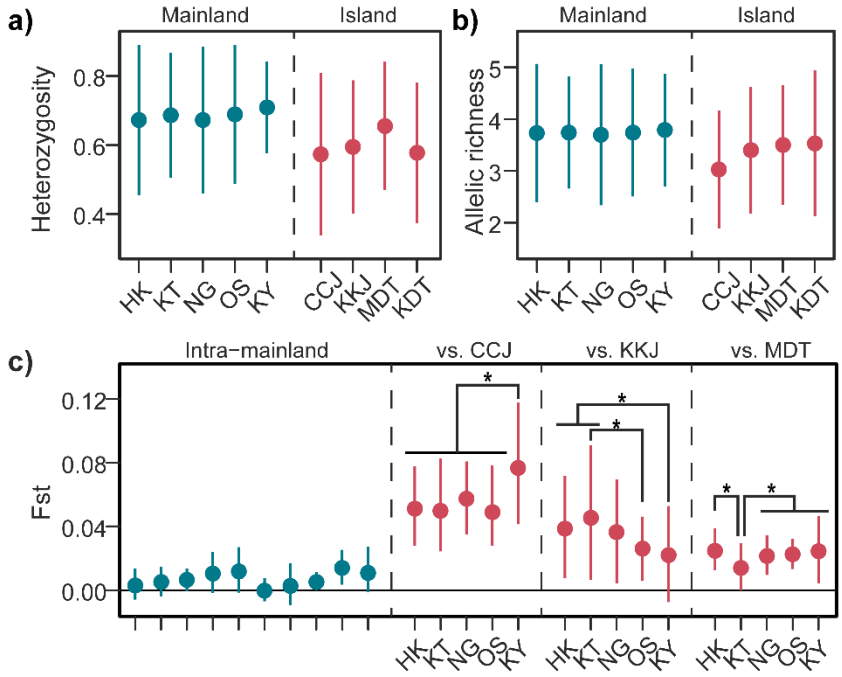

a)
Mainland
Island
Heterozygosity
0.8
0.6
0.4
HK
KT
NG
OS
KY
CCJ
KKJ
MDT
KDT
b)
Mainland
Island
Allelic richness
5
4
3
2
HK
KT
NG
OS
KY
CCJ
KKJ
MDT
KDT
c)
Intra−mainland
vs. CCJ
vs. KKJ
vs. MDT
Fst
0.12
0.08
0.04
0.00
*
*
*
*
*
HK
KT
NG
OS
KY
HK
KT
NG
OS
KY
HK
KT
NG
OS
KY

Figure 3

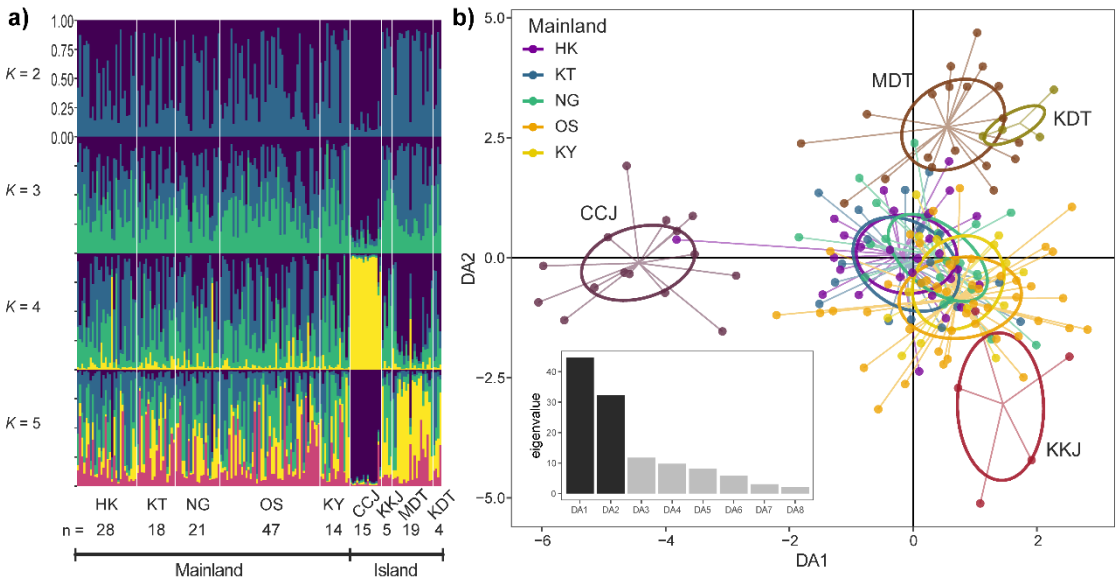
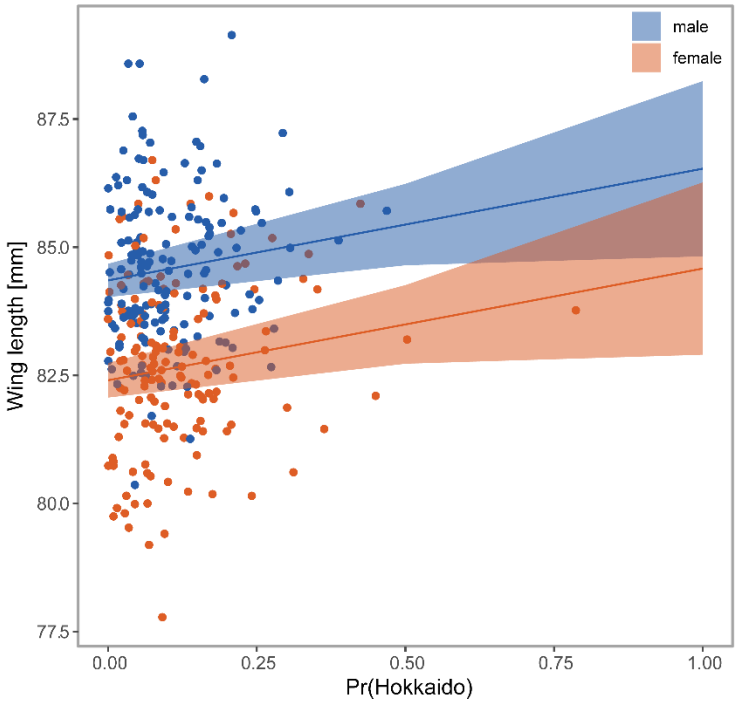

a)
1.00
0.75
0.50
0.25
0.00
K = 2
K = 3
K = 4
K = 5
HK KT NG OS KY CCJ KKJ MDT KDT
n = 28 18 21 47 14 15 5 19 4
Mainland
Island
b)
Mainland
HK
KT
NG
OS
KY
MDT
KDT
CCJ
KKJ
DA2
DA1
5.0
2.5
0.0
−2.5
−5.0
−6
−4
−2
0
2
eigenvalue
DA1 DA2 DA3 DA4 DA5 DA6 DA7 DA8

Figure 4


male
female
87.5
85.0
82.5
80.0
77.5
Wing length [mm]
0.00
0.25
0.50
0.75
1.00
Pr(Hokkaido)

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