A simple population viability analysis of Tancho (*Grus japonensis*) in southeastern Hokkaido, Japan

Yoshiyuki Masatomi, Seigo Higashi, Hiroyuki Masatomi

Yoshiyuki Masatomi, Seigo Higashi

Graduate School of Environmental Earth Science,

Hokkaido University

Kita 10, Nishi 5 Kita-ku, Sapporo 060-0810,

JAPAN

E-mail: tome@ees.hokudai.ac.jp

Tel: +81-11-706-2252

Fax: +81-11-706-4864

Hiroyuki Masatomi

Kita 8, Nishi 18 Chuo-ku, Sapporo 060-0008,

JAPAN

Abstract

We employed population viability analysis (PVA) to estimate future population trends and extinction risk of Tancho, the Japanese or Red-crowned crane (*Grus japonensis*). The stage matrix was based on 15-year data collected by counting the number of wintering cranes and following the survivorship of banded cranes. The accidental death rate was estimated from the number of dead or seriously injured cranes collected in the Kushiro Municipal Zoo. Consequently, the accidental death rate was found to increase each year at 0.072%/year during the recent 14 years and 0.132%/year during final six years. The carrying capacity (*K*) was estimated from the mean mire area within the territory of a breeding pair and the geographic information system data in southeastern Hokkaido. Accordingly, *K* was estimated to be 1,659 in this area. Using the stage matrix, accidental death rates and *K* (and 20%-lower *K*), the simulation was conducted under three conditions; (1) the increase of accidental death, (2) the limitation of carrying capacity, and (3) the concurrent occurrence of carrying capacity limitation and accidental death increase. As the result, the extinction probability during 100 years was zero, although the accidental death rate increased at the current rate of 0.132% per year. Therefore, by artificial feeding in winter, the Japanese population of Tancho reached the adequate level, which seems sustainable unless some catastrophic factors seriously damage the population. To raise the tolerance to catastrophic factors, we discuss the probability of their distributional expansion to western or northern Hokkaido and even to Honshu.

Keywords Artificial feeding · Extinction risk · Japanese crane · PVA · Wildlife management

Introduction

There are two isolated populations of Tancho—the Japanese or Red-crowned crane (*Grus japonensis*)—in northeastern Asia; one is a Japanese resident population inhabiting eastern Hokkaido and the other is a continental population breeding in China and Russia and wintering in the Korean Peninsula and east coast of China (Meine and Archibald 1996). The continental population is estimated to be about 1,200 in China and about 400 in the Korean Peninsula during winter (Delany and Scott 2003). They migrate to northernmost China and Far-East Russia for breeding during spring and return to the wintering regions in autumn (Higuchi et al. 1998). The migration distance is 1,000–3,000 km. Most of the cranes in China winter in the Yancheng Nature Reserve, Jiangsu Province. Although the number of individuals increased until the middle of the 1990s in this reserve (Ma 2002), it is not clear whether the upward trend indicated actual increase of the continental Tancho or only the loss of habitats in other wintering areas.

Until the mid 18th century, the Japanese population bred in northern Japan and some of them wintered in central Japan. However, they faced a crisis of extinction in the late 19th century due to hunting and habitat destruction (Masatomi 2000). Although they were once considered extinct, about 20 Tancho birds were rediscovered in 1924 in the Kushiro Mire, southeastern Hokkaido. At that time, some tens of Tancho were considered to be alive in the whole of southeastern Hokkaido. Since then, protection activities primarily by artificial feeding in winter were conducted and the number of birds has increased to about 1,000 (Masatomi 2000, Masatomi 2005). The density of breeding pairs reached more than ten times that found in China (Fen and Li 1985). With the growth of population, the following problems have occurred in the southeastern Hokkaido: increase in death due to traffic accidents, the saturation of carrying capacity in both the breeding and wintering habitats, excessive concentration at artificial feeding stations in winter, and agricultural damage by the increased population (Masatomi 2000). For the sustainable conservation of the Japanese population, it is important to estimate the population trend and extinction risk in the future.

In the present study, therefore, we employed a population viability analysis (PVA), which is defined as the process of evaluating the synergistic effects of various threats faced by populations or species on their risk of extinction, or decline, and their chances of recovery within defined time frames (Frankham et al. 2002). PVA is useful for wildlife management by assessing the impact of various factors on the population trend and extinction risk and by evaluating alternative management options for the recovery of endangered species (Brook et al. 1997, Marmontel et al. 1997, Mirande et al.

1997, Ratner et al. 1997).

Study Area and Materials

In this study, we analyzed data collected in eastern Hokkaido (Fig. 1) where the monthly mean temperature ranges from −7.9 °C (January) to 18.5 °C (August) and annual precipitation is ca. 1,100 mm including about 60 cm thick snowfall in winter. In this area, most cranes overwinter around some feeding stations, and there are four major feeding stations (Fig. 1C) where the cranes are provisioned with corn from early November to late March. Most of them initiate dispersal in February and March. In low moors dominated by reeds, each pair of cranes builds a nest 90–300 cm in diameter and lays 1 to 2 eggs. The incubation continues for about a month, and chicks being very precocious follow their parents for foraging shortly after hatching. The cranes' diet includes mud snails, earthworms, crayfish, loaches, horsetails, buds of reed, and many kinds of wildlife. Parents are accompanied by juveniles until the beginning of the following breeding season. In this study, the cranes were divided into three growth stages—juvenile, a young experiencing the first winter with pre-molting brown feathers and dark-tipped remiges without a red crown; sub-adult, a premature experiencing the second winter with dark-tipped remiges; and adult, a reproductive individual experiencing the third or later winter.

Methods

Data used in this study

The third author and his colleagues have conducted detailed surveys since the 1980s, and we analyzed the following data collected by them from 1990 to 2004; (1) aerial surveys of breeding pairs, conducted during April and May or in addition, June, every year; (2) population census of all individuals and juveniles every winter at feeding stations; (3) discovery data of banded individuals surveyed every winter; and (4) number of accidentally killed cranes. Since the Tancho is designated as an endangered bird, most of the dead or seriously injured cranes were collected by the Kushiro Municipal Zoo for the last two decades. In addition, we measured the area of low moors by analyzing vegetation maps (The National Survey on the Natural Environment, Ministry of the Environment, Japan) using GIS software ArcView8.3 (Environmental Systems Research Institute, Inc).

Simulation of the future population dynamics using stage matrix

From the above data, we calculated factors for a stage matrix that were used for simulating future population dynamics of the Tancho. Link et al. (2003) estimated age-specific survival rates, and fecundity of Whooping cranes from the number of juveniles and adults including subadults, based on a 64-year data of their population dynamics. However, our analysis is based on data collected for only 15 years, and therefore we estimated age-specific survival rates and fecundity from the data on banded cranes. Since the ratio of undiscovered survivors among all banded survivors was as low as 0.52% (3/580) in our surveys, the banded crane data were highly reliable. In the simulation performed by RAMAS Metapop (Akçakaya 2002), we set up the following three cases and tried 10,000 replications of simulation for each case. In these simulations, the parameter errors were not taken into consideration.

Case 1: increase in accidental death. In order to estimate the future trend of mortality due to accidents, the interannual fluctuation of accidental death rate was calculated from the data collected by the Kushiro Municipal Zoo.

Case 2: limitation of carrying capacity. The carrying capacity was estimated from the maximum number of breeding pairs in the study area. For this, we used data on the distribution of breeding pairs and the area of low moors measured from vegetation maps using ArcView8.3.

Case 3: concurrent occurrence of carrying capacity limitation and increase in accidental death. In this analysis, we used the mortality rates and carrying capacities calculated for cases 1 and 2, respectively.

Results

Estimation of stage matrix factors

The survival rate at each age stage was estimated from data of 172 chicks banded in the breeding seasons of 1990–2001 (Table 1). In this sampling, 40 chicks (23.3%) were dead before the first wintering season, and the other 132 chicks had grown into juveniles, which were regarded as age 1. The survival rate at each age stage was estimated from the data of banded cranes by using program MARK (White and Burnham 1999). The estimated survival rate was 0.918 ± SE 0.024 at age 1; 0.921 ± 0.027 at age 2; 0.927 ± 0.028 at age 3; 0.925 ± 0.032 at age 4; and 0.945 ± 0.016 at age 5+ (Table 2).

Since it was difficult to accurately confirm whether each banded adult had a juvenile in the flocks of cranes at the feeding stations, mean fecundity rate of adults was not directly, but indirectly estimated from the data of banded cranes. First, the number of sub-adults in i-th year (S_i) was estimated by $0.918J_{i-1}$ where J_{i-1} is the number of juveniles in the previous year. Next, the number of adults in the i-th year (A_i) was estimated by $T_i - J_i - S_i$ where T_i is the total number of wintering individuals in the i-th year. Finally, a fecundity rate in the i-th year was estimated by J_i/A_{i-1}, and the mean value 0.157 ± SD 0.033 was employed as the fecundity rate of adults.

Moreover, we made a stage matrix with standard deviations (Table 3). Elasticities and sensitivities were remarkably lower in fecundity rates than in survival rates, suggesting that the adoption of an age-independent fecundity rate 0.157 does not significantly distort the results of simulation. Life expectancy at each age was 15.7–17.2 years. The initial abundances in the simulation were represented by the age structure in 2004 (cf. Table 1).

Simulation of future population dynamics

Case 1: increase in accidental death

During 1991–2004, 1–17 cranes per year died from accidents (Table 1). As shown in Fig. 2 where the accidental death rate in each year is calculated by D_i/T_i (cf. Table 1), the accidental death increased by 0.072% per year during 1991–2004 and 0.132% per year during 1999–2004. Accordingly, the simulation of 100-year population dynamics was conducted with two assumptions of increase in accidental death rate per year (hereafter, ADR), that is, 0.072% and 0.132% increase per year (Fig.

3A). Because of the long generous protection and artificial feeding in winter, the Tancho cranes in Japan have been deeply habituated to people. Therefore, we assume that the risk of accidental death by collision with vehicles and man-made structures will increase yearly (time-dependence) because the cranes will frequently enter the zone of human activity. The accidental death rate will be related to density (density-dependence); however, currently we do not have any concrete data on this matter. Instead, we have focused on the importance of increased risk of accidental death by habituating to people.

In ADR = 0.072%, the mean population size reached the maximum of ca. 9,400 after about 80 years, and thereafter decreased to ca. 8,000. In ADR = 0.132%, the mean population size reached the maximum of ca. 3,300 after about 45 years, and thereafter decreased to ca. 350. Among these values of death rate, none of 10,000 trials reached extinction after 100 years. Case 1 suggests that the population increases for some decades, although the accidental death rate continues to increase every year.

Case 2: limitation of carrying capacity

In the aerial surveys in 2003 in seven regions containing 6.65–137.26 km^2 low moors (parameter H in Table 4), 10–88 breeding pairs were distributed at the mean distances of 1.72–4.06 km to the nearest pairs (L in Table 4). In this study, the territory size (U) was defined by $U = \pi(L / 2)^2$ and the area of low moor in each territory was measured using ArcView8.3. The average area of low moors in territories (W) was 0.18–1.35 km^2, and we calculated H/W to estimate the maximum number of pairs that can potentially breed in each region. As a consequence, a total of 520 pairs were estimated to be able to breed in these regions. Based on the data in Table 1, the linear regression between the total number of individuals (T) and the number of breeding pairs (B) was given by $T = 3.235B - 29.738$ ($R^2 = 0.928$, $p < 0.0001$); viz. $T = 1{,}659$ when $B = M = 520$. In this estimation, the present population structure was assumed to be maintained in the future. Therefore, we set up the carrying capacities (K) at 1,659 and 1,327 (20% lower) in the estimation of future population dynamics (Fig. 3B).

In $K = 1{,}327$ and 1,659, the mean population size reached the equivalent of about 1,300 and 1,650, after approximately 10 and 15 years, respectively. Even after 100 years, none of 10,000 trials reached extinction in both K values.

Case 3: concurrent occurrence of carrying capacity limitation and increase in accidental death.

Case 3.1: $K = 1{,}327$ with increase of accidental death rate (Fig. 4A)

The mean population size increased for about 10 years up to 1,300 in both values of ADR, maintained the level of 1,300 in ADR = 0.072% but decreased to 1,150 in ADR = 0.132% after 50 years**,** and then to 980 and 120 in ADR = 0.072% and ADR = 0.132%, respectively, after 100 years. In both ADR values, none of 10,000 trials reached extinction of population even after 100 years.

Case 3.2: K = 1,659 with increase of accidental death rate (Fig. 4B)

The mean population size increased for about 15 and 20 years up to 1,650 in ADR = 0.072% and 0.132%, respectively. Thereafter, it decreased to about 1,600 (ADR = 0.072%) and 1,450 (ADR = 0.132%) after 50 years and then to 1,230 (ADR = 0.072%) and 150 (ADR = 0.132%) after 100 years. In both ADR values, none of 10,000 trials reached extinction of population even after 100 years.

From these results, the following points are important for the conservation of the Tancho population. The distinct effect of ADR on the population trends later than that of K. Once their population reaches a maximal level; however, ADR will depopulate cranes. The turning point will occur earlier under the condition of low K values. The simulations with the concurrence of K limitation and the increase of accidental death suggest that the crane population will be less than 1,000 after about 60 (K = 1,327) and 70 (K = 1,659) years in ADR = 0.132%.

Discussion

On the basis of empirical evidence, Thomas (1990) suggests that a population size of 10 is far too small, 100 is usually inadequate, 1,000 is adequate for species of normal variability, and 10,000 should permit medium to long-term persistence of birds and mammals that show strong fluctuations in population size. In the present study, the carrying capacity in southeastern Hokkaido was estimated to be 1,659 and the extinction probability during 100 years was zero, although the accidental death rate increased at the current rate of 0.132% per year, suggesting that the Tancho population is sustainable unless catastrophic factors such as typhoons and pathogenic disease seriously damage the population. Though the Louisiana population of Whooping cranes has ever been endangered to extinction by a hurricane (Meine and Archibald 1996), fortunately Hokkaido is rarely attacked by typhoons unlike other main islands of Japan. Instead of catastrophic storms, pathogenic infections seem more plausible in the Tancho because the bottleneck effect at the beginning of 20th century remarkably reduced their genetic diversity. Hasegawa et al. (1999) analyzed the nucleotide sequence of the mitochondrial control regions of Tancho and detected only two haplotypes from 15 individuals of the Hokkaido population, while seven haplotypes were detected from 14 individuals of the continental population distributed in Far

Eastern Eurasia. This suggests a low diversity of the major histocompatibility complex (MHC), which can be an indicator of the cranes' immunological tolerance to pathogenic infections (Jarvi et al. 1995).

To avoid catastrophic depopulation, it is thus reasonable to enhance the Hokkaido population of the Tancho by expanding their distribution outside southeastern Hokkaido. On Kunashiri Island about 20 km from Hokkaido (Fig. 1), an isolated pair of Tancho was observed in the summer 1975 and a nest of Tancho was found in 1982, suggesting that some cranes have been breeding in Kunashiri and wintering in southeastern Hokkaido since the 1970s and 1980s by crossing over the 20 km wide strait. A few brooding pairs of Tancho were observed in Abashiri (ca. 120 km north of Kushiro) in the spring of 2000 (Masatomi et al. 2000) and in the Sarobetsu Mire (ca. 320 km northwest of Kushiro) in the spring of 2004 (Fig. 1). This was probably the first recovery of breeding pairs in northern Hokkaido since the mid 19th century (Masatomi et al. 2004). Since then, breeding has been confirmed in these areas almost every year and some non-breeders have been reported from other areas including the Lake Utonai, Yufutsu wildland, and Biei, which are located 160–220 km west of Kushiro.

However, these cranes evidently return to southeastern Hokkaido for wintering, probably due to the lack of appropriate artificial feeding stations, except in southeastern Hokkaido. In addition, deep snow cover seems to be another factor preventing the cranes from wintering in western or northern Hokkaido where the mean depth of snow cover in mid-winter exceeds 100 cm, while the southeastern Hokkaido has only about 60 cm deep snow cover even during mid-winter. The deep snow cover would disturb their foraging and roosting in unfrozen streams.

Paleographic evidence shows that many Tancho cranes migrated from Hokkaido to Honshu for wintering until the 19th century. We considered the migrating subpopulations to be extinct because of overhunting and/or habitat destruction in Hokkaido and Honshu; while a few non-migrating subpopulations survived in southeastern Hokkaido (Masatomi 2000). The migrating subpopulations may be distributed in the snow-rich areas, while the non-migrating subpopulations were probably distributed in the snow-poor areas such as southeastern Hokkaido. Even in the snow-rich areas of Hokkaido, however, the nonfreezing streams are not rare, unlike northern China and Far-East Russia, where most of the streams are frozen in winter and the entire Tancho subpopulations migrate for wintering around the unfrozen streams of Korea and central China (Meine and Archibald 1996, Higuchi et al. 1998). Therefore, artificial feeding in the snow-rich areas of Hokkaido probably enables the cranes to winter in their natural habitats. If they cannot winter in the snow-rich areas, the expansion of their breeding habitats will result in overpopulation at wintering areas in southeastern Hokkaido, and the cranes will be endangered by pathogenic infections.

In Hokkaido, cranes are compelled to be dependent on artificial feeding in order to maintain present population levels during winter, irrespective of their preferences. Because the ground is covered with snow and many rivers and lakes freeze up, it becomes difficult, if not impossible, for the cranes to get their natural diet from fields. Furthermore, they tend to feed at a site in the vicinity of their roost if there is enough food available. Therefore, the combined package of roosting and feeding place is regarded as the principal factor determining their dispersal to other wintering sites. On the other hand, it is considered that natural habitat, including food resources, is an important factor in dispersal of breeding pairs. Where there is decreased availability of natural diet or low efficiency of feeding, the cranes that have overcome their innate fear of human beings as a result of habitual contact, approach cultivated fields and eat farm products. If their population increases, the extent of agricultural damage is also likely to increase. However, these cranes cause agricultural damage even if the population size is small (i.e. the density is low). Therefore, farmers dislike cranes in close proximity to their lands. Hence, it can be concluded that dispersal of cranes can be restricted by putting into practice the measures that prevent cranes from coming close to these farmlands. The artificial feeding and taming of cranes have been a serious problem for preservation activities.

At present, the amount of natural diet available in the field is considerably less, compared to the 1950s when artificial feeding started, because of the destruction of over half the wetlands in southeastern Hokkaido. If artificial feeding is completely ceased and the cranes entirely depend on natural resources, the population would greatly decrease and might become extinction at the worst. As the cranes are habituated to people, however, they would receive fodder in the cultivated fields during fall and forage on the compost near farmhouses during winter. Despite the food provided by the people, the amount of food without artificial feeding obviously would fail to maintain the present and sufficient population size. Therefore, feeding assistance is unavoidable in this situation. To maintain a viable population size, it is desirable for cranes to live independently in their natural environment as much as possible by restoring the wetland ecosystem, preserving natural habitats, and dispersing cranes into the non-use wetlands.

Considering a more independent wild life of Tancho, the Hokkaido population is expected to migrate voluntarily to Honshu, which is separated from Hokkaido by about 20 km of the Tsugaru Strait (Fig. 1). It is not difficult for cranes to fly over the 20 km strait, as indicated by the migration between Kunashiri Island and Hokkaido. In addition, the migration to Honshu depends on the conservation of habitats in Honshu where the cranes are able to stay during winter.

In this paper, the carrying capacity is estimated using the assumption that the present population structure will be maintained in the future. In addition, the territory size is estimated based on the present breeding status, namely, the mean distance to the nearest nest. Although in this method K depends on the territory size, to accurately estimate K, accumulation of concrete data on territory size is necessary. We wish to analyze that data and estimate the carrying capacity more accurately in the future.

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Table 1 Data required for estimating values of stage matrix. The survival rate at each stage was estimated from the data of banded chicks (cf. Table 2). The survival rate 0.918 of sub-adult was used for calculating S_i

Year	Individuals (T_i)	Breeding pairs (B_i)	Juveniles (J_i)	Sub-adults (S_i)*	Adults (A_i)**	Banded chicks***	Accidental death (D_i)
1990	-	-	38	-	-	10	-
1991	453	148	58	35	360	15	2
1992	505	161	74	53	378	15	5
1993	522	171	54	68	400	10	4
1994	569	167	52	50	467	15	1
1995	500	182	50	48	402	10	2
1996	600	187	55	46	499	21	6
1997	619	218	59	50	510	12	4
1998	615	214	74	54	487	18	5
1999	706	215	103	68	535	18	2
2000	740	243	80	95	565	14	11
2001	771	263	92	73	606	14	8
2002	887	290	119	84	684	20	17
2003	898	273	122	109	667	17	13
2004	950	282	104	112	734	14	10

*$S_i = 0.918 \times J_{i-1}$; **$A_i = T_i - J_i - S_i$; ***The data after 2001 were not included for estimation of survival rate.

Table 2 Estimated survival rate, standard error and 95% confidence interval at each age stage by program MARK

	Survival rate	SE	Lower CI	Upper CI
Age 1	0.918	0.024	0.855	0.954
Age 2	0.921	0.027	0.850	0.960
Age 3	0.927	0.028	0.851	0.965
Age 4	0.925	0.032	0.833	0.968
Age 5+	0.945	0.016	0.903	0.970

Table 3 A stage matrix used for simulation, with other matrices calculated from the stage matrix using the software RAMAS Metapop. Life expectancy was calculated by $\sum_{i=1}^{\infty} \left| T^i n_0 \right| \Big/ \left| n_0 \right|$ where T is the stage matrix excluded fecundity and $\left| n_0 \right|$ is the total number of initial individuals. The initial abundance, i.e. the age structure in 2004, was estimated from the number of juveniles (Table 1) and survival rate (Table 2) by $N_2 = S_1 \times J^{2003}$, $N_3 = \prod_{i=1}^{2} S_i \times J^{2002}$, $N_4 = \prod_{i=1}^{3} S_i \times J^{2001}$, and $N_5 = T^{2004} - \sum_{i=1}^{4} N_i$ where N_i is the initial abundance at *i*-age, S_i is the survival rate at *i*-age, J^k is the number of juveniles at *k*-year, and T^{2004} is the number of individuals in 2004

Stage matrix

	1	2	3	4	5+
1	0	0	0.157	0.157	0.157
2	0.918	0	0	0	0
3	0	0.921	0	0	0
4	0	0	0.927	0	0
5+	0	0	0	0.925	0.945

Standard deviations

	1	2	3	4	5+
1	0	0	0.033	0.033	0.033
2	0.024	0	0	0	0
3	0	0.027	0	0	0
4	0	0	0.028	0	0
5+	0	0	0	0.032	0.016

Elasticities

	1	2	3	4	5+
1	0	0	0.010	0.009	0.070
2	0.089	0	0	0	0
3	0	0.089	0	0	0
4	0	0	0.079	0	0
5+	0	0	0	0.070	0.584

Sensitivities

	1	2	3	4	5+
1	0.089	0.077	0.067	0.059	0.476
2	0.103	0.089	0.077	0.068	0.549
3	0.118	0.102	0.089	0.078	0.632
4	0.120	0.104	0.090	0.079	0.641
5+	0.122	0.106	0.092	0.081	0.654

Life expectancy

Age	1	2	3	4	5+
	15.7	16.1	16.5	16.8	17.2

Initial abundances

Age	1	2	3	4	5+
	104	112	101	72	561

Table 4 Data required for estimating carrying capacity

	Region						
	Tokachi	Kushiro	Bekanbeushi	Kiritappu	Nemuro	Lake Furen	Notsuke Peninsula
Area of low moor (km^2) (*H*)	20.45	137.26	91.05	16.21	6.65	47.88	7.82
Number of breeding pairs	32	88	27	10	15	70	14
Mean distance to the nearest nest (km) (*L*)	2.30	2.17	2.63	1.86	1.74	1.72	4.06
Territory (km^2)							
Average size (*U*)*	4.15	3.68	5.42	2.73	2.38	2.32	12.95
Average area of low moor (*W*)	0.39	0.77	1.35	0.57	0.18	0.36	0.29
Maximum number of breeding pairs (*M*)**	52	179	67	28	36	131	27

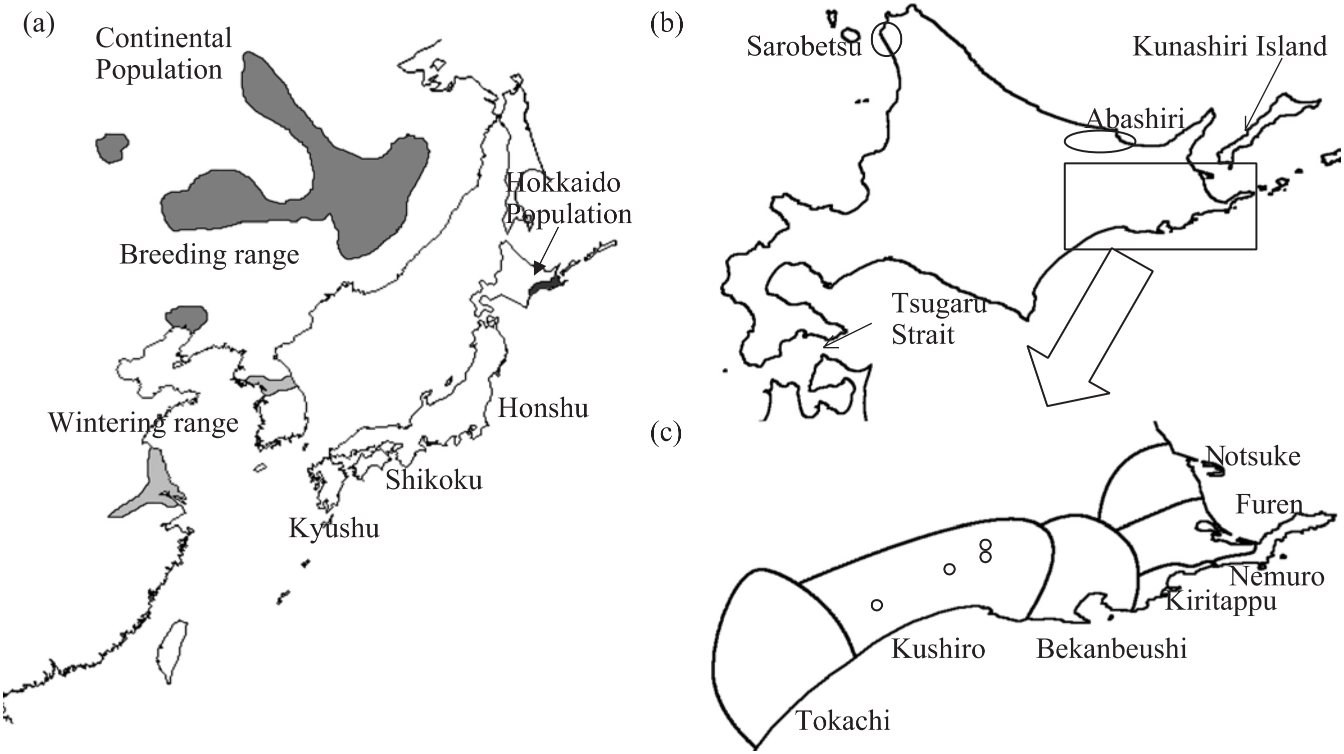
*$U = \pi(L/2)^2$; **$M = H/W$

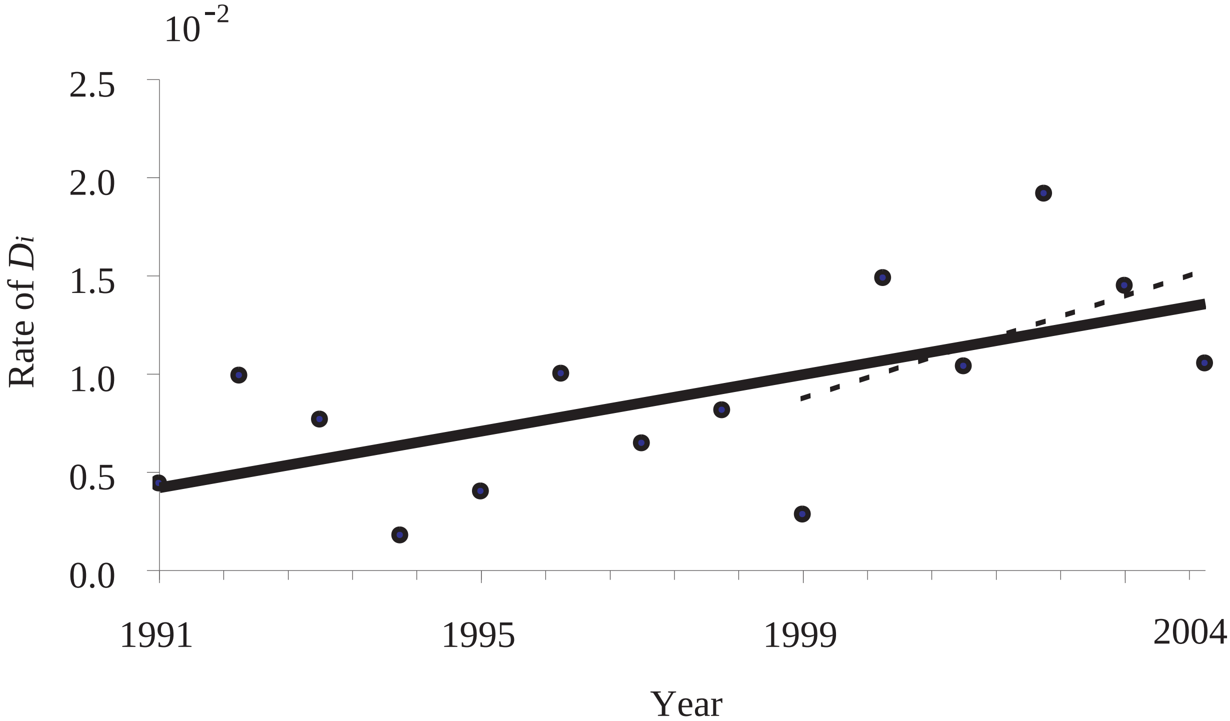
Fig. 1 Distribution of Red-crowned Crane (*Grus Japonensis*) (**A**) and study area (**B**, **C**). In **C**, the study area is divided into seven regions. Four major artificial feeding stations are shown in the Kushiro region

Fig. 2 Interannual fluctuation of accidental death rate calculated by D_i/T_i (cf. Table 1). Two lines are linear regressions during 1991–2004 (solid line: slope $S = 0.072 \times 10^{-2}$) and 1999–2004 (dotted line: $S = 0.132 \times 10^{-2}$), respectively

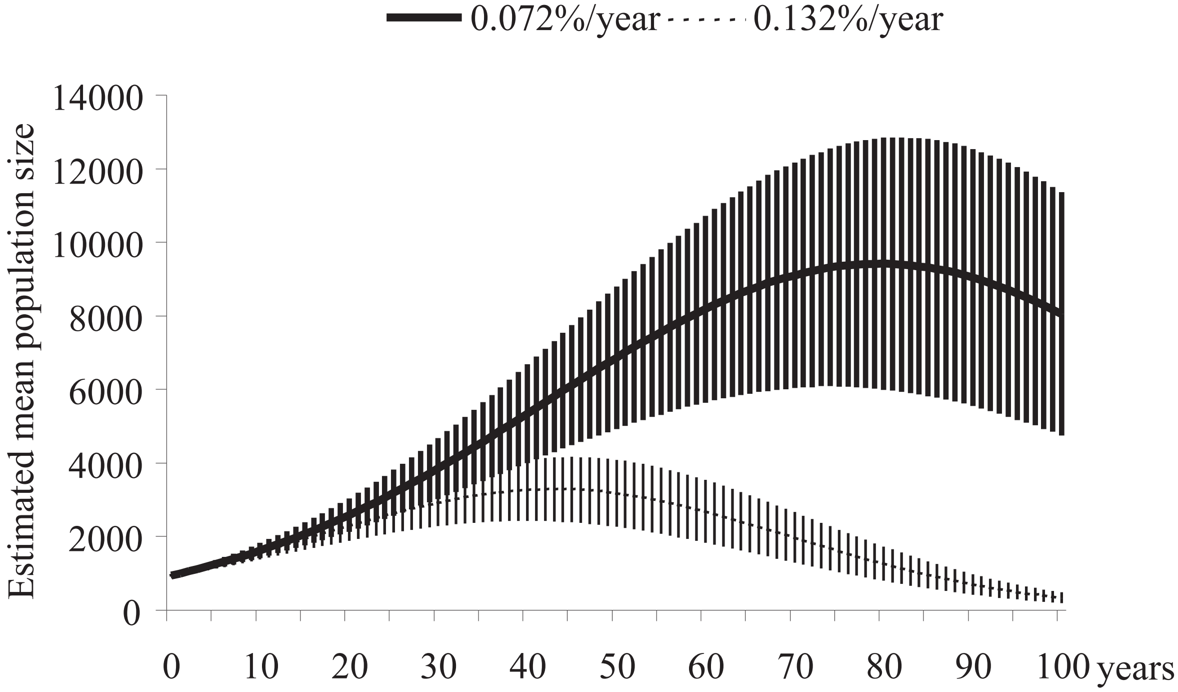
Fig. 3 Future population dynamics with standard deviation estimated in two cases of accidental death (**A**) and two cases of carrying capacity (**B**)

Fig. 4 Future population dynamics with standard deviation estimated in the combination of carrying capacities and accidental death rates

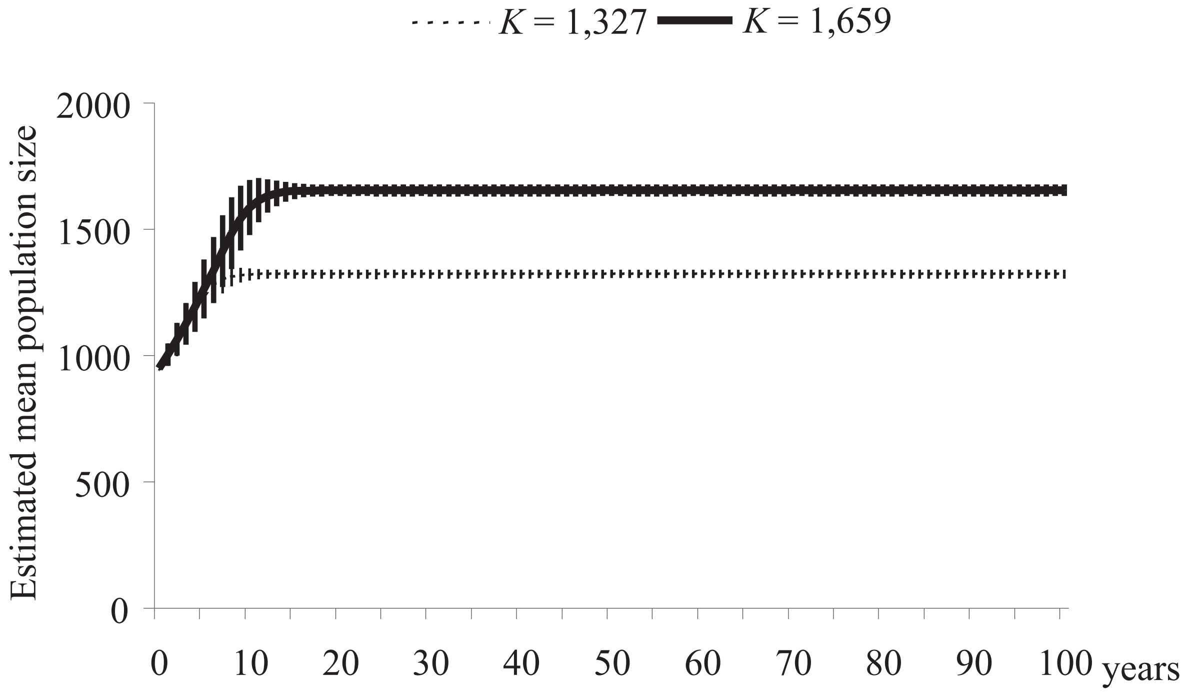

(a)
Continental Population
Breeding range
Hokkaido Population
Wintering range
Honshu
Shikoku
Kyushu
(b)
Sarobetsu
Kunashiri Island
Abashiri
Tsugaru Strait
(c)
Notsuke
Furen
Nemuro
Kiritappu
Kushiro
Bekanbeushi
Tokachi

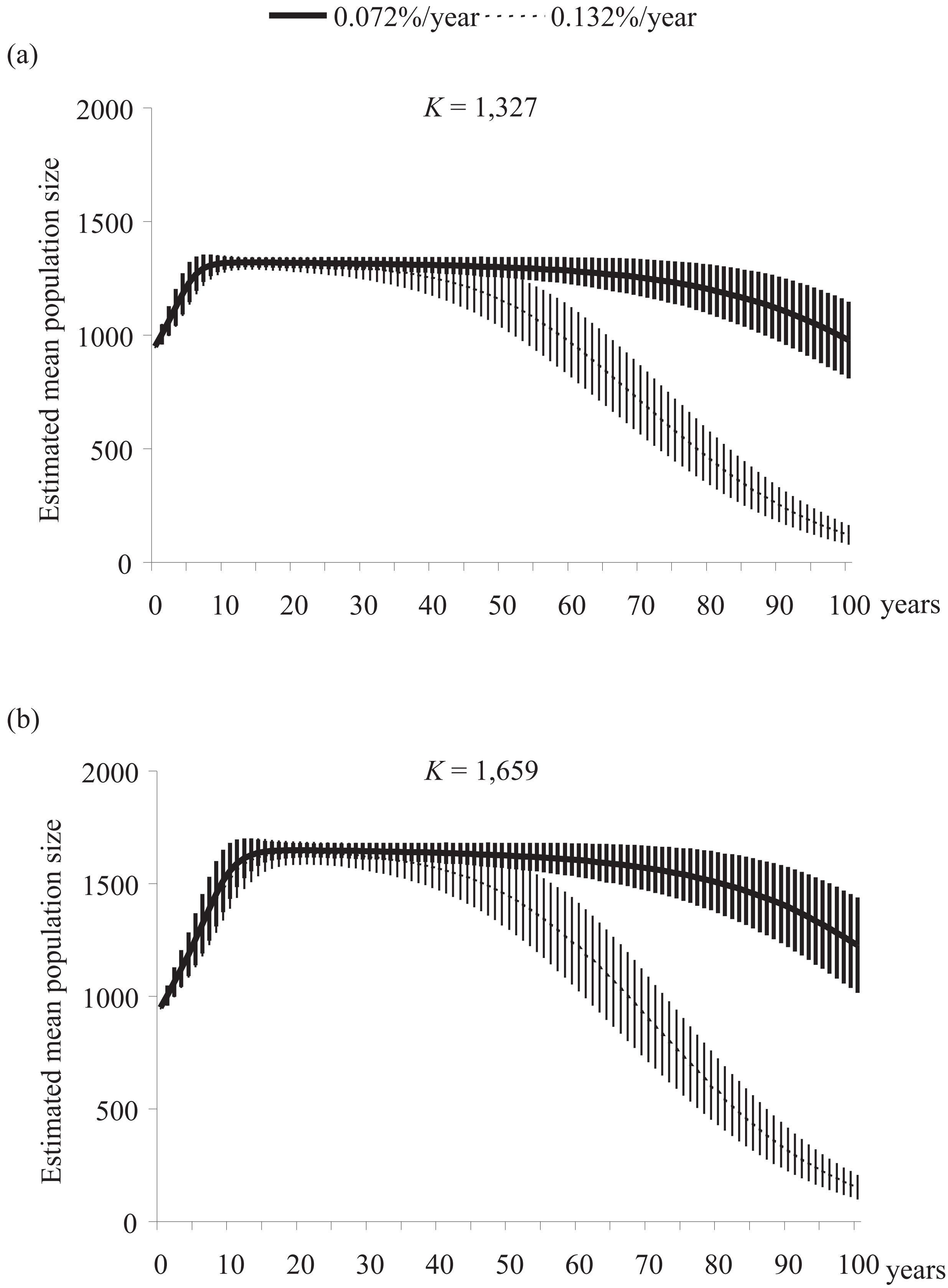

10^-2
2.5
2.0
1.5
1.0
0.5
0.0
Rate of Di
1991
1995
1999
2004
Year

(a)


0.072%/year
0.132%/year
Estimated mean population size
14000
12000
10000
8000
6000
4000
2000
0
0
10
20
30
40
50
60
70
80
90
100
years

(b)


K = 1,327
K = 1,659
Estimated mean population size
2000
1500
1000
500
0
0
10
20
30
40
50
60
70
80
90
100
years


0.072%/year
0.132%/year
(a)
K = 1,327
Estimated mean population size
2000
1500
1000
500
0
0
10
20
30
40
50
60
70
80
90
100
years
(b)
K = 1,659
Estimated mean population size
2000
1500
1000
500
0
0
10
20
30
40
50
60
70
80
90
100
years