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Abstract.—Waterbird survival rates are a key component of demographic modeling used for effective conservation of long-lived threatened species. The Swan Goose (*Anser cygnoides*) is globally threatened and the most vulnerable goose species endemic to East Asia due to its small and rapidly declining population. To address a current knowledge gap in demographic parameters of the Swan Goose, available datasets were compiled from neck-collar resighting and telemetry studies, and two different models were used to estimate their survival rates. Results of a mark-resighting model using 15 years of neck-collar data (2001-2015) provided age-dependent survival rates and season-dependent encounter rates with a constant neck-collar retention rate. Annual survival rate was 0.638 (95% CI: 0.378-0.803) for adults and 0.122 (95% CI: 0.028-0.286) for first-year juveniles. Known-fate models were applied to the single season of telemetry data (autumn 2014) and estimated a mean annual survival rate of 0.408 (95% CI: 0.152-0.670) with higher but non-significant differences for adults (0.477) vs. juveniles (0.306). Our findings indicate that Swan Goose survival rates are comparable to the lowest rates reported for European or North American goose species. Poor survival may be a key demographic parameter contributing to their declining trend. Quantitative threat assessments and associated conservation measures, such as restricting hunting, may be a key step to mitigate for their low survival rates and maintain or enhance their population. *Received 8 December 2015, accepted 29 January 2016.*

Key words.—*Anser cygnoides*, demography, neck-collar, survival rate, Swan Goose, telemetry.

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Population growth in long-lived birds is more strongly affected by survival than fecundity (Lebreton and Clobert 1991), and expected lifespan level increases exponentially with increasing survival rate (Ebbinge *et al.* 1991). Therefore, knowledge of the survival rates of long-lived and large-bodied waterbirds such as geese and swans is a key requirement for effective population management and conservation actions. In accordance with the favorable conservation status of many waterbird populations in North America and in Europe (Wetlands International 2010), adaptive management programs have been implemented to harmonize long-term conservation aims with short-term harvest regulation for North American and European geese populations (Alisauskas *et al.* 2011; Madsen *et al.* 2015), based upon population survival rate estimates (e.g., Powell *et al.* 2004; Trinder *et al.* 2005; Kéry *et al.* 2006; Fox *et al.* 2010). However, few survival rates have been estimated for Asian goose species despite the fact that almost all goose populations and many other waterfowl in East Asia are declining (Wetlands International 2010) and several of them have declined even to critical levels attributed to rapid habitat loss and uncontrolled hunting (Syroechkovskly 2006).

The Swan Goose (*Anser cygnoides*) is a globally threatened species listed as vulnerable in the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) (Batbayar *et al.* 2011; Birdlife International 2015). As an endemic species to East Asia, the Swan Goose mainly breeds in eastern Russia and northern Mongolia and winters primarily in southern China with some in South Korea (Kear 2005; Batbayar *et al.* 2011). Because its small and rapidly declining population is confined to a small geographical range that is contracting, the Swan Goose has become the most vulnerable goose species in this region (Poyarkov 2006). The major threats to Swan Geese likely include uncontrolled hunting, loss and degradation of breeding and molting wetlands, anthropogenic disturbance, and unfavorable climate conditions such as prolonged drought (Goroshko 2004; Poyarkov 2005; BirdLife International 2015; Tao *et al.* 2015).

Neck-collars and telemetry have been used widely for demographic studies of goose populations (Schmutz and Morse 2000), including the study of the migration of Swan Geese (Batbayar *et al.* 2011). The East Asian network of observers and bird band recovery schemes are poorly developed compared to those in North America and Europe, but Swan Goose neck-collar projects conducted since 2000 (Poyarkov 2006) have produced some important results regarding site connectivity and migration routes. For instance, the neck-collar resighting program identified that the Han River Estuary in South Korea is a key staging site for Swan Geese breeding in the Russian Far East (Poyarkov 2006) and that the Yangtze River watershed in China is a wintering area for birds breeding in the Daurian Region at the border of Russia, Mongolia, and China (Xu 2008) (Fig. 1). A recent satellite telemetry study (Batbayar *et al.* 2011) identified detailed migration timing and patterns of the Swan Geese breeding in northeastern Mongolia that use the Yalu River Estuary at the China-North Korea border as a key staging site and Poyang Lake in southern China as a major wintering area. These data showed that Swan Geese from Dauria and the Russian Far East may have separate, non-overlapping migration corridors, supporting the hypothesis that they have two discrete breeding populations (Poyarkov 2006).

However, many other aspects of the migration ecology and life cycle of the Swan Goose remain unknown; for instance, their breeding range is not clearly defined and the wintering areas of the Russian Far East population remain uncertain. In addition, survival rates, a key demographic fundamental for waterbird management and conservation, have never been estimated for the Swan Goose (Kear 2005). Here, we synthesized available resightings of neck-collared individuals and data from recent telemetry studies to provide the first estimate of survival rates for the threatened Swan Goose.

METHODS

Study Areas

This study covers the geographical range of the Swan Goose in East Asia, including parts of the Russian Federation (Russia), People's Republic of China (China), Mongolia, and the Republic of Korea (South Korea) (Fig. 1). It focuses on the breeding areas in the Daurian Region around the borders of northeastern Mongolia, Russia and China, the lower reaches of the Amur River in the Russian Far East, and stopover and wintering areas in China and South Korea.

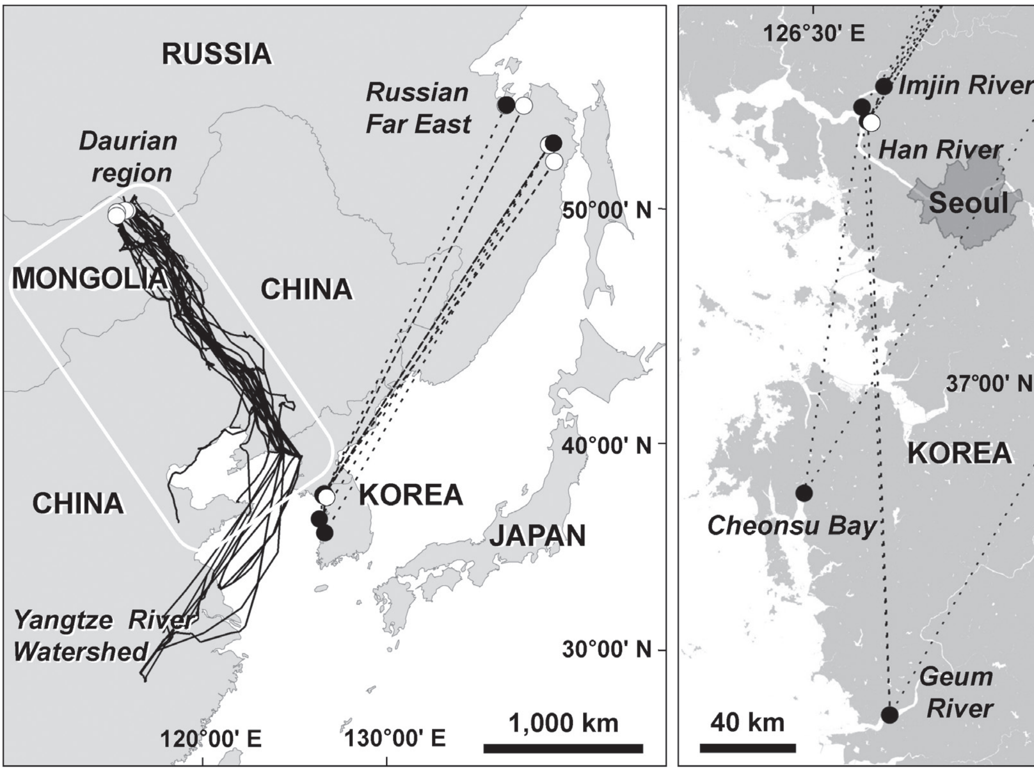

Figure 1. Study area and migration routes of two populations of the Swan Goose in East Asia. Solid lines indicate the autumn migration routes of 40 Swan Geese tracked by GPS-GSM transmitters in 2014. Dotted lines represent the linkages of 28 neck-collared Swan Geese between marking and resighting sites between 2001 and 2015. Open circles are capture and marking sites in Mongolia, the Russian Far East, and South Korea, while filled circles are wetlands with resighting reports in South Korea and Russia. The open box outlined in white indicates the extent of the telemetry data used in this study. The enlarged area in the right panel indicates detailed resighting and capture sites in South Korea.

Resighting Geese Marked with Neck-collars

We used marking and resighting data from Swan Geese (n = 63; hereafter geese) reported from Russia and South Korea (Fig. 1). In the Russian Far East, 60 geese (44 juveniles and 16 post-molting adults) were captured and marked with blue neck-collars (with combinations of three white engraved letters and numbers) in July and August between 2001 and 2008. At Udyl Lake (52° 10′ N, 139° 52′ E), two juveniles were marked in 2001, 11 geese in 2003, five in 2005, and 34 in 2006. Three geese were marked at Kizi Lakes (51° 33′ N, 140° 07′ E) in 2006, and five more individuals were marked and released at Nikolaya Bay (53° 36′ N, 138° 22′ E) in 2008. In South Korea, three adults were captured with a cannon net and marked with white neck-collars (engraved with a black letter and two figures) at a staging site at Gongreung Stream (37° 45′ N, 126° 41′ E) near the Han River estuary in March 2003.

We visited staging and wintering areas in South Korea to observe neck-collared geese and collect resighting reports (with the support of the Waterbird Network Korea, a nationwide non-governmental organization) from all available sources, including official bird banding reports, personal records of individual birdwatchers and volunteers, ornithological and environmental organizations, media, published and unpublished material. We also received data from Russian researchers and the Bird Ringing Centre of Russia about the fate and recovery of neck-collared geese.

We compiled 133 observational reports of individual neck-collared geese, excluding unreadable neck-collars, between October 2003 and March 2015 (Fig. 2). These reports were almost exclusively live bird observations, except for two cases from two geese marked in South Korea that were recovered dead and reported by hunters in Russia. On the basis of likely variation in observation probabilities, we defined four reporting seasons comprising three months: summer (June-August), autumn (September-November), winter (December-February), and spring (March-May). The original 133 observations were summarized into 74 resighting events by removing repeated reports of the same individuals within each 3-month sampling period. This resulted in 137 encounter histories composed of 63 marking and 74 resighting events: 61 in the summer, 40 in the autumn, 10 in the winter and 26 in the spring (Fig. 2). We defined an ‘observation’ as any individual event confirming the occur-

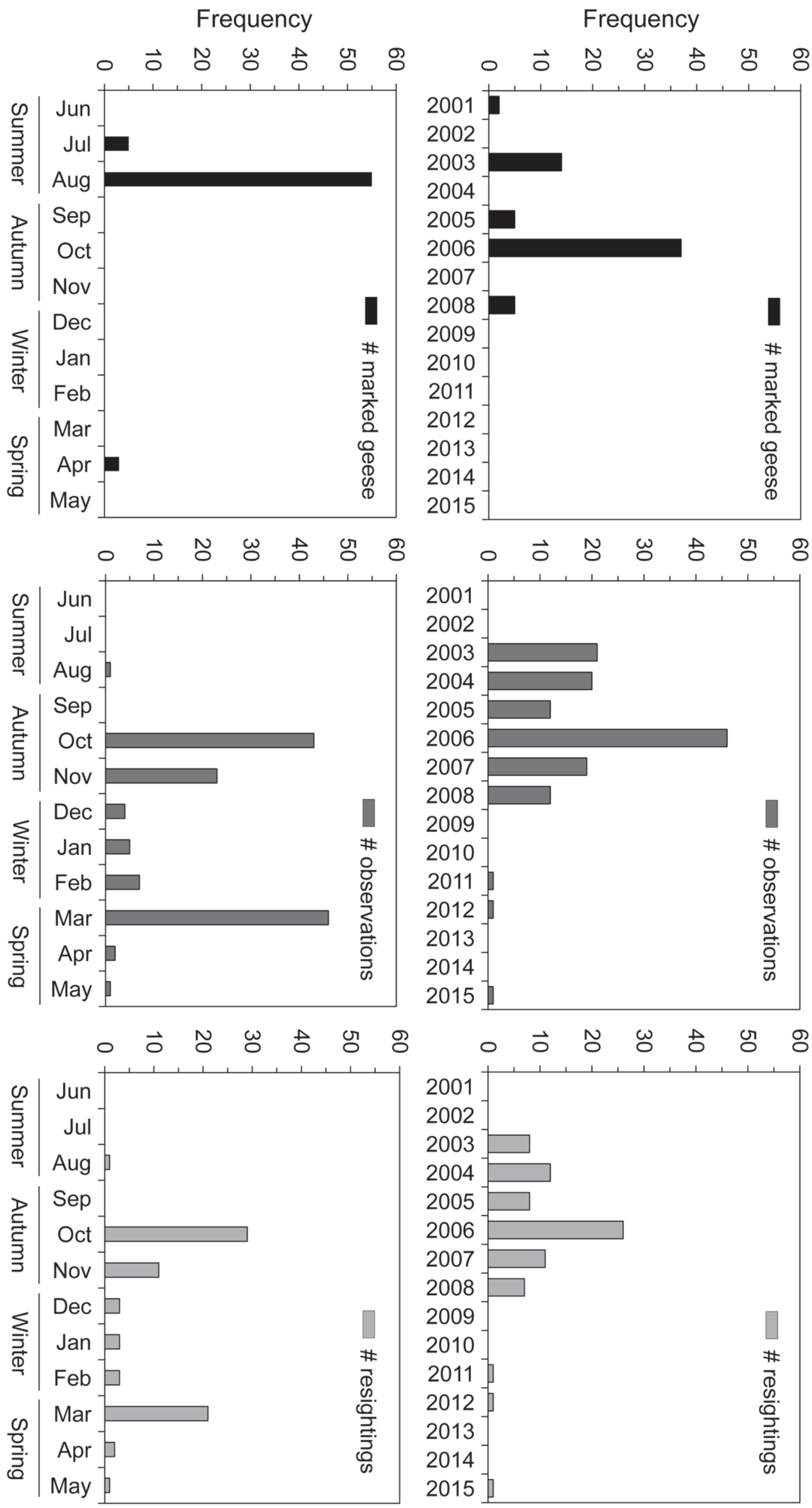

Figure 2. The frequency and distribution of 63 markings, 133 observations, and 74 resightings of Swan Geese by year (upper panels) and month (lower panels) in the Russian Far East and South Korea between 2001 and 2015.

rence of marked birds (e.g., recapture, recovery, harvest) regardless of its fate, 'resight' as a summarized event of all confirmed observations during a sampling period omitting repeated observations in the same period, and 'encounter' including both resight and capture for marking. Because of the limited number of marked birds and encounter reports over the study period, in addition to their site fidelity in a limited range, we assumed that the number of marked birds changed between sample periods with mortality but not emigration.

Tracking Geese Marked with Transmitters

We captured geese by herding flightless adults and juveniles with boats and kayaks into corral traps from 23 to 31 July 2014 in northeastern Mongolia (Fig. 1). A total of 49 transmitters were deployed on 49 Swan Geese in addition to neck-collars at four lakes: Bus Lake (49° 44′ N, 115° 09′ E), Galuut Lake (49° 44′ N, 115° 17′ E), Chukh Lake (49° 31′ N, 114° 39′ E), and Khaichiin Tsagaan Lake (49° 41′ N, 114° 40′ E). These transmitters (20 from Microwave Telemetry, Inc.; 20 from Ecotone, Inc.; six custom made by the Chinese Academy of Sciences, China; and three custom made by the Korea Institute of Environmental Ecology, South Korea) collected Global Positioning System (GPS) location fixes on programmed duty cycles (varying from 1- to 360-min intervals depending on solar conditions) and transmitted the accumulated data when connected to commercial Global System for Mobile (GSM) cellular phone networks. GSM networks are poor in remote regions of the breeding area, so the transmitters did not start to send location data until they encountered GSM networks in China during fall migration. All transmitters (< 60 g) were less than 2.0-2.5% of the body mass of the geese.

Signal loss from a transmitter may represent the death of a goose, mechanical failure, or physical loss. Thus, assuming that signal loss from tracked geese represents mortality may underestimate survival. We reviewed location fixes and metadata (i.e., height, speed, voltage of battery, activity and temperature sensor data) of geese where their signals were lost and visited the sites whenever possible to determine their fate and retrieve transmitters. Thus, mortality events were confirmed although some signal loss occurred with unknown fates.

Modeling Survival

The Cormack-Jolly-Seber (CJS) model assumes no loss of markers on marked individuals, but this assumption is often violated in wild bird populations (Laake *et al.* 2014). Loss of neck-collars may result in biased estimates of survival rates and abundance in mark-resighting studies (Pollock *et al.* 1990; Gauthier *et al.* 2001); thus, we used a hidden Markov model (HMM) to integrate marker loss in a CJS survival model (Laake *et al.* 2013, 2014) including age-, season-, and time-dependent variables. To examine the effects of age and season on survival (ϕ), resighting (p), and marker retention (τ) rates, we used four seasons and two age groups as explanatory variables. Individuals were readily assigned to juvenile or adult classes at the time of capture through differences in their plumage and size: geese in their first year of life were regarded as juveniles, and geese that had survived past their first wintering season were considered as adults. Sex was identified through cloacal examination. Survival rates corrected for marker loss were obtained by dividing the estimated survival rate from the HMM by the marker retention rate (τ) over the period (Pollock *et al.* 1990).

Daily survival rates (*S*) of geese during migration were estimated with known-fate models (Cooch and White 2014). Encounter histories were developed from daily telemetry detections regardless of duty cycles, and individuals with lost signals from unknown fates were censored. Models that varied by time, age, and sex were tested.

We used R packages 'marked' (Laake *et al.* 2013) and 'Rmark' (Laake 2013), linked to Program MARK (Cooch and White 2014) in the statistical program R (R Development Core Team 2015). The best model was selected by comparing Akaike's Information Criterion corrected for small sample sizes (AIC_c) among models and selecting the model with the lowest AIC_c value. However, we also considered models with ΔAIC_c of < 2 as competing models, and we applied model averaging to calculate parameters when a single best model was not identified (Burnham and Anderson 2002). Survival estimates are presented as means with standard errors (SE) or 95% confidence intervals (CI).

Results

Neck-collar and Telemetry Data

Between October 2003 and March 2015, a total of 28 out of 63 neck-collared geese (44.4%) were resighted in South Korea and Russia 18.5 ± 4.3 months after marking (median: 8.4 months; range: 0.8-102.7 months; *n* = 28) (Figs. 1-3). Resighted geese comprised 17 marked as adults and 11 marked as juve-

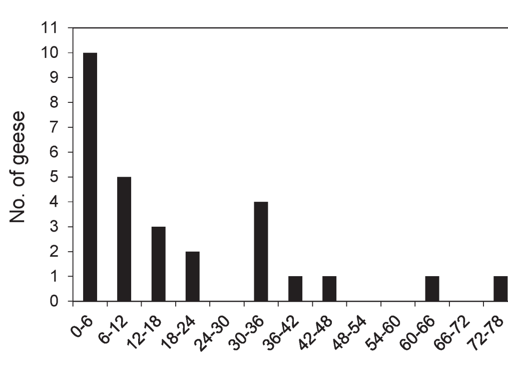

Figure 3. Time interval (months) between the initial marking and the last resighting of neck-collared Swan Geese marked in the Russian Far East and South Korea between 2001 and 2015.

niles, and resighting averaged 2.7 ± 0.5 times each (median: 2; range: 1-8; $n = 28$). The ratio of adults and juveniles at the time of marking was significantly different from that of resighted birds ($\chi^2_1 = 6.345$, $P = 0.012$), indicating a higher probability of resighting amongst geese marked as adults. Two out of 19 adults and 33 of 44 juveniles were never resighted after the initial marking and release. The seasonal frequency distribution of the known 133 observations demonstrated that marked geese were most frequently reported during migration in the autumn (32.3% in October and 17.3% in November) and the spring (35.3% in March) in South Korea, while only two reports were available in the Russian Far East in April and August (Fig. 2).

A total of 40 of 49 geese (14 adults and 26 juveniles) were tracked from 1 September to 30 November 2014 during their autumn migration from Mongolia to China (Fig. 1). The geese were tracked for 68.0 ± 3.9 days (median: 78; range: 8-91 days; $n = 40$), and seven mortalities were confirmed from one adult and six juveniles during the 3,640 tracking days (40 birds for 91 days). Signal loss occurred for 20 geese, and they were censored, while 13 geese were still active at the end of the study period in the autumn.

Survival Rates of Neck-collared Geese

We found three competitive parsimonious models in the analysis of the survival (ϕ), resighting (p), and marker retention rates (τ) of neck-collared geese (Table 1). The top candidate model, based on the lowest AIC_c value for survival (ϕ) and resighting (p) rates was $\phi_a p_s \tau_c$, indicating that the survival rate was best explained by dependence on age, while the resighting rate was affected by season (Table 1). However, two other models ($\phi_{a*s} p_s \tau_c$, $\phi_{a*s} p_{a*s} \tau_c$) also were competitive, and all of the candidate models suggested a constant marker retention rate.

Adults had higher survival rates than juveniles according to the model averaged estimates: quarterly (3-month) survival rates of adults and juveniles were 0.889 ± 0.040 (95% CI: 0.768-0.941) and 0.584 ± 0.082 (95% CI: 0.404-0.721) and corresponded to an annual survival rate of 0.624 (95% CI: 0.370-0.785) for adults and 0.119 (95% CI: 0.027-0.279) for juveniles. Resighting rates were not constant during seasons, but no significant difference between seasons was detected: 0.426 (95% CI: 0.293-0.558) in the spring, 0.250 (95% CI: 0.154-0.381) in the breeding season, 0.304 (95% CI: 0.225-0.395) in the autumn, and 0.363 (95% CI: 0.277-0.454) in the winter. Marker retention rate was constant across the seasons (0.994 ± 0.006, 95% CI: 0.961-0.999) with an annual marker retention rate of 0.977 ± 0.023 (95% CI: 0.852-0.997). Corrected annual survival rates incorporating marker loss were 0.638 (95% CI: 0.378-0.803) in adults and 0.122 (95% CI: 0.028-0.286) in juveniles.

Survival Rates of Transmitter-marked Geese

We obtained data from three adults and 10 juveniles for 91 days from September to

Table 1. Competitive parsimonious models in the analysis of the quarterly survival (ϕ) and resighting (p) rates of Swan Geese (*Anser cygnoides*) with marker retention rate (τ) based on resighting of neck-collared individuals between 2001 and 2015. Daily survival rate (S) was estimated based on telemetry data collected in autumn of 2014. For each model, the difference (ΔAIC_c) between the current corrected Akaike's Information Criterion (AIC_c) and the lowest value, AIC_c weight, number of estimated parameters, and deviance are reported. Subscripts *a*, *s*, and *sex* denote age-, season-, and sex-dependent, while *c* means constant.

Model	ΔAIC_c	AIC_c Weights	No. Parameters	Deviance
Neck-collar				
$\phi_a p_s \tau_c$	0.000	0.518	5	279.967
$\phi_{a*s} p_s \tau_c$	0.905	0.278	7	276.872
$\phi_{a*s} p_{a*s} \tau_c$	1.951	0.130	9	273.918
Telemetry				
S_c	0.000	0.489	1	45.415
S_a	0.844	0.320	2	44.256
S_{sex}	1.881	0.191	2	97.330

November 2014, while signals were lost for 27 birds including seven confirmed mortalities. The top candidate model for daily survival of migrating geese (S_c) suggested a constant daily survival rate, but two other models incorporating age (S_a) and sex (S_{sex}) effects were competitive. The model averaged estimate of daily survival was 0.998 ± 0.001 (95% CI: 0.996-0.999), indicating a quarterly survival rate of 0.799 ± 0.071 (95% CI: 0.624-0.904) during autumn migration and an annual survival rate of 0.408 (95% CI: 0.152-0.670). There was no statistical difference in the daily survival rates between the two age groups (0.998 in adults and 0.997 in juveniles) because they had overlapping 95% CIs (0.994-0.999 both in adults and juveniles). Annual survival rates were estimated as 0.477 (95% CI: 0.111-0.738) in adults and 0.306 (95% CI: 0.118-0.624) in juveniles.

Discussion

We studied individual Swan Geese marked with neck-collars or transmitters to estimate their survival rates from two different breeding areas. While differences in methods precluded direct comparison of survival between these populations, we calculated a mean overall annual survival rate of 0.477-0.638 for adults and 0.122-0.306 for juveniles. Thus, our findings suggest that low survival rates of juveniles may be a limiting demographic factor for Swan Geese.

Survival rates are highly variable for geese among species (Kear 2005; Baldassarre 2014) and populations (Powell *et al.* 2004; Trinder *et al.* 2005; Fox *et al.* 2010), as well as by age (Schmutz *et al.* 1994; Schmutz and Ely 1999; Powell *et al.* 2004; Alisauskas *et al.* 2006), sex (Schmutz and Ely 1999) and year (Schmutz *et al.* 1994; Powell *et al.* 2004; Alisauskas *et al.* 2006). In addition, marker effects may result in reduced survival (Schmutz and Morse 2000; Alisauskas and Lindberg 2002; Alisauskas *et al.* 2006; Caswell *et al.* 2012). Neck-collars or transmitters attached to neck-collars have been reported to lower mean survival rate by 17% in Emperor Geese (*Chen canagica*; Schmutz and Morse 2000), 0.6-23% in Canada Geese and 0.4-22% in Greater White-fronted Geese (*A. albifrons*; Alisauskas and Lindberg 2002), and 18-31% in Ross's Geese (*C. rossii*; Caswell *et al.* 2012) compared to individuals without those markers. Averaging the four upper limits of survival (23%) and applying them to our results (0.477-0.638 for adults and 0.122-0.306 for juveniles) would yield conservative maximum annual survival rates of 71-87% for adults and of 35-54% for juveniles. If the mean of the lower survival limits (9%) are applied, adjusted annual survival rates may be as low as 57-73% for adults and 21-40% for juveniles. A further study quantifying marker effects on survival is required to estimate a robust demographic parameter of Swan Geese.

We were unable to compare survival rates of other goose species in East Asia because of the lack of available estimates for other species in this region. However, from studies of North American and European goose populations, annual survival rates of geese typically ranged from 64-95% with lower survival of juveniles (e.g., Kear 2005; Trinder *et al.* 2005; Fox *et al.* 2010; Baldassarre *et al.* 2014). The results indicate that the annual survival rates for Swan Geese, especially juveniles, were lower than for European or North American goose populations, supporting the contention that this species has a strongly declining population trend (BirdLife International 2015), as do other goose populations in Asia (Syroechkovskly 2006). In general, the frequent and widespread spring wildfires on breeding grounds in the Daurian steppe (Goroshko 2012), as well as the current drought that affects abundance, extent and quality of breeding wetlands (Tao *et al.* 2015), seem to be important threats to the Swan Goose populations. In the Yangtze River watershed of China where Swan Geese spend the winter, water extraction, water level regulation, declining water quality, and expansion of intensive aquaculture reduce availability of preferred wintering wetlands (Fox *et al.* 2008, 2011; Zhang *et al.* 2011), concentrating geese at fewer sites and increasing their susceptibility to diseases (such as highly pathogenic avian influenza), illegal hunting, and pollution or poisoning at remaining key wetlands (BirdLife International 2015).

Our estimates of age-dependent survival rates between adult and juvenile Swan Geese differed by population. A mark-resighting model based on 14 years of field data for the Russian Far East population showed a significant difference in annual survival rates (0.638 in adults vs. 0.122 in juveniles), while results from the small telemetry dataset in the Daurian population showed no significant differences (0.408 combined) between ages. Differences in age ratios between marked and resighted birds in the Russian Far East population suggested geese marked as adults had a higher chance of being resighted than geese marked as juveniles, and this was consistent in studies where adults had higher survival rates than juveniles (e.g., Schmutz *et al.* 1994; Powell *et al.* 2004; Alisauskas *et al.* 2006). Nevertheless, it is unclear which factors specifically cause the low survival in juveniles of the Russian Far East population. However, it is noteworthy that two of three geese marked in Korea were killed by Russian hunters on the breeding grounds just 26 and 122 days after marking, implying that unregulated hunting may be the greatest threat to this species as has been suggested (Goroshko 2001, 2004; Poyarkov 2005; BirdLife International 2015). Neck-collar marked juveniles of Ross's Geese were twice as vulnerable to harvest as marked adults (Alisauskas *et al.* 2006), and, similarly, differential harvest by age as well as high hunting pressure may explain the low juvenile survival of Swan Geese in the Russian Far East and their unknown wintering grounds in China. At least three of seven confirmed mortalities in the telemetry data are suspected to be related to poaching, and this also suggests high hunting pressures on the Daurian population in China. In conclusion, our findings highlight conservation concerns about the low survival, especially of juveniles, where illegal hunting and trapping remains a serious problem in many parts of the staging, wintering, and breeding grounds of the Swan Goose (BirdLife International 2015).

Although the best model fit to the neck-collar study data did not support a seasonal difference in the survival rates, two other competitive models indicated seasonal effects as was shown for other goose species (Schmutz and Ely 1999; Gauthier *et al.* 2001; Hupp *et al.* 2008). Therefore, the annual survival rate estimate using the short-term telemetry data may be biased due to simple extrapolation of the autumn survival rate. The use of long-term telemetry will help estimate robust survival rates for the Swan Goose and identify key areas along its flyway (including unknown wintering grounds) to improve site management and conservation.

A Swan Goose captured in South Korea was confirmed to have lost its neck-collar (R5V, marked as juvenile in August 2006, recaptured in March 2015) based on its metal leg band (Y. S. Choi, unpubl. data). This record is the first and only confirmation of neck-collar loss, and it showed that a Swan Goose could survive > 103 months in the wild while retaining its neck-collar for > 76 months. The estimated marker retention rate in our hidden Markov model was established from this single report, and it may be another source of biased survival rate estimates. Nevertheless, our data indicate that the annual retention rate of neck-collars in Swan Geese was 97.7 ± 2.3%, which was similar to the 95.0 ± 0.8% reported in adult Greater Snow Geese (*C. caerulescens atlantica*; Gauthier *et al.* 2001).

These are the first survival estimates for Swan Geese, but additional neck-collar and telemetry studies will provide more fundamental baseline demographic information for this threatened goose species. Most importantly, quantitative assessments of the threats and pressures on populations together with associated conservation measures aimed at mitigating the low survival rates, especially of juveniles, would be useful to help stabilize or enhance the population growth of the Swan Goose.

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