

Abundance of Tule Geese *Anser albifrons elgasi* in the Pacific Flyway 2003–2019

DAN R. YPARRAGUIRRE^{1,*}, TODD A. SANDERS²,
MELANIE L. WEAVER¹ & DANIEL A. SKALOS¹

¹California Department of Fish and Wildlife, Wildlife Branch, 1010 Riverside Parkway,
West Sacramento, California 95605, USA.

²United States Fish and Wildlife Service, Division of Migratory Bird Management,
1211 SE Cardinal Court, Suite 100, Vancouver, Washington 98683, USA.

*Correspondence author. E-mail: danyparraguirre577@gmail.com

Abstract

Tule Greater White-fronted Geese *Anser albifrons elgasi* (Tule Geese) may be the least abundant of North American goose subspecies and thus are a conservation concern. However, existing Tule Goose abundance estimates are either outdated, unpublished or lack estimates of precision. Annual estimates of Tule Goose abundance were derived by expanding estimates of radio-marked goose abundance by the ratio of total to radio-marked geese from mark-resight data. Tule Geese ($n = 1,160$) were captured and ringed during 2003–2019 primarily at an autumn migration stopover area in eastern Oregon, and 505 were also marked with plastic collars with unique codes and VHF radios. About 19,900 resightings (live encounter by radio telemetry or visual sightings) of radio-marked Tule Geese were made, primarily during autumn and winter in Oregon and California. The mean (\pm s.e.) annual abundance of Tule Geese in the autumn was $14,703 \pm 1,455$ (95% CI = 11,852–17,555, $n = 17$). There was no evidence of a trend in Tule Goose abundance during this period; the annual growth rate was $-1.89 \pm 1.84\%$ (95% CI = -5.63 – 2.00 , $t_{16} = 1.05$, $P = 0.311$, n.s.). Point estimates of annual abundance were variable (range = 6,992–33,342) and lacked precision (mean CV = 26%, range = 19–41%). The uncertainty was primarily associated with the variance of total to marked goose ratio estimates compared to estimates of radio-marked goose abundance. Winter distribution of Tule Geese generally appears to be unchanged from information from the 1980s and 1990s. Mean annual survival probability was lower for female (0.724 ± 0.038 , 95% CI = 0.643–0.792) than for male (0.823 ± 0.029 , 95% CI = 0.758–0.874) leg-ringed only geese, and for radio-marked geese (0.610 ± 0.028 , 95% CI = 0.553–0.664) compared to leg-ringed only geese (0.786 ± 0.027 , 95% CI = 0.727–0.834). The mark-resight method provides a means to monitor abundance of Tule Geese; however, improvements are needed to increase the precision of estimates, particularly regarding estimation of the ratio of total to marked geese. The stable

trend in abundance and the moderate survival rates suggest that managers may need to assess current management strategies carefully if Tule Geese abundance is to be maintained or increased.

Key words: *Anser albifrons elgasi*, mark-resight, survival, telemetry, winter distribution.

Abundance estimates of Tule Greater White-fronted Geese *Anser albifrons elgasi* (hereafter Tule Geese) have been sporadic and lack estimates of precision (Scott 1949; Bauer 1979; Timm *et al.* 1982; Wege 1984; Pacific Flyway Council 1991), have been presented but not yet published in full (Orthmeyer *et al.* 1992, 1998; Trost & Harb 1995), are qualitative (“fewer than”, Ely *et al.* 2006; Fox & Leafloor 2018), or are based on a range of published and unpublished information (Deuel & Takekawa 2008). At least in part, this is a consequence of overlap in autumn and winter distribution of the Tule Goose and the Pacific Greater White-fronted Goose *A. a. sponsa* (after Banks 2011, hereafter PGWFG; previously *A. a. frontalis*) (Swarth & Bryant 1917; Bellrose 1980; Timm *et al.* 1982; Ely & Dzubin 1994; Orthmeyer *et al.* 1995; Banks 2011), where it is difficult to distinguish between the two subspecies during field observations, and also because the Tule Goose breeding range is remote and isolated (Timm *et al.* 1982; Ackerman *et al.* 2004; Densmore *et al.* 2006; Ely *et al.* 2007, 2017). Despite the periodic and disparate approaches and lack of appropriate statistical methods in describing the abundance of Tule Geese, statements about population size during 1949–1991 ranged from < 1,000 individuals (Scott 1949) to *c.* 5,000 (Wege 1984), and < 10,000 birds (Pacific Flyway Council 1991; Ely *et al.* 2006). Unpublished estimates

of the Tule Goose population size using quantitative methods ranged from *c.* 6,000 to *c.* 8,000 (Orthmeyer *et al.* 1992; Trost & Harb 1995) or < 10,000 in published estimates without measures of precision or descriptions of specific methodology (Deuel & Takekawa 2008; Fox & Leafloor 2018). The Tule Goose has been classified as “Endangered” (under the U.S. Endangered Species Preservation Act of 1966 from 1967–1970; USFWS 1967); as “Vulnerable” (Callaghan & Green 1993; Green 1996; Young *et al.* 2013, citing IUCN Criterion D2); and as a “Species of Special Concern” in California (Deuel & Takekawa 2008). Baldassarre (2014) concluded that Tule Geese represent the smallest population of geese in the world, and Fox and Leafloor (2018) identified only one subspecies (the Lesser Canada Goose *Branta canadensis parvipes*) with fewer estimated geese.

Three subspecies of Greater White-fronted geese are recognised in North America (Banks 2011) and are managed as separate populations (Pacific Flyway Council 1991, 2003, 2015). The Tule Goose is the largest and darkest morphologically (Krogman 1979; Bellrose 1980; Orthmeyer *et al.* 1995; Ely *et al.* 2005). It breeds along river drainages that flow into the Cook Inlet of Alaska (Bellrose 1980; Timm *et al.* 1982; Ely & Dzubin 1994; Ely *et al.* 2007, 2017) and winters in the Central Valley of California. The PGWFG breeds on the

Yukon-Kuskokwim Delta and Bristol Bay lowlands of Alaska and also winters in California and in western Mexico. The Mid-Continent Population (Miller *et al.* 1968) of the Interior Greater White-fronted Goose *A. a. gambelli* (Banks 2011) breeds in central and northern Alaska and across northern Canada but migrates and winters in the middle of the south-central North American continent and the eastern half of Mexico (Ely & Dzubin 1994).

Efforts to monitor the annual abundance of Tule Geese commenced in 1978 with coordinated ground counts of the birds during autumn migration (Pacific Flyway Council 1991). These censuses were possible because numbers of sympatric PGWFG were low (O'Neil 1979), facilitating separation of subspecies during the field observations and thus allowing an assessment of Tule Goose numbers at this time. As the abundance of PGWFG increased in the 1990s, their autumn migration patterns also changed, resulting in more temporal and spatial overlap with Tule Geese in the Sacramento Valley (Pacific Flyway Council 2003), thereby making census counts of Tule Geese less feasible. Also, the management community recognised that coordinated census counts during migration could result in biased indices of abundance associated with systematic changes in migration timing and detection probability. By 2009, the abundance of PGWFG was *c.* 450,000 birds and census counts of Tule Geese during autumn migration were abandoned. Efforts to estimate the abundance of Tule Geese by sampling methods were initiated in the 1990s (Orthmeyer *et al.* 1992, 1998; Trost

& Harb 1995), and the results led to this study.

Previous reports have described the migration patterns and winter distribution for Tule Geese (Timm *et al.* 1982; Wege 1984; Hobbs 1999; Ely *et al.* 2006). The geese leave their nesting area on the Cook Inlet, Alaska, in August–early September and stage at the Summer Lake Basin (42.95°N, 120.78°W, Fig. 1) and the Harney Basin (43.46°N, 119.06°W) of southern Oregon, and also at the Klamath Basin (42.14°N, 121.74°W) of southeastern Oregon and northeastern California (Bauer 1979; Timm *et al.* 1982; Ely & Dzubin 1994) during autumn migration. The first birds arrive at their primary wintering area in the Sacramento Valley as early as September, where their main roosting and foraging sites are located on and around the Sacramento, Delevan and Colusa National Wildlife Refuges (39.31°N, 122.10°W, Fig. 1). Small numbers of Tule Geese also use wintering sites further southeast in the Butte Sink (39.27°N, 121.91°W) and south in the Suisun Marsh (38.18°N, 122.17°W, see Fig. 1) and in the Sacramento-San Joaquin River Delta (38.03°N, 121.53°W; Wege 1984). Some historical accounts indicate that Tule Geese made regular use of the Butte Sink and the Suisun and Napa Marshes (38.20°N, 122.35°W) in the early 20th century (Swarth & Bryant 1917; Moffitt 1926, 1938; Wege 1984), whilst more recently Hobbs (1999) found that small numbers of Tule Geese continue to winter in the Butte Sink.

Because Tule Geese are of conservation concern, managers need reliable information on their status. Additionally, because

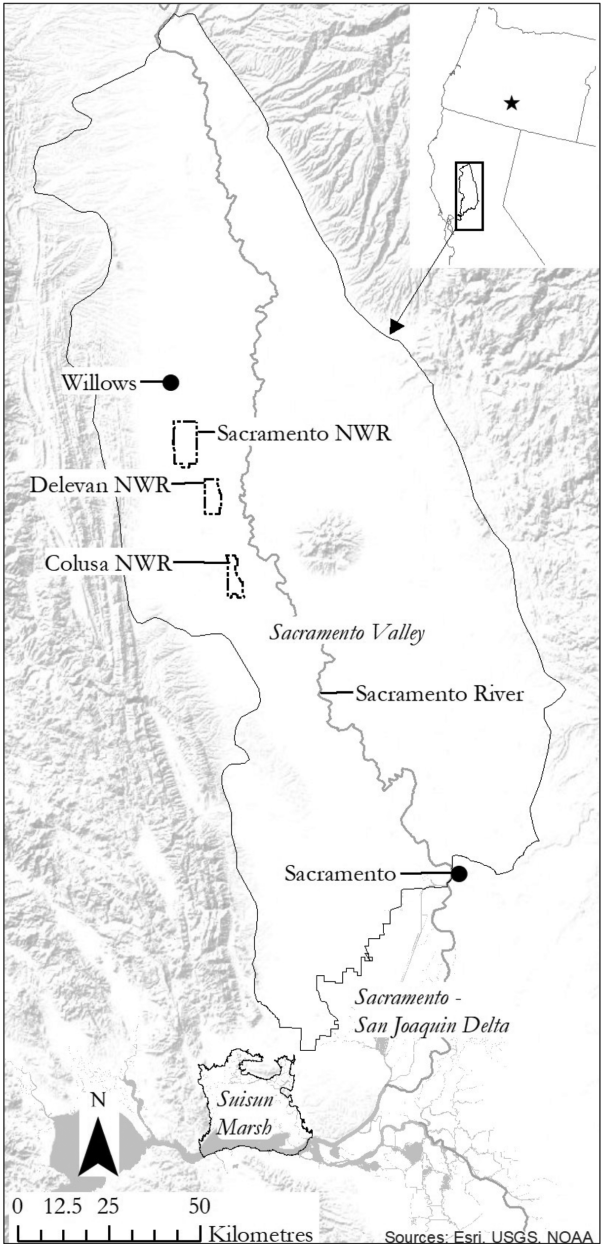


Figure 1. Marking and survey areas for Tule White-fronted Geese in Oregon and California, USA. The primary marking location was Summer Lake Wildlife Area, Oregon, as indicated by star in the inset. Mark-resight surveys were conducted primarily at the Summer Lake Wildlife Area and the Sacramento, Delevan and Colusa National Wildlife Refuges in the Sacramento Valley, California.

PGWFG have grown in abundance from *c.* 73,000 in 1979 to *c.* 647,000 in 2017 (Olson 2019), there has been an increase in public demand to address agricultural depredation complaints and to provide additional opportunities for hunting PGWFG. PGWFG abundance is 58% above its long-term (1979–2018) population average, resulting in more liberal hunting regulations. Special regulations (shorter open seasons; lower daily bag limits), however, remain in place to limit Tule Goose harvest in its primary migration and wintering areas in Oregon and California, and these restrictions are a source of contention among hunters. Assessment of the efficacy of regulations intended to protect the Tule Geese depends on reliable estimates of their population size, trends in numbers, distribution and other demographics. A mark-resight study therefore was conducted during 2003–2019 to estimate autumn abundance of Tule Geese associated with the Summer Lake Basin of Oregon and the Sacramento Valley of California. Secondary objectives were to determine winter distribution and annual survival rates for the subspecies.

Methods

Mark-resight methods were used to estimate annual abundance and to determine the winter distribution of Tule Geese. Resightings were defined as a live encounter of a radio-marked goose located by telemetry or observation of a neck collar post-marking. Annual estimates of Tule Goose abundance were derived by expanding an estimate of radio-marked goose abundance by the ratio of total to radio-

marked geese each year, using the models and procedures described by Sanders and Trost (2013). Also, standard leg rings and citizen-reported ring recoveries were used to estimate annual (September–August) survival rates and determine the winter distribution of Tule Geese.

Field procedures

Tule Geese were captured by rocket-netting at gritting sites at the Summer Lake Wildlife Area (SLWA), Oregon (Fig. 1) during September and October 2003–2019. For each captured goose, the subspecies was ascertained based on physical appearance and verified by bill measurement, with the bird's age class (juvenile or adult) and sex determined by plumage and cloacal characteristics (Bellrose 1980; Orthmeyer *et al.* 1995). Each Tule Goose was ringed with an aluminium leg ring issued by the U.S. Geological Survey Bird Banding Laboratory (BBL). To avoid marking pairs and increase independence of our data, the most numerous sex in each capture event was fitted with a blue plastic neck collar inscribed with a unique 2- or 3-character white alpha numeric code and a VHF radio that transmitted a unique radio frequency (Advanced Telemetry Systems model A3590, Isanti, Minnesota, USA). Total weight of the collar and radio was *c.* 50 g. Because geese were trapped in waist-deep water, all captured geese were held in a quiet, darkened building both during handling and for 12–24 h after handling to allow drying and release as a group back at the trap site during daylight hours.

Field surveys to estimate ratios of the total number of Tule Geese counted to the

number of radio-marked Tule Geese in the flocks were conducted systematically during 2003–2019 (years were defined as September through August and referenced by the earlier year), primarily during September–January at staging and wintering areas in Oregon and California. During on-the-ground field surveys, observers followed prescribed routes during midday roosting periods to count and identify the radio-marked birds and also to count unmarked geese identified as Tule Geese based on their morphological characteristics (Swarth & Bryant 1917; Bauer 1979; Bellrose 1980). Only visual methods were used during these ratio counts in order to maintain equal probability of detecting radio-marked (collared) and unmarked geese. To the extent possible, the identity of each radio-marked goose encountered was recorded during ratio counts using visual methods; however, radio telemetry was used to confirm marked goose identification after the ratio count in cases where the collar code was only partially recorded.

Observers used the tally method to count radio-marked and unmarked Tule Geese within a flock, where a sample of geese – those with necks fully visible during a single scan – were examined for the presence or absence of a marker with certainty (Ganter & Madsen 2001; Sanders & Trost 2013). Observers either had previous experience or received individual training on identification of Tule Geese and radio-marked birds. Observers made a concerted effort to survey all flocks of White-fronted Geese that could be located without knowingly sampling the same flocks more than once per day. During 2003–2014, field surveys

occurred one day in each of four to six periods during autumn–winter on the Summer Lake Wildlife Area, Klamath Basin, Sacramento, Delevan and Colusa National Wildlife Refuges, and the Grizzly Island Wildlife Area. During this period, field crews typically consisted of two observers to reach consensus on subspecies identification (77% of flock observations were from paired observers). During 2015–2019, field surveys were conducted daily over two, 1-week periods during November–December and only on and adjacent to Sacramento, Delevan and Colusa National Wildlife Refuges (Fig. 1) and each area was surveyed by a single individual. During all years, surveys were conducted on publicly owned wildlife areas during the midday roosting period after Tule Geese had returned from foraging flights in the morning because foraging could occur in varying locations on private agricultural lands where access was limited.

Additional telemetry searches for radio-marked Tule Geese were conducted each autumn and winter from the air (about 10 times per year) throughout the Sacramento Valley, in the Summer Lake Basin, Klamath Basin, Suisun Marsh areas, and occasionally in the Napa-Sonoma Marsh Wildlife Area. Searches for radio-marked geese were also conducted by ground in the Sacramento Valley (about 1–2 times per week). Elsewhere, aerial telemetry searches for radio-marked Tule Geese were conducted periodically by the Alaska Department of Fish and Game, U.S. Fish and Wildlife Service and by U.S. Geological Service personnel during summer in the Cook Inlet area of Alaska.

Abundance, winter distribution and survival rate

To ensure data integrity, only resightings of radio-marked geese verified as being consistent with marking records (*i.e.* collar and radio frequency identifications and logical encounter dates) were used in assessments. Almost all telemetry records were from normal radio signals (95.8%), but occasionally some were mortality signals (determined by a doubling of the pulse rate of the radio signals), which could indicate either goose mortality or radio malfunction. Telemetry encounters by mortality signal were included in the assessment only if there were ≥ 1 normal signal thereafter or a mortality signal or subsequent visual encounter(s) from a different location. Only radio-marked geese with an active radio were considered in the estimation of radio-marked goose abundance and ratio of total to radio-marked geese. Using only active radios maintained equal detection probability among geese for marked goose abundance estimation, and symmetry between estimates of radio-marked goose abundance and ratio of total to radio-marked geese.

Radio-marked goose abundance was estimated using a closed capture robust design model in Program MARK (White & Burnham 1999). Annual resighting data were partitioned into two secondary sampling occasions: September–October, primarily in the Summer Lake Basin; and November–January, primarily in central California, in relation to goose presence in these regions. Thus, the model included 34 sampling occasions (17 primary across years and two secondary within year). Banding and resighting data were included in the first

sampling occasion and only resighting data in the second occasion each year. Resightings of the few geese radio-marked during winter in the Sacramento Valley ($n = 15$, January–February, 2004–2006) and observed the same year were omitted because marking occurred during the second secondary sampling occasion.

To test hypotheses about the presence and form of temporary emigration (Markovian, even, random, none; see Kendall *et al.* 1997; Sanders & Trost 2013), which could bias abundance estimates, and time effects in survival and temporary emigration probabilities, 14 robust design models were constructed (Table 1). To be a temporary emigrant is to be a member of the population but unavailable for capture (resighting) in a given primary sampling occasion (Kendall *et al.* 1997). The form of temporary emigration specifies how individuals move between observable and unobservable states between sampling occasions. We assumed that the resighting probability varied over time, but that conditional sighting (p) and resighting probabilities (c) were the same within each primary occasion (*i.e.* $c_{i,j} = p_{i,j}$ in all robust design models). To ensure that all parameters included in the Markovian and random emigration models were identifiable when all parameters were time specific, we set probabilities of remaining a temporary emigrant (γ) and probabilities of becoming a temporary emigrant (γ') as equal for the last two sampling occasions ($\gamma'_k = \gamma'_{k-1}$ and $\gamma''_k = \gamma''_{k-1}$, where k = total number of primary sampling occasions); otherwise, these parameters are confounded with the survival probability S_{k-1} (Kendall *et al.* 1997).

Table 1. Closed robust design models considered in the estimation of population demographics for Tule Geese during September–January 2003–2019. Models ranked by model fit and parsimony based on Akaike’s Information Criterion corrected for sample size (AIC_c). Model parameters are: annual survival probability (S), probability of becoming a temporary emigrant (γ'), probability of remaining a temporary emigrant (γ''), conditional sighting probability (p) and resighting probability (ϕ). See Sanders and Trost (2013) and/or Kendall *et al.* 1997 for detailed description of model parameters. We assumed that resightings probability varied over time (primary occasion i), but that conditional sighting (p) and resighting probabilities (ϕ) were the same between secondary sample occasions (j) within each primary occasion (*i.e.* $c_{i,j} = p_i$). To provide identifiability of all parameters for the Markovian and random emigration models when all parameters were time specific, we set as equal for the last two sampling occasions ($\gamma'_k = \gamma'_{k-1}$ and $\gamma''_k = \gamma''_{k-1}$, where k = total number of primary sampling occasions); otherwise, these parameters are confounded with the $_{k-1}$ (Kendall *et al.* 1997).

Model	Movement	AIC _c	Delta AIC _c	AIC _c Weight	Likelihood	Parameters
$S_p \gamma'' = \gamma', c_{ij} = p_{ij}$	Random	2,359	0.000	0.952	1.000	51
$S_p \gamma'' = (1 - \gamma'), \gamma', c_{ij} = p_{ij}$	Even-flow	2,365	6.340	0.040	0.042	51
$S_p \gamma'' = 0, \gamma' = 1, c_{ij} = p_{ij}$	None	2,369	10.290	0.006	0.006	51
$S_p \gamma'' = \gamma'_p c_{ij} = p_{ij}$	Random	2,374	15.350	0.000	0.001	66
$S_p \gamma''_i = (1 - \gamma'_p), \gamma'_p c_{ij} = p_{ij}$	Even-flow	2,377	17.830	0.000	0.000	66
$S_p \gamma''_i = (1 - \gamma'_p), \gamma'_p c_{ij} = p_{ij}$	Even-flow	2,379	20.060	0.000	0.000	51
$S_p \gamma''_i = (1 - \gamma'), \gamma', c_{ij} = p_{ij}$	Even-flow	2,390	31.100	0.000	0.000	36
$S_p \gamma'', \gamma', c_{ij} = p_{ij}$	Markovian	2,391	32.070	0.000	0.000	52
$S_p \gamma'', \gamma', c_{ij} = p_{ij}$	Markovian	2,396	36.770	0.000	0.000	37
$S_p \gamma''_p \gamma'_p c_{ij} = p_{ij}$	Markovian	2,391	32.460	0.000	0.000	66
$S_p \gamma''_p \gamma'_p c_{ij} = p_{ij}$	Markovian	2,416	57.230	0.000	0.000	79
$S_p \gamma'' = 0, \gamma' = 1, c_{ij} = p_{ij}$	None	2,393	34.690	0.000	0.000	36
$S_p \gamma'' = \gamma', c_{ij} = p_{ij}$	Random	2,383	24.750	0.000	0.000	36
$S_p \gamma'' = \gamma'_p c_{ij} = p_{ij}$	Random	2,390	31.630	0.000	0.000	51

Goodness of fit of the fully time-dependent models was assessed qualitatively by adjusting the variance inflation factor (\hat{c}) for extra binomial variation to determine the point at which it influenced model selection. Model selection was based on model fit and parsimony using Akaike's Information Criterion (AIC_c , $QAIC_c$) corrected for sample size (Burnham & Anderson 2002).

For comparison with radio-marked goose abundance estimates, the minimum number of radio-marked geese known to be in the population each year was determined from all resightings data within and across years (*i.e.* not restricted to September–January in the Summer Lake Basin and Sacramento Valley).

Counts of marked and unmarked geese to estimate the ratio of total to radio-marked geese were restricted to those from the Sacramento Valley during October–January, in order to avoid any bias that may result from observing geese in Oregon just after marking and prior to these newly marked geese distributing throughout the population. Any flocks that contained a radio-marked goose that could not be verified as marked or unmarked (*i.e.* identification and active *vs.* inactive radio status) were excluded from the ratio estimations to avoid potential bias associated with unconfirmed marking status. Multiple linear regression was used to evaluate evidence for change in the ratio during October–January while controlling for year. Finally, log linear regression was used to evaluate the trend in annual estimates of total Tule Goose abundance.

True survival (S) and recovery (f) probabilities were estimated from Tule Goose band recovery data using a Brownie

“dead recovery” model (Brownie *et al.* 1985) in Program MARK (White & Burnham 1999). Band recovery data through to the end of February 2020 were received from the BBL for Tule Geese captured and ringed during 2003–2019. Additional recovery information from our radio-marked geese was obtained from reports made directly to us via the telephone number provided on each radio collar. Only recoveries resulting from a bird being shot or found dead (with the mortality radio signal used to find radio-marked geese that were not reported) during September–March (hunting season) were included. Recovery models were constructed to test *a priori* hypotheses about population demographics considering year, age class (hatch year, HY; and after hatch year, AHY), sex, and marker type (leg ring only or leg ring and radio collar). The most general model was $S(\text{year, age class, sex, marker})$, and $f(\text{year, age class, sex, marker})$. Alternative models were constructed with all combinations of year, age class, sex, and marker main effects in S and f . We evaluated model fit using estimates of \hat{c} (median method) and the point at which it influenced model selection.

The winter distribution of Tule Geese was determined by examining resightings (telemetry or visual encounter) of radio-marked geese and citizen-reported recoveries (shot or found dead during hunting season) of study geese, including both those with a leg ring only and those with a leg ring and radio-marker. The resightings and reported recoveries from this study were compared with the reported recoveries of Tule Geese ringed during earlier studies. Ringing for these other studies occurred in California,

Oregon and Alaska (C.R. Ely, pers. comm.). Estimates are reported as the mean \pm s.e.

Results

Marking and resighting

A total of 1,160 Tule Geese were leg-ringed from 2003–2019, of which 505 were radio-marked, providing an annual mean of 29.7 individuals tagged with radio transmitters ($n = 17$ years, range = 17–59 birds/year). Radio-marked geese were marked primarily (96%, 484 birds) at Summer Lake in September (461) and October (23), but also in the Sacramento Valley (2005–2007, 2011, and 2019) during September (2), October (4), January (5) and February (10). All but two radio-marked geese were adults, and most (68%, 345) were male. The 655 Tule Geese marked with leg rings only were marked primarily (92%) at Summer Lake (52 in Sacramento Valley); 43% (284) were male and 31% (204) were juveniles.

A total of 19,860 resightings of the radio-marked geese were recorded during 2003–2019, most (88%, 17,450 resightings) in the Summer Lake Basin (23%, 4,659) or Sacramento Valley (64%, 12,791), and most (84%, 14,604) of those during September–January. Telemetry was the primary method (97%, 19,197 *vs.* visual only 3%, 663) for resighting geese. The last telemetry resighting for each of the radio-marked geese was mostly (88%, 435 of 494) less than three years post-marking (34% at < 1 year, 32% at < 2 years, 22% at < 3 years, and 11% at < 4 years). Considering only telemetry resightings, the mean number of unique radio-marked geese resighted per year during resightings occasions (September–

January) was 59.1 birds ($n = 17$, range = 45–88, Table 2). The mean number of radio-marked geese known to be in the population each year based on all within-year telemetry resightings data was 60.7 geese (range = 47–90) and based on all within- and across-years resightings data was 60.9 geese (range = 47–90) (Table 2).

Ratio counts of radio-marked and unmarked geese in the Sacramento Valley during October–January were recorded for 4,909 flocks; most (90%, 4,410) counts were about equally distributed in months October–December inclusive (range = 26–32%). The mean number of counts per year was 289 ($n = 17$, range = 53–512) and the mean number of geese examined for the presence of a radio collar per year was 6,122 (range = 1,465–13,432) (Table 3). Most (92.4%, 4,538) of the ratio counts were conducted by eight of 16 individuals; the remaining eight individuals each contributed $\leq 3.6\%$ of the ratio count data. Two individuals recorded 44% (2,174) of the ratio counts. The mean annual ratio of total to marked geese ranged from a low of 147 ± 35 in 2008 to a high of 412 ± 134 in 2006 (Table 3). There was no evidence that the mean ratio changed by month during October through January (estimated change in ratio = 30.0 ± 40.7 total per marked goose, 95% CI = -51.7 – 111.8 , $R^2 = 1.3\%$, $t_{49} = 0.74$, $P = 0.464$, n.s.). However, beginning in 2015, all ratio counts were restricted to November–December.

Radio-marked and total goose abundance

Of all the robust design models considered for estimating abundance of radio-marked

Table 2. Estimated annual abundance (\bar{m}), standard error (s.e.), and lower (LCI) and upper (UCI) 95% confidence intervals of marked Tule Geese from a closed robust design model using data from September–January, 2003–2019. Also included are the unique annual numbers of radio-marked Tule Geese known to be in the population based on live encounters (telemetry/visual) in the Summer Lake Basin and Sacramento Valley during September–January (U), those determined to be in the population from all in and among year resighting data (U'), and those encountered during robust design sampling occasions ($n1$ is resighted during sampling occasion 1 in Sep–Oct, $n2$ is resighted during sampling occasion 2 during Nov–Jan, and $m2$ is resighted during both sampling occasions).

Year	U	U'	$n1$	$n2$	$m2$	Closed robust design			
						\bar{m}	s.e.	LCI	UCI
2003	47	47	47	46	46	47.0	0.0	47.0	47.0
2004	60	60	60	47	47	60.0	0.0	60.0	60.0
2005	50	51	44	42	36	51.4	1.4	50.3	57.4
2006	81	82	81	63	63	81.0	0.0	81.0	81.0
2007	88	90	85	82	79	88.2	0.5	88.0	91.1
2008	75	77	74	61	60	75.2	0.5	75.0	78.3
2009	53	55	48	45	40	54.1	1.2	53.2	59.4
2010	58	63	58	53	53	58.0	0.0	58.0	58.0
2011	53	58	50	50	47	53.2	0.5	53.0	56.3
2012	59	62	56	51	48	59.5	0.8	59.1	63.3
2013	50	50	50	45	45	50.0	0.0	50.0	50.0
2014	56	57	54	53	51	56.1	0.4	56.0	58.3
2015	59	60	58	55	54	59.1	0.3	59.0	60.9
2016	56	56	45	56	45	56.0	0.0	56.0	56.0
2017	60	62	57	56	53	60.2	0.5	60.0	63.1
2018	45	50	44	41	40	45.1	0.3	45.0	47.2
2019	54	55	52	48	46	54.3	0.6	54.0	57.4

geese and temporary emigration, the top two models had 99.2% of the support in data based on AIC_c weight (Table 1). Both models included year-specific survival and non-year-specific movement, but differed

in the form of temporary emigration (*i.e.* random *vs.* even flow) with the random movement model having 95.2% of the weight. The random movement model indicated the level of temporary movement

Table 3. Estimated ratio (\hat{R}) of total (marked and unmarked) to radio-marked Tule Geese, standard errors (s.e.), and lower (LCI) and upper (UCI) 95% confidence intervals during October–January in the Sacramento Valley, 2003–2019. Associated statistics include number of geese examined for a marker (g), number of marked birds (m), number of observed flocks (f) and mean number of marked geese per observed flock (\bar{m}).

Year	g	m	f	\bar{m}	\hat{R}	s.e.	LCI	UCI
2003	13,432	36	353	0.10	373.1	72.4	231.1	515.1
2004	1,671	11	53	0.21	151.9	44.8	64.1	239.7
2005	1,465	5	91	0.05	293.0	119.5	58.8	527.2
2006	3,293	8	154	0.05	411.6	134.4	148.1	675.1
2007	4,338	23	278	0.08	188.6	40.0	110.3	266.9
2008	6,750	46	327	0.14	146.7	35.4	77.4	216.1
2009	6,951	28	345	0.08	248.3	55.8	138.9	357.6
2010	6,156	21	347	0.06	293.1	79.3	137.8	448.5
2011	9,861	44	512	0.09	224.1	42.4	141.0	307.2
2012	7,931	29	269	0.11	273.5	80.0	116.7	430.2
2013	4,829	22	227	0.10	219.5	65.7	90.7	348.3
2014	3,027	19	148	0.13	159.3	42.3	76.4	242.2
2015	6,546	40	420	0.10	163.7	32.1	100.6	226.7
2016	6,258	19	368	0.05	329.4	91.2	150.7	508.1
2017	8,246	29	375	0.08	284.3	68.8	149.5	419.2
2018	6,047	39	281	0.14	155.1	34.5	87.4	222.7
2019	7,275	24	361	0.07	303.1	90.8	125.2	481.0

rate was on average $0.021 \pm 0.010/\text{year}$, (95% CI = 0.008–0.054). The variance inflation factor (\hat{c}) was increased from 1–4 to evaluate the effect of possible extra binomial variation influence on model selection. The top model remained one that included random temporary emigration and accounted for $\geq 54.3\%$ of AIC_c weight, whereas the second top model included

even flow temporary emigration and $\leq 24.5\%$ of weight.

Radio-marked goose abundance estimates from the top model averaged 59.3 birds (range = 45.1–88.2) per year and were precise (mean CV < 1%) (Table 2). The estimates were slightly greater than the number of unique individuals encountered each year during resighting occasions (mean

difference = 0.3 geese, range = 0–1.4), but were slightly lower than the number of marked geese known to be in the population from all within- and among-year resightings data (mean difference = –1.6 geese, range = –5.0–0.4) (Table 2). Resighting probabilities were high (≥ 0.78) each year in each resighting occasion; the mean was 0.954 ± 0.007 (95% CI = 0.938–0.966) for the first occasion and 0.886 ± 0.010 (95% CI = 0.864–0.904) for the second occasion each year. The mean annual resightings probability during both sampling occasions combined averaged at $0.974 \pm 0.010/\text{year}$ (95% CI = 0.946–0.988). Although we used dead recovery data to estimate annual survival rates, the closed robust design model provided a survival estimate from live encounter data for comparison. The mean annual radio-marked adult survival rate was

0.537 ± 0.016 (95% CI = 0.505–0.568), but this reflects both survival and radio status.

The annual abundance estimates of radio-marked geese were expanded by the ratio of total to radio-marked geese to derive total (marked and unmarked) population size (Fig. 2). Resultant point estimates were variable from year to year (range = 6,992–33,342) and lacked precision (mean CV = 26%, range = 19–41%). This was primarily due to the variability and variance of annual ratio estimates *vs.* radio-marked bird abundance (Fig. 2, Tables 2 and 3). The mean annual abundance of Tule Geese in the autumn was $14,703 \pm 1,455$ (95% CI = 11,852–17,555, $n = 17$). There was no evidence of a trend in abundance of Tule Geese during this period; the annual growth rate was $-1.89 \pm 1.84\%$ (95% CI = –5.63–2.00, $t_{16} = 1.05$, $P = 0.311$, n.s.).

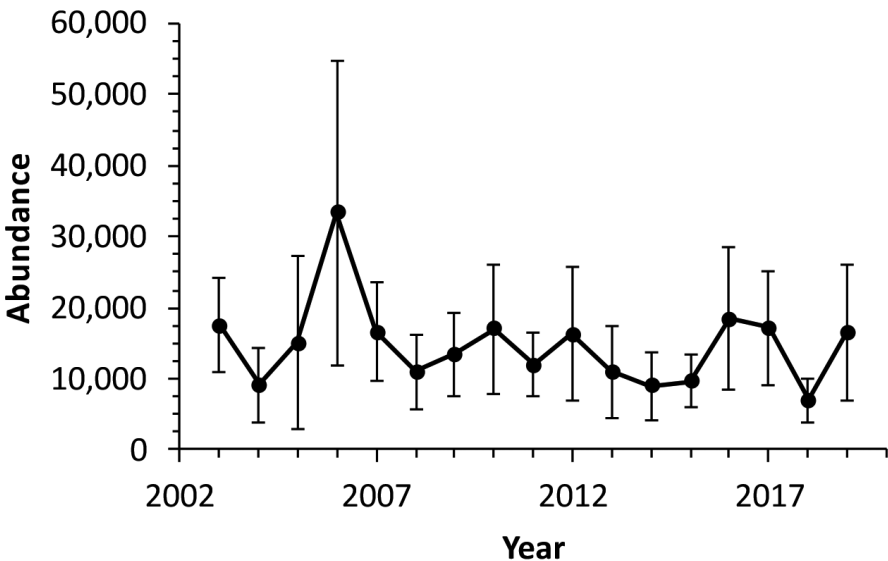


Figure 2. Estimated annual abundance of Tule Geese and 95% confidence intervals in Summer Lake Basin and Sacramento Valley during September–January, 2003–2019.

Annual survival and winter distribution

The Brownie “dead recovery” model goodness-of-fit test statistics did not indicate a lack of fit of our most general model; $\hat{c} = 1.00$, so no adjustments were made for over-dispersion. Increasing \hat{c} from 1–4 made no difference in the model most supported by the data. The best fitting models included sex and/or marker type effects on survival and recovery probabilities and had 95.2% of the AIC_c weight combined (Table 4). The next best fitting models indicated age and/or marker type effects on survival and recovery probabilities but these had only 4.1% of the AIC_c weight combined. The best fitting model, which had 74.2% of the AIC_c weight, included sex and marker type effects on survival and marker type as affecting recovery probabilities. Annual survival probability from our top model was 7.0–10.0% lower for females than for males (Table 5). Recovery probabilities were 8.5% higher for radio-marked geese than for leg-ringed only geese, but this included the increased probability of finding dead geese due to telemetry (Table 5). Mean annual survival and recovery probabilities for leg-ringed only geese were 0.786 ± 0.027 (95% CI = 0.727–0.834) and 0.045 ± 0.006 (95% CI = 0.035–0.058), respectively, whereas for radio-marked geese it was 0.610 ± 0.028 (95% CI = 0.553–0.664) and 0.131 ± 0.012 (95% CI = 0.109–0.157).

The distribution of resighted radio-marked Tule Geese was similar to the distribution of recovered Tule Geese that were shot or found dead (and subsequently reported) during the September–March

hunting season (Fig. 3, Table 6). For Tule Geese radio-marked during autumn, mostly in the Summer Lake Basin, there was a high probability of being resighted during September–March (annual mean = 0.974 ± 0.010), by locating individuals using telemetry equipment in the few areas where we concentrated our efforts – primarily in the Summer Lake Basin during autumn and the Sacramento Valley and Suisun Marsh during winter (90.4% of all encounters, Table 6). Recovery distributions of both radio-marked and leg-ringed only geese were not dependent on resighting survey efforts, but rather on citizen recovery and reporting. Both leg-ringed and radio-marked goose recoveries indicated a similar distribution of Tule Geese during autumn and winter, primarily in the Summer Lake Basin during autumn and in Sacramento Valley and Suisun Marsh during winter. Reports of Tule Geese marked in Alaska and the Sacramento Valley during earlier studies indicated an autumn and winter recovery distribution similar to the geese marked in the current study (Table 6). There were a few ($n = 9$) recoveries scattered more broadly, *e.g.* in Alberta, Saskatchewan, Washington, Nevada, Kansas, Texas and Mexico; however, these appear to be anomalies. In total, and similar to the resightings data, the recoveries from the three data sets all indicate that the primary (90–97% of each recovery distribution) wintering area of Tule Geese is the Sacramento Valley and Suisun Marsh, with geese passing through the Summer Lake and the Klamath Basins during migration, and possibly also wintering to some extent in the Klamath Basin.

Table 4. Brownie band recovery models considered in the estimation of survival (S) and recovery (f) rates for Tule Geese during September–January 2003–2019. Models ranked by model fit and parsimony based on Akaike’s Information Criterion corrected for sample size (AIC_c). Variables considered included sex, age class (HY and AHY), group (leg-ringed only *w.* leg-ringed and radio-marked), and year (time).

Model	AIC _c	Delta AIC _c	AIC _c Weight	Likelihood	Parameters	Deviance
{S(sex, group), f(group)}	2035	0.0	0.742	1.000	6	433.2
{S(sex, group), f(sex, group)}	2039	3.7	0.118	0.159	8	432.8
{S(group), f(group)}	2040	5.1	0.057	0.077	4	442.3
{S(group), f(sex, group)}	2041	6.1	0.035	0.047	6	439.3
{S(age, group), f(group)}	2042	7.0	0.022	0.030	5	442.2
{S(age, group), f(age, group)}	2042	7.3	0.019	0.026	6	440.4
{S(age, sex, group), f(age, sex, group)}	2045	9.6	0.006	0.008	12	430.5
{S(age), f(age, group)}	2062	26.9	0.000	0.000	5	462.1
{S(group), f(time, group)}	2075	40.3	0.000	0.000	36	411.0
{S(sex), f(sex)}	2077	42.2	0.000	0.000	4	479.4
{S(sex, group), f(sex)}	2081	45.8	0.000	0.000	6	478.9
{S(time, group), f(group)}	2084	49.3	0.000	0.000	33	426.5
{S(), f()}	2085	50.1	0.000	0.000	2	491.3
{S(age), f(age)}	2085	50.1	0.000	0.000	4	487.3
{S(age, group), f(age)}	2087	52.1	0.000	0.000	5	487.3
{S(time, group), f(time, group)}	2113	78.0	0.000	0.000	65	385.0
{S(time), f(time)}	2119	84.1	0.000	0.000	33	461.2
{S(time, sex), f(time, sex)}	2132	96.5	0.000	0.000	66	401.2
{S(time, age), f(time, age)}	2152	117.1	0.000	0.000	64	426.3
{S(time, sex, group), f(time, sex, group)}	2184	149.1	0.000	0.000	125	312.2
{S(time, age, sex, group), f(time, age, sex, group)}	2282	246.6	0.000	0.000	180	261.3

Table 5. Estimated survival and recovery probabilities, standard errors (s.e.), and lower (LCI) and upper (UCI) 95% confidence intervals for leg-ringed only (LR) and radio-marked (RM) Tule Geese marked during September–October in the Summer Lake Basin (5 in Sacramento Valley), 2003–2019.

Parameter	Estimate	s.e.	LCI	UCI
Survival rate				
Male LR	0.823	0.029	0.758	0.874
Female LR	0.724	0.038	0.643	0.792
Male RM	0.633	0.032	0.569	0.692
Female RM	0.563	0.043	0.478	0.644
Recovery rate				
LR	0.046	0.006	0.036	0.059
RM	0.131	0.012	0.109	0.157

Discussion

Abundance

Understanding the abundance and trends in wildlife populations, especially those subject to harvest, is essential for the conservation of species and biodiversity (Runge *et al.* 2004). Here we use mark-resight methods to obtain quantitative, model-based, estimates of Tule Goose abundance, which provide the first published, repeatable method for monitoring numbers and trends for this subspecies. Although the annual estimates of abundance were somewhat imprecise (mean CV = 26%), they indicate a mean annual autumn population size of *c.* 15,000 geese. These results confirm that Tule Geese are among the smallest populations of geese in the world (Fox & Leafloor 2018). Although not directly comparable, because of differences in estimation methods,

our abundance estimates are however greater than those from the 1990s (Orthmeyer *et al.* 1992, 1998; Trost & Harb 1995). We found no evidence of a trend in abundance during 2003–2019.

Our estimates of Tule Goose abundance are applicable to the geese associated with our primary study area: at least one of the areas where we concentrated our resighting efforts during September–January; primarily at the Summer Lake Basin (in September–October), and in Sacramento Valley and Suisun Marsh (in November–January; the main winter study area, see discussion on winter distribution below). For these staging and wintering areas, we found strong evidence of temporary emigration to unobservable states among years, but the level of movement was small. The probability of emigrating (becoming unobservable) was 2.1% and the probability

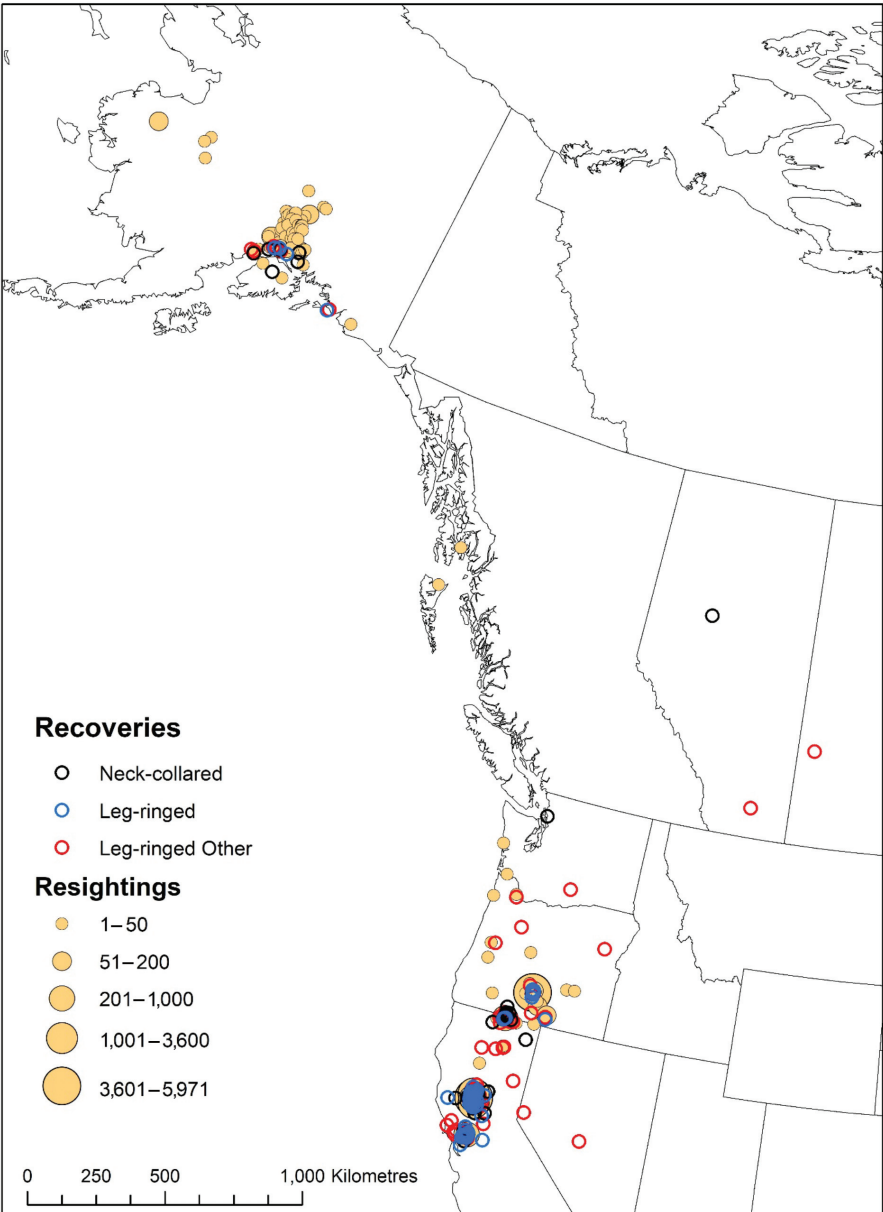


Figure 3. Distribution of Tule Goose encounters in this study include, for years 2003–2019 inclusive: (1) resightings of radio-marked geese and citizen-reported recoveries of radio-marked geese shot or found dead during the hunting season (Neck-collared), (2) citizen-reported recoveries of leg-ringed only geese shot or found dead (Leg-ringed); and, for years 1980–2015: (3) citizen-reported recoveries of leg-ringed geese from earlier (1980–2015) studies (Leg-ringed Other).

Table 6. Distribution (%) of Tule Goose encounters based on data from this study during 2003–2019 and from earlier studies during 1980–2015. Data from this study includes resightings (Live) of radio-marked geese (RM), citizen-reported recoveries of radio-marked geese shot or found dead during hunting season (Dead), and citizen-reported recoveries of leg-ringed (LR) only geese shot or found dead. Data from other studies includes citizen-reported recoveries of leg-ringed only geese. Aggregate totals include Summer Lake Basin (SL), Sacramento Valley (SV), Suisun Marsh (SM), Alaska (AK), and Klamath Basin (KB).

State/province	This study			Other studies
	Live	Dead		Dead
Region	RM	RM	LR	LR
Alaska	6.6	5.1	3.6	6.5
Oregon	23.5	24.4	12.7	15.9
Summer Lake	23.5	21.8	11.8	11.2
Klamath Basin	0.0	2.6	0.9	2.3
California	69.9	69.2	83.6	73.4
Klamath Basin	3.0	10.3	3.6	6.5
Sacramento Valley	64.4	50.0	59.1	54.7
Suisun Marsh	2.5	7.1	18.2	8.9
Alberta	0.0	0.6	0.0	0.5
British Columbia	< 0.1	0.0	0.0	0.0
Saskatchewan	0.0	0.0	0.0	0.5
Washington	< 0.1	0.6	0.0	0.5
Nevada	0.0	0.0	0.0	0.9
Kansas	0.0	0.0	0.0	0.5
Texas	0.0	0.0	0.0	0.9
Mexico	0.0	0.0	0.0	0.5
Total	100.0	100.0	100.0	100.0
SL-SV	87.9	71.8	70.9	65.9
SL-SV-SM	90.4	78.8	89.1	74.8
SL-SV-SM-AK	96.9	84.0	92.7	81.3
SL-SV-SM-AK-KB	99.9	96.8	97.3	90.2
Sample size	19,860	156	110	214

of immigrating (becoming observable) was 97.9% each year (*i.e.* the probability of remaining observable among years was 97.9%). Completely random movement in and out of a study area does not introduce bias to estimators from closed-population methods, although it decreases precision (Kendall 1999). Thus, our abundance estimates apply to the observable and unobservable population (the “super-population”) associated with our primary study area. We resighted radio-marked geese with a high (97.4%) probability each year in the few areas we focused our efforts because radio telemetry was our primary method of resighting geese, and Tule Geese exhibited strong fidelity to these areas.

Our data provide some evidence that our abundance estimates may underestimate Tule Goose abundance in the Pacific Flyway and for the subspecies (*i.e.* outside of our primary study area). Abundance point estimates of radio-marked geese were on average about 1.6 geese fewer than those known to be in the population from all within- and across-year resightings data (*i.e.* all resightings data including summer resightings in Alaska). However, the number of radio-marked geese known to be in the population from all resightings data was within the upper 95% confidence interval of the estimated number of marked geese each year by a mean of 0.6 ± 0.6 geese. A potential negative bias in the point estimate on average of 1.6 radio-marked geese per year equates to about 397 total geese, based on a mean ratio of total to radio-marked geese of 248. Although nearly all Tule Geese appear to winter in the Sacramento Valley, there is evidence that some geese may stray

to other areas in western North America (Table 6). Despite the potential small negative bias of 397 geese per year, mark-resight sampling restricted to Summer Lake Basin and Sacramento Valley during September–January appears to be effective at providing a slightly conservative population estimate for Tule Geese associated with these areas, and with other areas in California, Oregon, and Alaska where resightings have occurred (*i.e.* the Pacific Flyway).

Use of VHF radio as a means of locating geese for subsequent resighting occasions resulted in high encounter probabilities (97.4%) and annual estimates of marked goose abundance with low variance (mean $CV < 1\%$). For analysis of radio-marked goose abundance, we included September capture data in addition to resightings data in the first secondary sampling occasion (*i.e.* September–October) each year. Heterogeneity of capture and survival probabilities between capture and sighting events usually result in a lack of fit of data in the model (Sheaffer & Jarvis 1995). Because resighting probabilities were especially high, excluding capture data resulted in a total time series difference of five fewer marked geese over 17 years. Including capture data provided slightly more information and did not lead to model lack of fit.

No general, robust procedures are currently available for assessing model fit and estimation of a variance inflation factor to account for extra-binomial variation (*i.e.* model lack of fit) for robust design models (White & Burnham 1999; White 2002). We found little evidence, however, for concern

about lack of model fit in the robust design models presented here. Increasing variance inflation values had little effect on model selection and no consequence for demographic parameter estimates, nor for conclusions about the status of the population.

Our annual sampling occasion was prolonged (5 months) and occurred across the autumn staging and wintering areas to allow for maximum movement of the marked population during and between sampling occasions within a year. We expected geese to move randomly in and out of areas that could be surveyed within the study area during and especially between secondary sample occasions (Hobbs 1999). Thus, each sampling occasion approximated to a random sample of all geese whose travels included the observable areas at some point during sampling. Recruitment was not a factor in our closed-capture study design because few geese were marked after September–October, and we excluded resightings data from these birds in that year. Some mortality occurred during sample occasions, but we expected rates to be similar for radio-marked and unmarked geese (*i.e.* no change in the ratio of total to radio-marked geese) and for seen and unseen marked geese (*i.e.* no bias in radio-marked goose abundance estimates). The robust design and Lincoln-Petersen closed population estimators are robust to mortality during and between secondary sample occasions (Kendall 1999), except that abundance estimates apply to the larger population of marked geese that occurs at the beginning of the first secondary sampling occasions in each year (here

September). Neck collar loss and radio failure may have occurred during secondary sampling occasions. However, neck collar loss and radio failure are equivalent to mortality when estimating abundance of marked animals from resightings data, so are not of concern except for the period to which estimates of abundance apply (*i.e.* abundance estimates apply to the larger population of marked geese that occurs at the beginning of the first secondary sampling occasion each year).

Two underlying assumptions of the total to marked ratio estimator are that marked individuals are distributed randomly in the population, and that marked and unmarked individuals have an equal probability of being examined and classified correctly (Sheaffer & Jarvis 1995). Our ratio estimates from wintering areas in the Sacramento Valley should be unbiased because birds are primarily marked in autumn at a migration stopover area at SLWA in Summer Lake Basin, and substantial mixing of marked and unmarked geese occurs before arriving at wintering areas. Also, we marked only males or females in each capture event to reduce the probability of marking paired birds and increase independence of our data.

The ratio of the total goose count to the number of marked geese has a major influence on the expansion of marked geese to total population size (Sanders & Trost 2013). A substantial challenge in deriving abundance estimates for the Tule Geese was in determining the ratio of total to radio-marked geese because of ratio estimate variance (mean CV = 28%) associated with small sample sizes, which resulted both from difficulty in locating and identifying

flocks of Tule Geese amongst the more abundant PGWFG during ratio counts and also confirming whether individuals observed in the field were fitted with radio-markers. Early studies (Bauer 1979) described Tule Geese as secretive, apparently preferring small wetlands with dense cover, occurring in smaller flocks during autumn and winter, although occasionally larger flocks are observed (Deuel & Takekawa 2008).

Ideally, ratio sampling should be completed over a short period (few weeks) and the ratio estimate should apply to the same period as the estimate of marked goose abundance. We sampled ratios over a prolonged period (4 months, Oct–Jan) to increase sample size and reduce sampling variance, but marked goose abundance estimates in our study applied to the population in September. We found no evidence that the ratio of total to marked geese changed during our prolonged sampling period, and therefore biased counts. This may be because we radio-marked only adult Tule Geese, and the lower survival rate of radio-marked geese was offset by lower survival rate of juvenile geese relative to adults.

Another challenge in estimation of the ratio of marked to unmarked geese is subspecies identification with ocular equipment. Most (92.4%) of the ratio counts during our 17-year study were made by eight individuals that overlapped most of the years. Two observers, who contributed 44% of the ratio counts participated for all 17 years of the study. Each observer had experience in subspecies identification or was trained by the more experienced observers. To facilitate subspecies

identification consistency and training, we used two observers in each field crew for most of the ratio surveys in the beginning years of the study.

In a 2004 double-observer study in the Sacramento Valley, Takekawa *et al.* (2005) evaluated error in identification of Tule Geese and PGWFG by comparing novice and trained observers. One of the eight individuals that contributed most of the ratio counts used in our study conducted the training. Of 350 White-fronted Geese examined, $87\% \pm 11\%$ of geese identified as Tule Geese were likely classified correctly. Among birds classified as PGWFG, $8.4\% \pm 8.9\%$ were likely Tule Geese. These estimates may be improved by including observer experience. Thus, there may be a net bias in subspecies classification errors in that counts of unmarked Tule Geese may underrepresent the unmarked geese classified by up to 4.6% (*i.e.* ratio and abundance estimates could be up to 4.6% higher than we estimated). Orthmeyer *et al.* (1995) concluded that PGWFG from the Bristol Bay lowlands were closer in size to Tule Geese than the more abundant PGWFG from the Yukon-Kuskokwim Delta. This may have increased subspecific identification errors; however, PGWFG from the Bristol Bay lowlands were not generally in the Sacramento Valley during ratio counts (Ely & Takekawa 1996). Subspecies identification errors were not evaluated in our study, but we believe error was minimal given the observer training, experience, pairing, and the use of few observers over multiple years in our study.

The tally method used in our study, in which observers made a careful single scan

of the entire flock, ensured that marked and unmarked birds had an equal probability of being examined and classified correctly. The location of birds within the flock only occasionally permitted examination of individuals for presence of a marker, and there was constant mixing of geese within the flock. When observers cannot track which birds already have been observed, repeated scans result in a greater probability of encountering a marked bird compared to an unmarked bird and violates the assumption of equal detectability. Conversely, an approximation of the total numbers of birds in the flock size and scanning for marked birds only (the flock method; Ganter & Madsen 2001) can result in reduced probability of encountering a marked bird and violates the assumption of equal detectability.

Winter distribution

Previous studies defined the wintering distribution of Tule Geese as occurring primarily in the Sacramento Valley, and specifically in the areas associated with three National Wildlife Refuges and Suisun Marsh (Timm *et al.* 1982; Wege 1984; Hobbs 1999). Marked goose encounters from this study and summaries of citizen-encountered marked geese confirmed the primary use of Summer Lake Basin and Sacramento Valley by Tule Geese during autumn and winter. However, there is some evidence of minor changes in distribution within California, as marked geese were not encountered (resighted or recovered) in the Butte Sink during our 17-year study, in contrast to historical and previous reports (Swarth & Bryant 1917; Moffitt 1926; Wege 1984; Hobbs 1999).

From 2003–2019 inclusive, only one of 266 marked Tule Goose recoveries was away from the western states of the Pacific Flyway (in Alberta), whereas earlier ringing studies indicated a greater proportion occurring outside this area (9 of 214). All goose marking in this study occurred in either Oregon or California, whereas other studies (Timm *et al.* 1982; Ely *et al.* 2006) included Tule Geese marked in Alaska, including areas where moulting birds of different populations aggregate. We adhered to the bill measurement criteria (Orthmeyer *et al.* 1995) for identifying Tule Geese for inclusion in this study, because this method is considered to classify 92–96% of Tule Geese correctly. Thirty geese, visually identified as Tule Geese and reported to the BBL as such, were omitted because they did not meet the criteria; earlier investigations occurred before the biometric data were available for classification purposes. Nonetheless, some of the resightings reported in the earlier studies, further afield than our own records, were of birds marked in the Cook Inlet, the core Tule Goose breeding area (Timm *et al.* 1982). The eruption of the Redoubt Volcano in 1989 caused significant changes to both Tule Goose breeding habitat and the birds' use of that habitat (Ely *et al.* 2006), so changes in Tule Goose breeding distribution and population size may explain some of these small differences in winter distribution. On considering both the estimated population size and the number of birds detected in the Cook Inlet, Timm *et al.* (1982) hypothesised that not all Tule Geese nested in the Redoubt Bay area of the Cook Inlet. However, more recent information (Ely *et al.*

2006) suggests that Tule Geese were likely in the upper Cook Inlet, but that changes in moulting distribution have occurred. Thus, despite strong genetic evidence that the Tule Goose is a valid subspecies tied to the Cook Inlet (Ely *et al.* 2017), further investigation of the birds' use of summer areas is warranted.

Survival

Our annual survival rate estimates are the first reported for Tule Geese. We also found few estimates of survival rates for Greater White-fronted Geese in the Pacific Flyway and furthermore these estimates were for different time periods and derived by different methods (Timm & Dau 1979; Schmutz & Ely 1999). PGWFG had relatively low survival rates during the first period of study when abundance was declining (Timm & Dau 1979; O'Neil 1979), relatively moderate survival rates during the second period of study when abundance was stable, and relatively high survival rates during the third period of study when abundance was increasing (Schmutz & Ely 1999; Olson 2019). However, survival rates between study periods did not differ significantly and direct inferences about the relationship between survival and abundance were not possible (Schmutz & Ely 1999). Estimated adult survival rates for leg-ringed adult Tule Geese in this study appear slightly higher than the survival rate estimates of PGWFG from the period when abundance was stable, but lower than when abundance was increasing.

Our survival rate estimates of radio-marked Tule Geese are lower than that of leg-ringed birds (Table 5). This was not unexpected as many previous studies of

other species of geese have documented lower survival rates attributed to the neck collars (Hestbeck & Malecki 1989; Castelli & Trost 1996; Schmutz & Morse 2000; Alisauskas & Lindberg 2002; Alisauskas *et al.* 2006). The marked sample in this study was small relative to Tule Goose abundance (annual mean of 59 radio-marked birds in *c.* 11,000 total geese). Despite the reduced survival rates of radio-marked birds, however, we believe that the impact of annually radio-marking this small sample of geese is generally inconsequential to the status of the total population, whilst facilitating collection of Tule Goose abundance data important for informing management plans.

Conservation implications

We believe traditional breeding population surveys may not be a feasible method to measure the abundance of Tule Geese because of the remote and structurally complex habitat used by the geese during the summer months (Ely *et al.* 2006; Densmore *et al.* 2006). Attempts to census the entire population by making weekly counts of Tule Geese on autumn staging or wintering areas amongst the more abundant sympatric PGWFG are thought by managers to be impractical. The mark-resight method used here, with sampling restricted to Summer Lake Basin and Sacramento Valley during September–January, provides abundance estimates that are largely representative of the Tule Goose population, albeit somewhat conservative. Resultant abundance estimates may be useful for harvest management regulation setting and evaluating the efficacy of

regulations and management intended to ensure sustainability of the Tule Goose. We recommend that this approach to monitoring Tule Goose demographics be continued as an operational survey, with minor changes to study protocol intended to reduce the variance of the abundance estimates. The variance in ratio counts may be reduced by increasing the proportion of marked geese in the population and increasing the number of ratio counts. It may also be possible to estimate abundance of Tule Geese via our mark-resight protocol by using neck collars without radios, to increase the number of marked geese in the population, and to allow use of flocks with partially read marked-bird identifications (see Sanders & Trost 2013). Further, we strongly recommend that managers make a concerted effort to train observers in field protocols and proficient identification of subspecies and goose marking status to avoid bias in ratio counts, and therefore in total abundance estimation. Finally, this study was not designed to make inferences about the causes or changes in survival rates. However, given no evidence of an increasing trend in abundance during the last 17 years, the moderate survival rates over this period, and the conservation concern for Tule Geese, further investigations of survival rates, annually and seasonally, are warranted.

Acknowledgements

This project benefited by the earlier work done by Craig R. Ely, John Y. Takekawa, Dennis L. Orthmeyer and John G. Mensik. Field operations were a partnership with the Oregon Department of Fish and Wildlife

particularly Bradley D. Bales, Brandon S. Reishus, Martin J. St. Louis and staff at the SLWA; and the U.S. Fish and Wildlife Service, particularly Mike A. Wolder (deceased) and staff from the Sacramento NWR complex. Resightings in Alaska were made by the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service in Alaska, and the U.S. Geological Survey through Craig R. Ely. We thank all the other field technicians from all the agencies; over 17 years there were many. The manuscript was improved from the helpful review and suggestions by Joshua L. Dooley, John Y. Takekawa, and two anonymous reviewers. Financial support for this study was provided by Pittman-Robertson Federal Aid Funds to Wildlife under project G1998024, the California State Duck Stamp Account, and the Oregon Department of Fish and Wildlife.

References

- Ackerman, J.T., Takekawa, J.Y., Kruse, K.L., Orthmeyer, D.L., Yee, J.L., Ely, C.R., Ward, D.H., Bollinger, K.S. & Mulcahy, D.M. 2004. Using radio telemetry to monitor cardiac response of free-living tule greater white-fronted geese (*Anser albifrons elgasi*) to human disturbance. *The Wilson Journal of Ornithology* 116: 146–151.
- Alisauskas, R.T. & Lindberg, M.S. 2002. Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. *Journal of Applied Statistics* 29: 521–537.
- Alisauskas, R.T., Drake, K.L., Slattery, S. M. & Kellett, D.K. 2006. Neckbands, harvest and survival of Ross's geese from Canada's central arctic. *Journal of Wildlife Management* 70: 89–100.
- Baldassarre, G.A. 2014. *Ducks, Geese and Swans of North America. Vol. 1*. John Hopkins University Press, Baltimore, Maryland, USA.

- Banks, R.C. 2011. Taxonomy of Greater White-fronted Geese (Aves: Anatidae). *Proceedings of the Biological Society of Washington* 124: 226–233.
- Bauer, R.D. 1979. Historical and status report of the Tule White-fronted Goose. In R.L. Jarvis & J.C. Bartonek (eds.), *Management and Biology of Pacific Flyway Geese*, pp. 44–55. Oregon State University Press, Corvallis, Oregon, USA.
- Bellrose, F.C. 1980. *Ducks, Geese and Swans of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. 1985. *Statistical Inference from Band-Recovery Data – a Handbook*. 2nd edition. Resource Publication No. 156. Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C., USA.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multi Model Inference: a Practical Information Theoretic Approach*. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Callaghan, D.A. & Green, A.J. 1993. Wildfowl at risk, 1993. *Wildfowl* 44: 149–169.
- Castelli, P.M. & Trost, R.E. 1996. Neck bands reduce survival of Canada geese in New Jersey. *Journal of Wildlife Management* 60: 891–898.
- Densmore, R.V., Ely, C.R., Bollinger, K.S., Kratzer, S., Udevitz, M.S., Febringer, D.J. & Rothe, T.C. 2006. Nesting habitat of the Tule Greater White-fronted Goose *Anser albifrons elgasi*. *Wildfowl* 56: 37–51.
- Deuel, B.E. & Takekawa, J.Y. 2008. Tule Greater White-fronted Goose. In W.D. Shuford & T. Gardali (eds.), *California Birds Species of Special Concern: a Ranked Assessment of Species, Subspecies and Distinct Populations of Birds of Immediate Conservation Concern in California*. *Studies of Western Birds*. Vol. 1. Western Field Ornithologists, Camarillo, California and California Department of Fish & Game, Sacramento, USA.
- Ely, C.R. & Dzubin, A.X. 1994. Greater white-fronted goose (*Anser albifrons*) In A. Poole and F. Gill (eds.), *The Birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington DC, U.S.A.
- Ely, C.R. & Takekawa, J.Y. 1996. Geographic variation in migratory behavior of Greater White-fronted Geese (*Anser albifrons*). *The Auk* 113: 889–901.
- Ely, C.R., Fox, A.D., Alisauskas, R.T., Andreev, A., Bromley, R.G., Degtyarev, A.G., Ebbinge, B., Gurtovaya, E.N., Kerbes, R., Kondratyev, A.V. & Kostin, I. 2005. Circumpolar variation in morphological characteristics of Greater White-fronted Geese *Anser albifrons*. *Bird Study* 52: 104–119.
- Ely, C.R., Bollinger, K.S., Hupp, J.W., Derksen, D.V., Terenzi, J., Takekawa, J.Y., Orthmeyer, D.L., Rothe, T.C., Petula, M.J. & Yparraguirre, D.R. 2006. Traversing a boreal forest landscape: Summer movements of Tule Greater White-fronted Geese. *Waterbirds* 29: 43–55.
- Ely, C.R., Bollinger, K.S., Densmore, R.V., Rothe, T.C., Petula, M.J., Takekawa, J.Y. & Orthmeyer, D.L. 2007. Reproductive strategies of northern geese: why wait? *The Auk* 124: 594–605.
- Ely, C.R., Wilson, R.E. & Talbot, S.L. 2017. Genetic structure among greater white fronted goose populations of the Pacific Flyway. *Ecology and Evolution* 7: 2956–2968.
- Fox, A.D. & Leafloor, J.O. (eds.). 2018. *A Global Audit of the Status and Trends of Arctic and Northern Hemisphere Goose Populations*. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland.
- Ganter, B. & Madsen, J. 2001. An examination of methods to estimate population size in wintering geese. *Bird Study* 48: 90–101.
- Green, A.J. 1996. Analyses of globally threatened Anatidae in relation to threats, distribution,

- migration patterns, and habitat use. *Conservation Biology* 10: 1435–1445.
- Hestbeck, J.B. & Malecki, R.A., 1989. Estimated survival rates of Canada geese within the Atlantic Flyway. *Journal of Wildlife Management* 53: 91–96.
- Hobbs, J.H. 1999. Fall and winter distribution and habitat use of the Tule Greater White-fronted Goose (*Anser albifrons gambelli*) in the Sacramento Valley, California. M.Sc. thesis, Sacramento State University, Sacramento, California, USA.
- Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology* 80: 2517–2525.
- Kendall, W. L., Nichols, J.D. & Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563–578.
- Krogman, B.D. 1979. A systematic study of *Anser albifrons* in California. In R.L. Jarvis & J.C. Bartonek (eds.), *Management and Biology of Pacific Flyway Geese*, pp. 22–43. Oregon State University Press, Corvallis, Oregon, USA.
- Miller, H.W., Dzubin, A.X. & Sweet, J.T. 1968. Distribution and mortality of Saskatchewan-banded White-fronted Geese. *Transactions of the North American Wildlife and Natural Resources Conference* 33: 101–119.
- Moffitt, J. 1926. Notes on White-fronted and Tule Geese in central California. *The Condor* 28: 241–243.
- Moffitt, J. 1938. Environmental factors affecting waterfowl in the Suisun area, California. *The Condor* 40: 76–84.
- Olson, S.M. (comp.). 2019. *Pacific Flyway Data Book*. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, U.S. Department of Interior, Vancouver, Washington, USA.
- O'Neil, E.J. 1979. Fourteen years of goose populations and trends at Klamath Basin refuges. In R.L. Jarvis & J.C. Bartonek (eds.), *Management and Biology of Pacific Flyway Geese*, pp. 316–321. Oregon State University Press, Corvallis, Oregon, USA.
- Orthmeyer, D.L., Takekawa, J.Y. & Ely, C.R. 1992. Morphological difference in Greater White-fronted Geese Populations from the Pacific Flyway. In J.S. Sedinger & C.R. Ely (comps.), *Proceedings of the 7th North American Arctic Goose Conference and Workshop: Abstracts*, p. 88. California Maritime Academy Vallejo California, January 7–12, 1992. Available at http://www.naagconference.com/wp-content/uploads/2017/08/7th-naag_vallejo_1992.pdf (last accessed 6 September 2020).
- Orthmeyer, D.L., Takekawa, J.Y., Ely, C.R., Wege, M.L. & Newton, W.E. 1995. Morphological differences in Pacific Coast populations of Greater White-fronted Geese. *The Condor* 97: 123–132.
- Orthmeyer, D.L., Takekawa, J.Y., Ely, C.R., Mensik, J.G., St. Louis, M., Rothe, T.C. & Yparraguirre, D.R. 1998. Comparing population size estimates for the vulnerable Tule Greater White-fronted Goose subspecies from counts, collar observations, and radio locations. In K. Abraham, R. Rockwell, D. Ankney, B. Jefferies, R. Alisauskas & E. Cooch (comps.), *Proceedings of the 9th North American Arctic Goose Conference: Abstracts*, p. 60. Victoria, British Columbia, January 7–11, 1998. Available at http://www.naagconference.com/wp-content/uploads/2017/08/9th-naag_victoria_1998.pdf (last accessed 6 September 2020).
- Pacific Flyway Council. 1991. *Pacific Flyway Management Plan for the Tule Greater White-fronted Goose*. Pacific Flyway Study Committee, Vancouver, Washington, USA. Available at http://www.pacificflyway.gov/Documents/Tgwg_plan.pdf (last accessed 6 September 2020).
- Pacific Flyway Council. 2003. *Pacific Flyway Management Plan for the Greater White-fronted*

- Goose. Pacific Flyway Study Committee, Vancouver, Washington, USA. Available at http://www.pacificflyway.gov/Documents/Pgwg_plan.pdf (last accessed 6 September 2020).
- Pacific Flyway Council. 2015. *Management Plan for Midcontinent Greater White-fronted Geese*. Pacific Flyway Council, Vancouver, Washington, USA. Available at http://www.pacificflyway.gov/Documents/Mgwg_plan.pdf (last accessed 6 September 2020).
- Runge, M.C., Kendall, W.L. & Nichols, J.D. 2004. Exploitation. In W.J. Sutherland, I. Newton & R.E. Green (eds.), *Bird Ecology and Conservation: A Handbook of Techniques*, pp. 303–328, Oxford University Press, Oxford, UK.
- Sanders, T.A. & Trost, R.E. 2013. Use of capture–recapture models with mark resight data to estimate abundance of Aleutian cackling geese. *Journal of Wildlife Management* 77: 1459–1471.
- Schmutz, J.A. & Ely, C.R. 1999. Survival of greater white-fronted geese: effects of year, season, sex, and body condition. *Journal of Wildlife Management* 63: 1239–1249.
- Schmutz, J.A. & Morse, J.A. 2000. Effects of neck collars and radio transmitters on survival and reproduction of emperor geese. *Journal of Wildlife Management* 64: 231–237.
- Scott, P. 1949. Key to the wildfowl of the world. *Wildfowl* 2: 91–111.
- Sheaffer, S.E. & Jarvis, R.L. 1995. Bias in Canada goose population size estimates from sighting data. *Journal of Wildlife Management* 59: 464–473.
- Swarth, H.S. & Bryant, H.C. 1917. A study of the races of the White-fronted Goose (“*Anser Albifrons*”), occurring in California. *University of California Publications in Zoology* 17: 209–222.
- Takekawa, J.Y., Lee, J.L. & Ackerman, J.A. 2005. Estimating identification error for similar subspecies: distinguishing Tule Greater White-fronted Geese in the Pacific Flyway. In M. Lindberg & J. Schmutz (comps.), *Proceedings of the 11th North American Arctic Goose Conference: Abstracts*, p. 72. Reno, Nevada, USA, January 5–8, 2005. Available at http://www.naagconference.com/wp-content/uploads/2017/08/11th-naag_reno_2005.pdf (last accessed 6 September 2020).
- Timm, D.E. & Dau, C.P. 1979. Productivity, mortality, distribution, and population status of Pacific Flyway White-fronted Geese In R.L. Jarvis & J.C. Bartonek (eds.), *Management and Biology of Pacific Flyway Geese*, pp. 280–298. Oregon State University Press, Corvallis, Oregon, USA.
- Timm, D.E., Wege, M.L. & Gilmer, D.S. 1982. Current status and management challenges for Tule White-fronted Geese. *Transactions of the North American Wildlife and Natural Resources Conference* 47: 453–463.
- Trost, R.E. & Harb, L. 1995. Tule Greater White-fronted Goose mark-recapture survey. Unpublished Report to U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- United States Fish and Wildlife Service. 1967. *Native Fish and Wildlife: Endangered Species*. Federal Register. Vol. 32, No. 48. March 11, 1967. U.S. Department of the Interior, Fish & Wildlife Service, Washington DC, USA.
- Wege, M.L. 1984. Distribution and abundance of Tule Geese in California and southern Oregon. *Wildfowl* 35: 14–20.
- White, G.C. 2002. Discussion comments on: the use of auxiliary variables in capture–recapture modeling. An overview. *Journal of Applied Statistics* 29: 103–106.
- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement No. 1): S120–S139.
- Young, G., Williams, M., Hughes, B. & Hall, C. (eds.). 2013. *TWSG News. Bulletin of the IUCNSSC/Wetlands International Threatened Waterfowl Specialist Group, No. 16*. The Wildfowl & Wetlands Trust, Slimbridge, UK.