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Article *in* Wildlife Research · September 2015

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Intra-annual patterns in adult band-tailed pigeon survival estimates

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Abstract

Context. The band-tailed pigeon (*Patagioenas fasciata*) is a migratory species occurring in western North America with low recruitment potential and populations that have declined an average of 2.4% per year since the 1960s. Investigations into band-tailed pigeon demographic rates date back to the early 1900s, and existing annual survival rate estimates were derived in the 1970s using band return data.

Aims. The primary purpose of the paper was to demonstrate that the apparent paradox between band-tailed pigeon population dynamics (long-term steady decline) and breeding season survival rates (very high) can be explained by changes in survival probability during the remainder of the year.

Methods. We trapped Pacific coast band-tailed pigeons during two separate periods: we equipped pigeons with very high frequency (VHF) radio-transmitters in 1999–2000 (1999 = 20; 2000 = 34); and outfitted pigeons with solar powered platform transmitting terminal (PTT) transmitters in 2006–08 (n = 20). We used known fate models to estimate annual survival rates and seasonal survival variation among four periods based on an annual behavioural cycle based on phenological events (nesting, autumn migration, winter and spring migrations). We used model averaged parameter estimates to account for model selection uncertainty.

Key results. Neither body condition nor sex were associated with variation in band-tailed pigeon survival rates. Weekly survival during the nesting season did not differ significantly between VHF-marked (0.996; CI = 0.984–0.999) and PTT-marked pigeons (0.998; CI = 0.990–1.00). Model averaged annual survival of PTT-marked pigeons was 0.682 (95% CI = 0.426–0.861) and was similar to annual survival estimated in previous studies using band return data. Survival probability was lowest during both migration periods and highest during the nesting period.

Conclusions. Our survival estimates are consistent with those of prior studies and suggest that mortality risk is greatest during migration. Weekly survival probability during winter was nearly the same as during the nesting season; however, winter was the longest period and survival throughout winter was lower than other seasons.

Implications. We present the first inter-seasonal analysis of survival probability of the Pacific coast race of band-tailed pigeons and illustrate important temporal patterns that may influence future species management including harvest strategies and disease monitoring.

Additional keywords: known fate model, Pacific Northwest, *Patagioenas fasciata monilis*, platform transmitter terminals (PTT), radio-telemetry.

Received 30 September 2014, accepted 29 July 2015, published online 18 September 2015

Introduction

Understanding animal survival – or the corollary to survival, relative mortality risk – is central to developing effective management or research plans. By extending survival analyses to investigate temporal patterns in survival probability, we can often identify limiting environmental factors or behaviours and target management actions accordingly. Estimation of avian survival is typically accomplished using individuals marked with uniquely numbered leg bands or outfitted with radio-transmitters (Pollock *et al.* 1989; Millspaugh and Marzluff 2001; Murray 2006). Banding studies estimate survival probability between separate capture occasions (e.g. annually) while radio-telemetry studies allow for estimation on much shorter time scales (e.g. daily or weekly), which allow for greater discrimination of temporal patterns.

Estimating survival during shorter time scales may be particularly important when behaviour, habitats used, or threats to survival change greatly throughout the year. Seasonal disease outbreaks may have large effects on local animal populations that are episodic and may be hard to assess without long-term and widespread monitoring. Furthermore, estimating seasonal survival for migrating species or those with wide-ranging nomadic behaviours may be infeasible with traditional radio-telemetry using line-of-sight very high frequency (VHF) transmitters where individuals cannot be relocated as they move over large spatial extents. Recent technological advancements are enabling transmitters that communicate with satellites (e.g. platform transmitting terminal, PTT) to provide relocations on ever smaller devices. These satellite-communicating transmitters

reduce the need for observers to relocate radio-marked individuals from the ground and allow remote monitoring of individual location and status throughout the year (Webster *et al.* 2002; Gaidet *et al.* 2010).

The band-tailed pigeon (*Patagioenas fasciata*) is an example of a species in which detailed, but difficult to obtain, intra-annual survival information could improve management. Band-tailed pigeons (*Patagioenas fasciata*) are a migratory game bird occurring in the western states and provinces of the United States, Mexico and Canada. Two subspecies of band-tailed pigeon occur in North America. The interior race (*P. f. fasciata*) occurs in Arizona, Colorado, New Mexico, and Utah. The coastal race (*P. f. monilis*) occurs from British Columbia south into Baja California, primarily west of the Cascade and Sierra Nevada Crest. Band-tailed pigeons are a long-lived species (Wight *et al.* 1967; Silovsky 1969; Jarvis and Passmore 1992) with low productivity (1.08 eggs per clutch; Neff 1947; Wight *et al.* 1967; Leonard 1998). Population indices of band-tailed pigeon have declined an average of 2.3% per year throughout North America from 1966 to 2011 (Sauer *et al.* 2014). Despite increasingly restrictive harvest regulations and decrease in hunting pressure, the Pacific coast band-tailed pigeon population continued to decline 1.7% per year between 1980 and 2012 (Sauer *et al.* 2014). However, current estimates indicate that the Pacific coast population trend has remained stable over the last decade (Sauer *et al.* 2014).

Band-tailed pigeon populations can be substantially affected by two lethal parasites, *Trichomonas gallinae* and the recently described *T. stableri*, which is passed directly from one pigeon to another through food, water and crop milk (Stabler 1954; Cole 1999; Stromberg *et al.* 2008; Girard *et al.* 2014). Although most epizootic events can occur during any period of the year, the largest recorded outbreak occurred in California during the winter of 2006–07, when an estimated 43 059 band-tailed pigeons succumbed to this disease (Stromberg *et al.* 2008; Girard *et al.* 2014). Outbreaks of trichomoniasis in band-tailed pigeons also appear to be more frequent during winter and disease outbreaks are suspected of providing a major population regulation function (Girard *et al.* 2014).

Despite studies on band-tailed pigeons that date back to the early 1900s (Grinnell 1913), there has been little concerted effort to understand demographic parameters that could be useful to wildlife managers. Most published information on survival rates are derived using band return data, wherein annual survival ranged from 0.57 to 0.71 for Pacific coast populations (Wight *et al.* 1967; Smith 1968; Silovsky 1969; Jarvis and Passmore 1992). Leonard (1998) estimated high nesting season survival (0.963; 95% CI 0.922–1.00) among adult band-tailed pigeons in Oregon. The discrepancy between high nesting season survival rates and much lower annual survival rates from band return studies suggest that a substantial portion of mortality must occur during migration and/or on southern California or north-western Mexico wintering grounds (Leonard 1998).

Information on time-dependent survival is deficient in the literature and, thus, our study objectives were to: (1) use VHF radio-telemetry to estimate band-tailed pigeon nesting season survival at two locations in northern California from 1999 to 2000; (2) use PTT transmitters to estimate intra-annual patterns of band-tailed pigeon survival during behaviour states that

correspond to four phenologically based periods – nesting, autumn migration, winter, and spring migration; and (3) compare our estimates with prior research and provide baseline information to guide species and habitat management decisions. Specifically, we compared the nesting period PTT-based survival rates with VHF-based estimates of survival during the nesting season from this and previous studies. We also discussed the consistency of our non-nesting season survival rate estimates with previous observations that nesting season survival must be greater than survival during other seasons if annual survival obtained from banding studies is correct. Our research provides quantitative estimates to guide management targets towards periods of demographic importance.

Methods and study area

We captured band-tailed pigeons ($n = 54$) using box traps baited with cracked corn ($n = 48$; Smith 1968; Braun 1976) or rocket nets ($n = 6$; Schemnitz 1994) at known mineral sites and marked them with VHF-transmitters in 1999 and 2000. Twenty pigeons captured and marked with PTT-transmitters between 2006 and 2008 were caught in box traps ($n = 16$), spring-loaded Q-nets ($n = 3$), or mist nets ($n = 1$) at both residential bird feeders and baited mineral sites. Box traps measured $\sim 1.5 \times 1.5$ m with one hinged door held open using a 0.5 m pole to which a long cord was attached. All birds caught during 1999 and 2000 ($n = 54$) were captured in northern California and outfitted with a backpack mounted 9 g VHF transmitter (Model A1120, Advanced Telemetry Systems, Isanti, MN). Birds tracked using satellite telemetry (2006–08) were trapped in California ($n = 10$), Oregon ($n = 5$), Washington ($n = 6$), British Columbia ($n = 4$) and Nevada ($n = 1$) and outfitted with 12 g solar powered PTT-transmitters (Model PTT-100–12 g, Microwave Telemetry, Columbia, MD). Both transmitter styles were fastened to birds using 5/16" Teflon ribbon using a cross-keel backpack harness. Because PTT transmitters were solar-powered and continued transmitting for long durations, band-tailed pigeons that survived through one year were still available for analysis during the subsequent year(s). We retained individuals marked during previous years in the analysis, but treated each survival independently during each calendar year. We recorded morphometric measurements, which consisted of weight (g), flat wing (cm), tarsus length (cm) and culmen length (mm), and aged and sexed birds based on plumage (White and Braun 1978) and/or cloacal characteristics (Miller and Wagner 1955). Morphometric data were used to develop a body condition index from the residuals of a third order polynomial model estimated by linear regression ($\text{mass} = a \times \text{flat wing}^3$; Tella *et al.* 1995). We used this body condition index to evaluate potential confounding effects on survival.

Monitoring pigeons

VHF radio-marked birds were monitored on a daily basis using standard vehicle and hand-held telemetry techniques. We attempted to attain two locations each week in each of three different diurnal periods (morning, afternoon and evening). Locations from PTT-marked birds were transmitted every 106 hours. Mortalities were indicated based on characteristics of the relocation data and were visually checked and confirmed. Transmitted data from the PTT transmitters included both a

mortality code that registered when the transmitter did not move for 10 consecutive days and also included ambient temperature data. We identified mortalities by presence of the mortality signal, sudden and continuing drop in ambient (body) temperature measurements, and static relocation occurring for extended periods of time. Radio failure or unconfirmed mortalities were censored (Tsai *et al.* 1999).

Statistical analyses

The primary objective of our research was to estimate differences in band-tailed pigeon survival rates during four different periods of the year that represent different behaviours (nesting, wintering, and both spring and autumn migrations). Therefore, we developed a small set of *a priori* models investigating intra-annual variation in band-tailed pigeon survival estimated using PTT data. Separate models were developed to estimate survival probabilities during different combinations of all seasonal periods. Survival estimation using VHF data was collected only during the nesting season. Therefore, only a single model estimating the survival during this period was calculated. Models were computed in Program R (R Core Team 2008) with the package ‘RMark’, which calls the ‘known fate’ subroutine from Program MARK (White and Burnham 1999; Laake 2013). We calculated survival using a one-week interval period to correspond to the coarsest period wherein birds were relocated (Tsai *et al.* 1999). We evaluated several potential confounding variables that could influence survival probability. Specifically, we checked for changes in survival according to sex, body mass, body condition and during different years. Our diagnostic tests indicated insufficient support for any of these confounding hypotheses, as indicated by likelihood ratio tests (LRT) among nested models (LRT ~0.0 in all cases). Therefore, we limit presentation of our results to the intra-annual investigation that was our primary focus. We expected our analyses to have low statistical power due to low sample size and the statistical methodologies employed. Therefore, we used model averaged parameter estimates from the suite of *a priori* candidate models to estimate survival probability during individual phenologically based periods while accounting for model selection uncertainty (Anderson 2008).

Identification of phenological periods for both spring and autumn migration were based on observed migration timing across all PTT-marked individuals (i.e. a population-scale variable). However, an individual only migrates for a short portion of this time. Our estimated survival rate during migration is therefore unbiased during the band-tailed pigeon migration season, but survival during migration activity is biased by the non-migratory survival nesting and wintering behaviours that comprise a substantial portion of migration periods (Fig. 1). In an effort to directly estimate survival while pigeons were actively migrating, we estimate a modified migration survival probability as:

$$\text{Equation 1} : \hat{S}_T = \hat{S}_S^{N_s} \times \hat{S}_n^{N_n} \times \hat{S}_f^{N_f} \times \hat{S}_w^{N_w}$$

Where:

N_s, N_n, N_f and N_w =number of time periods (weeks in our analysis) spent migrating in spring, nesting, migrating in autumn and wintering, respectively

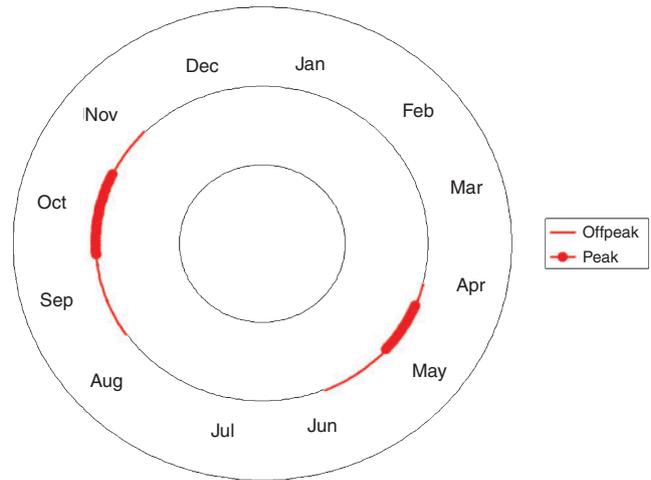


Fig. 1. Estimated migration period based on PTT information (shown in red). The off-peak period refers to the range of dates for which migration was observed among PTT-marked band-tailed pigeons. The peak period refers to the average start and end dates of migration among all PTT-marked individuals. The duration of time that an individual spent migrating during the spring migration averaged 19 days and 45 days during autumn migration (Casazza and Overton 2008).

S_s, S_n, S_f and S_w =interval (weekly) survival rate during spring migration, nesting, autumn migration and wintering, respectively

S_T =survival rate estimated across entire time period (e.g. annual survival rate).

And,

$$N_s + N_n + N_f + N_w = 52 \text{ weeks}$$

We used Eqn 1 to solve for the survival rate S_T under several *a priori* hypotheses regarding the timing of survival differences and potential covariates (models provided in supplementary material). N_s and N_f were estimated from PTT relocation data of band-tailed pigeon migration timing (USGS, unpubl. data). Equation 1 is equivalent to a weighted geometric mean of the season-specific weekly survival rates taken to the exponent of 52 to provide annual survival probability. Equation 1 was modified to a reduced model in our candidate model set that estimated survival in the special case where the survival rate is identical during either spring or autumn migration as well.

Results

Model averaged annual survival rate was 0.661 ± 0.092 (95% CI: 0.466–0.813) for band-tailed pigeons that were equipped with PTTs during 2006–08. Weekly survival rate was greatest during the nesting season (0.994) and winter (0.993) and lowest during spring and autumn migrations (0.989 and 0.990, respectively); however, there was substantial model selection uncertainty (Table 1) and confidence intervals overlapped among estimates during all periods (Fig. 2). Survival probabilities derived for each phenological period were: winter=0.879 (16 November to 29 March); spring migration=0.889 (30 March to 14 June); nesting=0.926 (15 June to 13 September); and autumn migration=0.913 (14 September to 15 November). The weekly

survival rate among 54 VHF-monitored band-tailed pigeons during the nesting seasons of 1999 and 2000 was 0.996 ± 0.003 (95% CI: 0.984–0.999). This estimate resulted in a derived survival across the 13-week nesting season of 0.949. Nesting season survival did not significantly differ between VHF and PTT data sources.

Band-tailed pigeon migration during the spring averaged 19 days in duration and autumn migration averaged 45 days ($n=35$; Casazza and Overton 2008). The duration of an individual’s migration activity was 31% and 59% of the total range of migration activity used to estimate survival rates. Using Eqn 1, we estimated weekly survival during active migration of 0.976 during spring and 0.989 during autumn (Fig. 2). The correlate to survival (S) is mortality risk ($M=1 - S$), resulting in a mortality risk of 0.024 during spring migration and 0.011 during autumn migration. These mortality risks are 4.05 and 1.94 times higher, respectively, than the mortality risk during the nesting season (0.006).

Discussion

To our knowledge, this study represents the first survival rate estimation of band-tailed pigeons throughout the annual cycle, and the first effort to assess survival differences across separate behavioural states throughout the annual cycle. Estimating differences in band-tailed pigeon survival among seasons has been a challenge largely because most studies have either used band recovery information or employed VHF-telemetry methods that could not accommodate for migration away from seasonal use areas. The primary purpose of this paper was to demonstrate that the apparent paradox between band-tailed pigeon population dynamics (long-term steady decline) and breeding season survival rates (very high) can be explained by changes in survival probability during the remainder of the year. Secondly, we demonstrate which periods are more likely to be responsible for such patterns. Survival appeared lower during migration than during either nesting or wintering periods despite the generally increased prevalence of disease in California during winter. We estimated similar nesting season survival rates (0.926) as those estimated in Oregon during 1993–95 by Leonard (1998; 0.963). In addition, our annual survival rates (0.661) are also similar to those reported by band-recovery data from adult band-tailed pigeons in Colorado (0.730; Kautz and Braun 1981), Oregon (0.709; Wight *et al.* 1967; and 0.637; Jarvis and Passmore 1992), and combined estimates for the Pacific coast population (WA, OR, CA = 0.648; Silovsky 1969).

Table 1. Candidate model set, including weight of evidence, used to model average seasonal variation in band-tailed pigeon survival
 K = number of parameters, AICc = sample size adjusted Akaike’s Information Criterion, $\Delta AICc$ = AICc difference from most parsimonious model

Model	K	AICc	$\Delta AICc$	AICc weight	Deviance weight
Null	1	106.60	0	0.276	51.24
Migration specific	2	106.68	0.082	0.265	49.32
Nesting specific	2	107.60	1.004	0.167	50.24
Winter specific	2	108.18	1.583	0.125	50.82
Winter, nesting and migration	3	108.57	1.973	0.103	49.20
Winter, nesting, spring migration and autumn migration	4	109.52	2.924	0.064	48.13

While our results are similar to annual survival estimates obtained from band-recovery data collected in the 1960s and 1970s (Wight *et al.* 1967; Smith 1968; Silovsky 1969) for the Pacific coast population, it is important to note that those data were collected during and shortly after a peak period of population decline when hunting was implicated as a major factor in adult mortality (Silovsky 1969). Substantial changes have occurred in the management of hunting pressure on this species. However, population indices and survival rates have not increased in response. Current hunting seasons for band-tailed pigeons along the Pacific coast coincide with the start of autumn migration. In British Columbia, Oregon, Washington and northern California a short 9- or 15-day season occurs in the last half of September following the start of migration but before peak migration (Fig. 1). Southern California has a 9-day late season band-tailed pigeon hunt occurring in the last half of December, but relatively few PTT band-tailed pigeons migrated into the southern California hunting zone (USGS, unpubl. data). The timing of current hunting seasons appears to balance the goal of offering hunting opportunities while minimising impacts to nesting band-tailed pigeons and harvest of non-resident birds.

We estimated that the lowest band-tailed pigeon survival occurred during spring and autumn migration, indicating that Pacific coast populations may be exposed to enhanced risk and mortality during their semi-annual migrations. Spring migration lasted an average of 19 days, while autumn migration lasted an average of 45 days, with an overall average of 740 km travelled

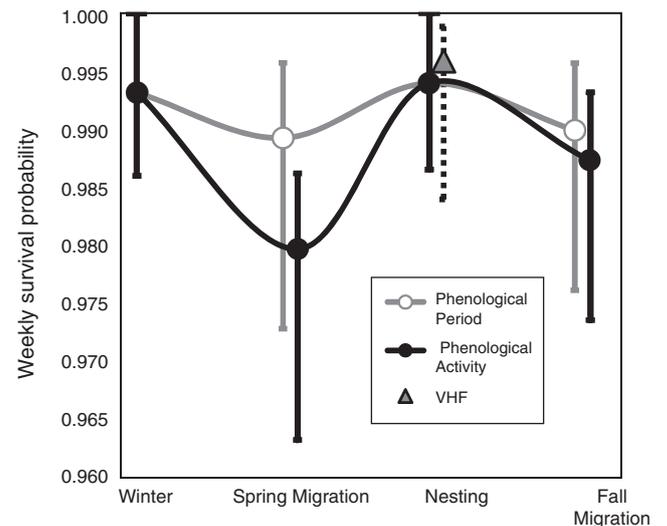


Fig. 2. Estimated intra-annual patterns in radio-marked band-tailed pigeon survival (95% confidence limits) within the Pacific coast range of the species. Survival rates of satellite-tracked birds (PTT) were estimated during seasonal periods (open circle, light grey line) and when specific behavioural activities (i.e. migration) actually occurred for individuals (solid circle, black line). Survival rate of ground-tracked birds (VHF; triangle symbol) was estimated only during the nesting season. Since individual migratory behaviour occurs during a portion of the total time that migration occurs, the risk of mortality during migratory activity is biased by survival rates of non-migration behaviour (light grey lines) and estimates of unbiased survival rates are provided for migratory activity (black line).

between winter and the nesting season ($n=35$; Casazza and Overton 2008). Conditions encountered during migration such as restricted food supplies, adverse weather, density-dependent predation and other migration-related events can have substantial effects on population levels (Sandercock and Jaramillo 2002; Sillett and Holmes 2002; Newton 2006).

Although our results indicate a relatively high winter survival rate, it is important to consider that outbreaks of trichomoniasis can be localised and have large effects on segments of band-tailed pigeon populations (Stromberg *et al.* 2008). The concentration of migrant and recently fledged birds in southern portions of the species range (i.e. California and Baja California) and at lower elevations (e.g. Sierra Nevada foothills) may increase the likelihood of disease transmission and trigger an epizootic event that could affect a disproportionate extent of the Pacific coast population (Girard *et al.* 2014). Such outbreaks are often episodic and locally distributed. Our analysis was not designed to detect localised differences in survival probability, which could indicate regions with lower survival than our estimates indicate. However, recent wintertime disease outbreaks of trichomoniasis (Girard *et al.* 2014) did not substantially overlap with locations used by migrating band-tailed pigeons (USGS, unpubl. data). Consequently, our results may show relatively high wintertime survival rates that could be unachievable if disease outbreaks occur with greater severity where migrating band-tailed pigeons settle.

Satellite telemetry provides a useful tool to estimate seasonal survival, but has limitations. For example, difficulty in differentiating mortality from PTT failure may inflate survival rates since known fate models assume a detection probability of 1.0 and that signal detection is uncorrelated with individual fate (Tsai *et al.* 1999). However, this often isn't the case, especially for PTT satellite transmitters. For example, solar powered transmitters may not transmit locations from the bottom of a canyon where there is insufficient sunlight to charge the batteries, whereas transmitters located in tree tops can charge and continue to transmit locations. Although this phenomenon may inflate survival rate by increasing the number of censored birds that could have actually been deaths (Tsai *et al.* 1999), we believe the effects here were negligible. For example, we investigated the robustness of our survival estimates to violations of these assumptions in a *post hoc* analysis that assumed every right-censored individual died at the moment of censoring. Although survival rates under this hypothetical scenario were much lower, the resulting estimates were not biologically feasible and did not influence our central findings regarding intra-annual survival patterns.

These study findings provide baseline information on annual and seasonal survival for band-tailed pigeons that were previously lacking. In particular, our finding that migration periods have a greater mortality risk for band-tailed pigeons may affect how cross-season population dynamics studies are interpreted. For example, survival rate estimation from banding studies may be improved by understanding migration behaviour across the landscape. Our results also indicate that we need greater understanding of the causes of lower survival during migration. In particular, it is important to know whether this increased mortality risk is density independent or density dependent. The prevalence of density-dependent mortality during migration could result in a situation where pre-migration harvest is a compensatory mortality

factor. This could allow managers to consider increased hunter opportunities through expanding band-tailed pigeon hunting seasons and/or bag limits. Lastly, the relatively high winter season survival we estimated may be impacted in years where *Trichomonas* prevalence, transmission and mortality is greater. Band-tailed pigeons are particularly susceptible to a virulent strain of *Trichomonas* that frequently causes local outbreaks in California during winter. Subpopulation survival monitoring in California may indicate location, extent and severity of disease outbreaks, help understand disease ecology, and inform action plans to manage outbreaks.

Much of our existing demographic knowledge about band-tailed pigeons was interpreted from banded birds and through harvest data during the 1960s and 1970s, a time when populations were experiencing significant declines and had much greater harvest pressure than exists today. For example, ~550 000 band-tailed pigeons were harvested from the three coastal states in 1968 (Western Migratory Upland Game Bird Committee 1994), whereas an average of 17 117 pigeons were harvested annually from 1999 to 2010 (Sanders 2013). Contemporary estimates using band recoveries would require intensive re-trapping efforts to compensate for reduced hunter recovery. Despite the limitations and potential biases associated with telemetry data, analysis of PTT data, coupled with local VHF data, may provide the best approach to understanding within-year temporal patterns in survival given the migratory nature of this species.

Acknowledgements

We would like to thank the many private landowners, technicians and volunteers who assisted in data collection and capture and are particularly indebted to A. Forde, M. Law, J. Schneiderman and D. Van Baren. We would also like to thank G. Wylie, D. Blankenship, D. Yparraguirre, M. Miller, P. Gore and L. Parker for administrative and technical assistance. This project was funded by the California, Oregon and Washington Departments of Fish and Wildlife, with matching funds from the Webless Migratory Game Bird Research Program through the USA Fish and Wildlife Service. We wish to acknowledge and thank the program administrators, D. Dolton and T. Cooper, and the Pacific region representatives, T. Sanders, B. Bales, D. Kraege, B. Bortner and A. Breault for their support. Additional funding was provided by the Western Ecological Research Center, USA Geological Survey. Approved Animal Care and Use Committee guidelines developed by the Western Ecological Research Center were followed before bird handling. Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the USA Government.

References

- Anderson, D. R. (2008). 'Model Based Inference in the Life Sciences.' (Springer Science: New York, NY.)
- Braun, C. E. (1976). Methods for locating, trapping, and banding band-tailed pigeons in Colorado. Colorado Division of Wildlife Special Report No. 39. Denver, CO.
- Casazza, M. L., and Overton, C. T. (2008). Breeding distribution and migration routes of Pacific Coast band-tailed pigeons. In 'Webless Migratory Game Bird Research Program, Project Abstracts – 2008'. (Ed. D. D. Dolton.) pp. 29–31. (USFWS: Laurel, MD.)
- Cole, R. A. (1999). Trichomoniasis. In 'Field Manual of Wildlife Diseases: General Field Procedures and Diseases of Birds'. (Eds M. Friend and J. C. Franson.) pp. 201–206. (USDI, Geological Survey – BRD: Washington, DC.)

- Gaidet, N., Cappelle, J., Takekawa, J. Y., Prosser, D. J., Iverson, S. A., Douglas, D. C., Perry, W. M., Mundkur, T., and Newman, S. H. (2010). Potential spread of highly pathogenic avian influenza H5N1 by wildfowl: dispersal ranges and rates determined from large-scale satellite telemetry. *Journal of Applied Ecology* **47**, 1147–1157. doi:10.1111/j.1365-2664.2010.01845.x
- Girard, Y. A., Rogers, K. H., Woods, L. W., Chouicha, N., Miller, W. A., and Johnson, C. K. (2014). Dual-pathogen etiology of avian trichomonosis in a declining band-tailed pigeon population. *Infection, Genetics and Evolution* **24**, 146–156. doi:10.1016/j.meegid.2014.03.002
- Grinnell, J. (1913). The outlook for conserving the band-tailed pigeon as a game bird of California. *The Condor* **15**, 25–40. doi:10.2307/1361868
- Jarvis, R. L., and Passmore, M. F. (1992). Ecology of band-tailed pigeons in Oregon. Report no. 6. (US Fish Wildlife Service Biological: Washington, DC.)
- Kautz, J. E., and Braun, C. E. (1981). Survival and recovery rates of band-tailed pigeons in Colorado. *The Journal of Wildlife Management* **45**, 214–218. doi:10.2307/3807888
- Laake, J. L. (2013). 'RMark: an R Interface for Analysis of Capture-Recapture Data with MARK.' (AFSC Processed Rep 2013–01, NOAA: Seattle, WA.)
- Leonard, J. P. (1998). Nesting and foraging ecology of band-tailed pigeons in western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, OR.
- Miller, W. J., and Wagner, F. H. (1955). Sexing mature Columbiformes by cloacal characters. *The Auk* **72**, 279–285. doi:10.2307/4081606
- Millsbaugh, J., and Marzluff, J. M. (Eds) (2001). 'Radio Tracking and Animal Populations.' (Academic Press: San Diego, CA.)
- Murray, D. L. (2006). On improving telemetry-based survival estimation. *The Journal of Wildlife Management* **70**, 1530–1543. doi:10.2193/0022-541X(2006)70[1530:OITSE]2.0.CO;2
- Neff, J. A. (1947). Habits, food, and economic status of the band-tailed pigeon. North American Fauna 58. (US Department of the Interior, Fish and Wildlife Service: Washington, DC.)
- Newton, I. (2006). Can conditions experienced during migration limit the population levels in birds? *Journal für Ornithologie* **147**, 146–166.
- Pollock, K. H., Winterstein, S. R., Bunck, C. M., and Curtis, P. D. (1989). Survival analysis in telemetry studies: the staggered entry design. *The Journal of Wildlife Management* **53**, 7–15. doi:10.2307/3801296
- R Core Team (2008). 'R: a Language and Environment for Statistical Computing. Version 2.0.0.' (R Foundation for Statistical Computing: Vienna.)
- Sandercock, B. K., and Jaramillo, A. (2002). Annual survival rates of wintering sparrows: assessing demographic consequences of migration. *The Auk* **119**, 149–165. doi:10.1642/0004-8038(2002)119[0149:ASROWS]2.0.CO;2
- Sanders, T. A. (2013). 'Band-tailed Pigeon Population Status, 2013.' (US Department of the Interior, Fish and Wildlife Service, Division of Migratory Bird Management: Washington, DC.)
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J., Jr, and Link, W. A. (2014). 'The North American Breeding Bird Survey, Results and Analysis, 1966–2012. Version 02.19.2014.' (USGS Patuxent Wildlife Research Center: Laurel, MD.)
- Schemnitz, S. D. (1994). Capturing and handling wild animals. In 'Research and Management Techniques for Wildlife Habitats. 5th edn'. (Ed. T. A. Bookhout.) pp. 106–124. (The Wildlife Society: Bethesda, MD.)
- Sillett, T. S., and Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**, 296–308. doi:10.1046/j.1365-2656.2002.00599.x
- Silovsky, E. D. (1969). Distribution and mortality of the Pacific coast band-tailed pigeon. Master's Thesis, Oregon State University, Corvallis, OR.
- Smith, W. A. (1968). The band-tailed pigeon in California. *California Fish Game Bulletin* **54**, 4–16.
- Stabler, R. M. (1954). *Trichomonas gallinae*: a review. *Experimental Parasitology* **3**, 368–402. doi:10.1016/0014-4894(54)90035-1
- Stromberg, M. R., Koenig, W. D., Walters, E. L., and Schweisinger, J. (2008). Estimate of *Trichomonas gallinae*-induced mortality in band-tailed pigeons, upper Carmel Valley, California, winter 2006–2007. *The Wilson Journal of Ornithology* **120**, 603–606. doi:10.1676/07-115.1
- Tella, J. L., Gortázar, C., López, R., and Osácar, J. J. (1995). Age related differences in biometrics and body condition in a Spanish population of alpine swift (*Apus melba*). *Journal für Ornithologie* **136**, 77–79. doi:10.1007/BF01647211
- Tsai, K., Pollock, K. H., and Brownie, C. (1999). Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. *The Journal of Wildlife Management* **63**, 1369–1375. doi:10.2307/3802856
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., and Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* **17**, 76–83. doi:10.1016/S0169-5347(01)02380-1
- Western Migratory Upland Game Bird Committee (1994). 'Pacific Flyway Management Plan for the Pacific Coast Population of Band-tailed Pigeons.' (Pacific Flyway Council: Portland, OR.)
- White, J. A., and Braun, C. E. (1978). Age and sex determination of juvenile band-tailed pigeons. *The Journal of Wildlife Management* **42**, 564–569. doi:10.2307/3800819
- White, G. C., and Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–138. doi:10.1080/00063659909477239
- Wight, H. M., Mace, R. U., and Batterson, W. M. (1967). Mortality estimates of an adult band-tailed pigeon population in Oregon. *The Journal of Wildlife Management* **31**, 519–525. doi:10.2307/3798134