Closed Robust Design Modeling of 2013 Saipan TMAPS Capture-recapture Data

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Abstract

The Tropical Monitoring Avian Productivity and Survivorship (TMAPS) program was established in 2008 to provide insights into the molt, phenology, and demography of landbirds on Saipan, Northern Marianas Islands. The TMAPS program has been operated in each year since 2008. However, sampling protocols and effort have varied among years due to variation in funding and competing objectives for which no single sampling protocol was ideal. Beginning in 2013, we implemented a temporally intensive sampling protocol (focused on mid-dry and mid-wet seasons) that increased net densities and sampling areas to provide station-specific estimates of population size and vital rates. Here we provide an initial assessment of the new sampling protocol based on application of a closed robust design model to capture-recaptue data for adult birds of three target species: Rufous Fantail (*Rhipidura rufifrons saipanensis*), Bridled White-eye (*Zosterops conspiculatus saypani*), and Golden White-eye (*Cleptornis marchei*). For Rufous Fantail, we also compared results of analyses that included only the original TMAPS net sites and analyses that also included nets established in 2013. We were able to estimate adult apparent survival rates between the 2013 dry season and wet season at the station-scale for Rufous Fantail and Golden White-eye. There were relatively few recaptures of Bridled White-eye, and we were only able to estimate an overall (i.e., station-constant) survival rate, which was very low (0.037). Inclusion of additional years of data will allow modeling of temporary emigration and improve survival-rate estimates. Population-size was estimated with sufficient precision to detect a variety of differences among stations and seasons. Initial capture probabilities were much higher than recapture probabilities suggesting strong net avoidance following initial capture. Comparison of results between reduced and full data sets for Rufous Fantail suggested substantial gain in precision in population size and survival-rate estimates and significant increases in recapture probabilities. Results suggest that the sampling protocol implemented in 2013 offers great potential as part of a long-term landbird monitoring effort on Saipan.

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Introduction

Application of standardized constant-effort mist netting and modern capture-recapture analytical techniques is an effective means of monitoring demographic rates of many landbird species (Robinson et al. 2009). Such an effort was initiated in North America by The Institute for Bird Populations (IBP) in 1989 with the establishment of the Monitoring Avian Productivity and Survivorship (MAPS) program (Desante et al. 1995; DeSante et al. 2004). The MAPS program is a cooperative network of over 1,000 constant-effort mist-netting stations operated across North America that has provided demographic data for $>$ 180 landbird species (DeSante and Kaschube 2009). Similar programs in Europe are central components of national and international bird-monitoring efforts (e.g., Peach et al. 2004). The MAPS program was endorsed in 1991 by the Monitoring Working Group of Partners in Flight (PIF) and the USDI Bird Banding Laboratory, and has attracted participation from many U.S. agencies, including the National Park Service, Department of Defense, Texas Army National Guard, USDA Forest Service, and Fish and Wildlife Service, as well as hundreds of independent banding-station operators.

IBP, in collaboration with the Division of Fish and Wildlife of the Commonwealth of the Northern Mariana Islands, established and operated the first six “Tropical MAPS” (TMAPS) stations on the island of Saipan in 2008, and these stations have been operated in each year since that time. The overall goal of this effort is to provide baseline data on trends, vital rates, and habitat associations for populations of up to nine bird species indigenous to Saipan to inform conservation strategies for this insular avifauna. Long-term goals of the TMAPS program on Saipan include: (1) providing annual indices of adult population size and post-fledging productivity (from constant-effort capture data); (2) providing annual estimates of adult population size, survival rates, proportions of residents, and recruitment into the population (from capture-recapture data); (3) relating avian demographic data to weather and habitat; (4) identifying population trends and proximate and ultimate causes of population change; and (5) applying these data to inform management.

In addition to the long-term goals, an initial aim of the TMAPS program was to gather basic information on the timing and extent of breeding and molt, and to better understand how these processes relate to abiotic drivers (rainfall, plant productivity). Due to competing goals, as well as annual variation in funding, the length of the field season during the initial 5 years of the TMAPS program was variable. We operated stations across what was thought to be the the primary breeding season for most species (Apr-Jul), but we also extended the field season into additional months of the year whenever funding allowed, and we were able to complete sampling that extended across a full year between Mar 2011 and Mar 2012. Sampling frequency largely followed the standard MAPS protocol of one day of mist-netting per 10-d period; however, we moved to a monthly 3-d 'pulse' protocol between Jul 2011 and Mar 2012 (to conform to a design more readily analyzed with modern capture-recapture methods). These extensive sampling efforts have yielded important insights into spatial and temporal variation in breeding (Saracco et al. 2014) and into the timing and extent of molt (Junda et al. 2012; Radley et al. 2011). But extended annual sampling or year-round banding is expensive, and avoidance of nets over time by birds may result in relatively inefficient demographic monitoring compared to more intensive sampling designs (Ruiz-Gutiérrez et al. 2012). In addition, numbers of captures and recaptures at a typical MAPS station (10 nets distributed over approximately 8 ha) are usually too few to allow application of capture-recapture models that require large samples to provide inferences about demographic parameters at the station-scale. For these reasons, we restructured the Saipan TMAPS sampling in 2013 to conform to a closed robust design model (Kendall et al. 1997; Kendall 1999), whereby two pulses (one in the mid-dry season, one in the mid-wet season) of mist netting are to be completed each year at original station net sites and at an additional array of net sites established at each station (increasing station boundaries in most cases).

Here we present results of analyses of the 2013 data set to provide station-specific estimates of adult population size during dry and wet seasons and estimates of adult survival between these two seasons for three target species: Rufous Fantail (*Rhipidura rufifrons saipanensis*), Bridled White-eye (*Zosterops conspiculatus saypani*), and Golden White-eye (*Cleptornis marchei*). For the most commonly captured species, Rufous Fantail, we also compared results of analyses that include only the original net sites and analyses that also included the net array established in 2013 to provide an initial indication of how inferences were affected by the extra effort and whether the level of effort expended in 2013 is justifiable as part of the longer-term TMAPS monitoring program.

Methods

Study Areas and Field Methods

Six study areas (TMAPS stations) were established across the island of Saipan in land cover types typical of Saipan and neighboring islands Tinian and Rota (see Saracco et al. 2014 for detail). Ten nets were established at each station across an area of approximately 8 ha (Desante et al. 2014), and these nets were operated annually with various levels of effort since 2008. In 2013, we sampled birds at the original 10 nets established at each TMAPS station plus up to two additional nets within this netting area (hereafter, net array A), as well as at an additional 10-12 nets (net array B) that we established at each station to enhance sample sizes and provide improved station-scale inferences about demographic rates. In all cases except at the Sabana Talofofo (SATA) station (where room for station expansion was most limited), the additional net array increased the overall sampling area of each station.

Sampling at each station was conducted within two 'pulses' of mist netting centered on the mid-dry season (April) and mid-wet season (Oct). For each net array and pulse, we conducted three consecutive days of mist-netting. We netted birds at only a single net array on each sampling day, and sampling was structured such that we cycled through net array A at each site before cycling through net array B. This design resulted in both net arrays at each station and pulse being sampled within a period of approximately 1 month, with samples across all stations for a given pulse spanneing a period of approximately 1.6 months (dry season pulse from 21 Mar-7 May; wet season pulse from 20 Sep-10 Nov). Mist-netting effort data (i.e.,

Table 1: Sampling effort at each of the six Tropical Monitoring Avian Productivity and Survivorship (TMAPS) stations on Saipan during 2013. Three days of mist-netting were completed for each station, net array, and season.

			Dry season (Mar-May)			Wet season (Sep-Nov)		
Station	Code	Net array	1	2	3	1	2	3
Bird Island Conserv. Area	BICA	A	59.33	72.00	56.00	53.33	54.67	71.33
		B	68.00	68.67	62.00	62.67	71.33	72.00
Kingfisher	KIFI	A	60.00	56.67	52.67	30.83	58.67	58.00
		B	58.67	60.00	60.00	56.67	53.33	19.17
Laderan Tangke	LATA	A	70.67	72.00	72.00	64.67	70.00	46.67
		B	60.00	70.67	70.67	68.00	48.00	71.33
Mount Tapochau	MTAP	A	52.00	60.00	60.00	58.00	60.00	59.33
		B	60.00	60.00	60.00	57.33	24.67	58.00
Obyan	OBYA	A	64.00	64.00	64.00	64.00	70.67	45.67
		B	56.00	40.00	48.00	47.33	62.00	63.33
Sabana Talofofo	SATA	A	60.00	58.00	60.00	56.67	47.83	58.67
		B	60.00	60.00	60.00	54.33	60.00	60.00

the number and timing of net-hours on each day of operation) were collected in a standardized manner by recording opening and closing times (to the nearest 10 min) for nets, as well as the time at which each net check commenced. We aimed to operate nets for six morning hours per day beginning 15 minutes after sunrise (on or near 05:30 AST). Inclement weather (mostly high sun and wind exposure) and high capture rates at some sites, however, resulted in variable effort among stations. A summary of mist-netting effort for each station, net array and pulse is presented in Table 1.

With few exceptions, all birds captured in mist nets were identified to species, age (young = 'hatching year'; adult = 'after hatching year'), and sex (based on Pyle et al. 2008; Radley et al. 2011) and banded with United States Geological Survey Biological Resources Division numbered aluminum leg bands if not already so marked. Band numbers of all recaptures were carefully recorded. We also collected ancillary data on skull pneumaticization, breeding condition, molt, wing length, and subcutaneous fat deposition (Desante et al. 2014).

Statistical Analysis

We applied closed robust design models (Kendall et al. 1997; Kendall 1999) to the 2013 TMAPS capture-recapture data for adult birds (i.e., birds aged “After-hatching-year” or older). The robust design consists of two levels of sampling: primary samples (here represented as the dry season and wet season samples) and secondary samples (individual sampling days for a station within each season). The model assumes population closure within primary samples and an open population between primary samples. We used these models to estimate adult population size at stations during the 2013 dry and wet seasons and adult apparent survival rates between these seasons. We also provide estimates of time-constant capture and recapture probabilities. It should be noted with just two pulses of data, we were unable to impose complex model structure on survival (e.g., time-since marking models to provide estimates of 'resident' survival; Pradel et al. 1997). In addition, we were not able to model temporary emigration parameters (a minimum of three pulses is needed). As additional years of data are accumulated, we will be able to model temporary emigration and add model complexity that should better reflect patterns of movement and demography in these populations.

For Rufous Fantail and Golden White-eye, we ran models in program MARK (White and Burnham 1999) that allowed adult population size (N) to vary by station and year, adult apparent survival (S) to vary as a function of station, and capture probability to vary between initial capture (p) and subsequent capture (c). We allowed capture probability to vary between initial and subsequent capture to reflect the hypothesis that birds become 'trap-shy' after initial capture (i.e., the $M_b$model of Otis et al. 1978; White 2008). We set the temporary emigration parameter γ'' equal to zero to make the survival parameters identifiable. As noted above, we will begin to be able to model temporary emigration once an additional pulse of data has been added to the data set. We also considered parameterizations for Rufous Fantail and Golden White-eye that modeled S as constant across stations, and we assessed support for these models compared to the staion-specific S models based on Aikaike's information criterion adjusted for small samples (AIC_c; Burnham and Anderson 2002) For Bridled White-eye, data were too sparse to estimate station-specific survival. For this species, we only report results from a model with S held constant across stations. For Rufous Fantail, we also ran models based on captures and recaptures from only the 10 nets represented by net array A.

Results

For Rufous Fantail and Golden White-eye, the two species with sufficient data for modeling station-specific survival, statistical support for the station-specific survival model was similar to support for the model with survival held constant. In both cases, the constant-survival model had the lowest $AIC_c$with the station-specific model within 2 AIC_c points ($\Delta AIC_c = 0.39$ for Rufous Fantail and$\Delta AIC_c = 1.10$ for Golden White-eye). Between-season adult apparent survival estimates for Rufous Fantail from the station-specific survival model ranged from 0.148 (SE = 0.080; 95% CI: 0.047-0.376) at the MTAP station to 0.498 (SE = 0.102; 95% CI: 0.309-0.688) at the OBYA station. For Golden White-eye, sufficient data were available to provide station-scale estimates of survival at just 3 of the 6 stations, BICA, LATA, and MTAP. Survival estimates at these stations were similarly low at LATA ($\hat{S} = 0.228; SE = 0.068; 95\%\text{CI} : 0.122 - 0.386$) and MTAP ($\hat{S} = 0.217; SE = 0.141; 95\%\text{CI} : 0.052 - 0.585$) and slightly higher at BICA ($\hat{S} = 0.292; SE = 0.081; 95\%\text{CI} : 0.161 - 0.470$). The constant adult apparent survival estimate for Bridled White-eye was extremely low ($\hat{S} = 0.037; SE = 0.027; 95\%\text{CI} : 0.009 - 0.143$).

Station-scale adult population size (N) was estimated with sufficient precision to detect a variety of significant differences among stations and seasons (Fig. 1). Although each species showed a somewhat unique spatial pattern of relative abundance, the BICA station tended to have the greatest abundance of all three species. Abundances of all three species tended to decline between the 2013 dry and wet seasons.

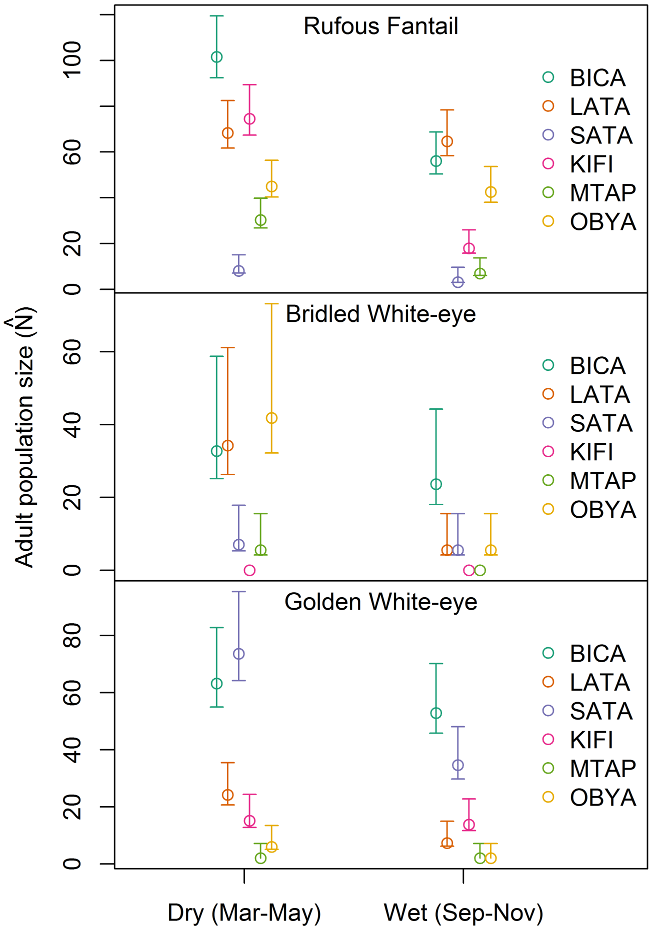

Figure 1: Estimates of station-scale adult population size (±95% confidence limits) during the 2013 dry and wet seasons at the six Tropical Monitoring Avian Productivity and Survivorship (TMAPS) stations on Saipan, Northern Marianas Islands.

For the Rufous Fantail data set that included only net array A, the model that allowed survival to vary by station received no support compared to a station-constant survival model$\Delta AIC_c = 10.91$; AIC_cmodel weight $= 0.00$). Station-specific estimates of adult apparent survival were (with the exception of MTAP) somewhat lower for the reduced (net array A) data set compared to the full data set, and data were insufficient to estimate survival with the reduced data set for the SATA station (Table 2). In addition, precision of survival estimates was substantially lower for the reduced data set compared to the full data set. The mean CV of survival rate estimates for the five stations where survival could be estimated averaged 51% for the reduced data set compared to 28% for the full data set. Initial capture probability estimates (p) were very similar for the two data sets (although slightly higher for the full data set; 0.43 v. 0.39); however, recapture probability was significantly higher for the full data set compared to the reduced data set (0.11 v. 0.05; Table 2). On average, Rufous Fantail population size estimates more than doubled with the full data set compared to the reduced data set (mean increase across stations and seasons of a 2.3 × over the reduced data set; Table 2), highlighting the increase in sampling area covered with the increased number of nets operated. Precision of population size estimates was also substantially improved for the full data set (average CV = 12%) compared to the reduced data set (average CV = 21%).

Table 2: Comparison of parameter estimates from closed robust design models applied to the complete 2013 Rufous Fantail data set and a reduced data set comprised only of captures and recaptures from net array A (10 nets). Parameter superscripts represent station codes (see Table 1); subscripts represent primary samples (i.e., dry [Mar-May] or wet [Sep-Nov] season).

	Full data set				Net array A only			
Parameter	Estimate	SE	95% lower	95% upper	Estimate	SE	95% lower	95% upper
S^{BICA}	0.31	0.06	0.21	0.44	0.20	0.08	0.08	0.42
S^{LATA}	0.44	0.08	0.29	0.60	0.27	0.11	0.11	0.52
S^{SATA}	0.18	0.16	0.02	0.66	0.00	0.00	0.00	0.00
S^{KIFI}	0.26	0.07	0.15	0.41	0.22	0.09	0.09	0.44
S^{MTAP}	0.15	0.08	0.05	0.38	0.20	0.13	0.05	0.55
S^{OBYA}	0.50	0.10	0.31	0.69	0.17	0.11	0.04	0.50
p	0.43	0.04	0.36	0.50	0.39	0.06	0.28	0.51
c	0.11	0.01	0.09	0.14	0.05	0.01	0.03	0.08
N^{BICA}_{dry}	101.53	6.61	92.40	119.51	40.90	4.93	35.22	56.55
N^{LATA}_{dry}	68.34	5.00	61.74	82.50	30.54	4.00	26.17	43.73
N^{SATA}_{dry}	8.08	1.47	7.14	15.02	2.01	0.94	2.00	6.13
N^{KIFI}_{dry}	74.48	5.31	67.41	89.36	38.31	4.70	32.96	53.35
N^{MTAP}_{dry}	30.22	2.98	26.84	39.80	16.31	2.64	13.83	26.10
N^{OBYA}_{dry}	44.98	3.80	40.29	56.37	18.90	2.90	16.06	29.31
N^{BICA}_{wet}	56.04	4.38	50.43	68.76	24.07	3.40	20.54	35.72
N^{LATA}_{wet}	64.65	4.82	58.35	78.38	39.60	4.82	34.09	54.95
N^{SATA}_{wet}	3.13	0.96	3.00	9.62	2.01	0.94	2.00	6.13
N^{KIFI}_{wet}	17.93	2.22	15.78	25.95	9.83	1.96	8.33	18.14
N^{MTAP}_{wet}	6.84	1.35	6.09	13.72	4.63	1.33	4.05	12.06
N^{OBYA}_{wet}	42.52	3.67	38.04	53.61	11.12	2.10	9.42	19.72

Discussion

TMAPS sampling protocols on Saipan during the 5-yr pilot program (2008-2012) aimed to address a broad range of goals, including providing basic understanding of the phenology and extent of breeding and molt and providing demographic data. As such, these protocols represented a compromise in approaches, none of which was ideally suited to addressing any particular goal. Although demographic analyses of the 5-yr data set have provided many important insights (Saracco et al. 2014), the mixture of sampling designs used prior to 2013 resulted in complicated analyses that were always well-matched to meeting demographic monitoring objectives. Revised protocols introduced in 2013 provide a bridge between the 2008-2012 monitoring program (via retention of original net sites) and long-term demographic monitoring protocols that are better matched to available analytical methods. Results presented here suggest great potential for the intensive sampling protocol adopted in 2013 to effectively monitor the population status and demographic rates of target landbird species on Saipan. Although we only consider adult birds here, the same basic methods could be applied to young birds to provide snapshots of age-specific abundances at two periods of the life cycle that, together, may accurately reflect annual productivity (Saracco et al. 2014).

Our capture-recapture analysis focused on estimating population size, N, adult apparent survival probability, ϕ, and parameters representing the annual probability of initial capture, c, and recapture, p. Population size estimates for each target species were estimated with sufficient precision to detect a variety of differences among stations and pulses, which suggests the overall utility of our approach for monitoring the year- and season-specific status of populations on our study areas. Although stations differ to some extent with respect to sampling area and net density, the increase in net numbers should facilitate spatial modeling that would allow density estimation that would be directly comparable among stations (by scaling abundances to account for differences in areal coverage among stations; Royle et al. 2013).

Survival-rate estimates provided here represent a complex mixture of movement off of study areas (both temporary and permanent emigration) and true survival. As such, these estimates were biased low to some degree. Future analyses with additional pulses of data will offer flexibility in modeling temporary and permanent emigration and survival-rate estimation approximating true survival rates (Kendall et al. 1997; Kendall 1999). Irrespective of interpretation of survival estimates presented here, we found it promising that relatively precise station-specific estimates of survival could be obtained with just two primary sampling periods for two of the target species (all but Brideled White-eye, which had extremely low overall survival between pulses in 2013). We found that the probability of initial capture was much higher than the probability of subsequent recapture for all species, suggesting strong net avoidance by birds following initial capture. This situation might be ameliorated by avoiding the use of fixed net sites within pulses altogether (i.e., moving nets each day; Marques et al. 2013); however, such a protocol might prove logistically difficult to implement in practice.

Population size estimates for Rufous Fantail from the full data set were 2.3 × larger then estimates based on analysis of just the original net sites. For some stations (e.g., BICA), new net sites had little overlap with the original sampling area, and so this magnitude of difference is not surprising, but in general there was some degree of overlap between the two net arrays (the extreme being at SATA, where the overall sampling area was essentially the same). Thus, the increase in population estimates also suggests that the increased net density provided by both net arrays sampled portions of the study area that were previously not sampled by the original net arrays. This too, might be expected, given typically high population densities of tropical island bird species (e.g., MacArthur et al. 1972) compared to temperate mainland forests, and original net densities based on MAPS protocols, which were designed for monitoring of temperate mainland bird populations (Desante et al. 2014). Nevertheless, these interpretations of differences in population estimates from the two data sets depend on the assumption that the population was closed over the approximately 1 month that it took to sample both net arrays at each station. Although we have not tested the validity of this assumption, we expect that local populations would be relatively stable during our sampling periods, which coincide with periods when the phenology of habitats is relatively stable (Saracco et al. 2014).

Comparison of survival-rate estimates for Rufous Fantail between the full and reduced data sets showed substantial increase in precision of estimates with the full data set. Although confidence intervals overlapped broadly for estimates from the two data sets, there was a tendency for estimates from the full data set to be higher, suggesting the potential importance of study area size in affecting apparent survival rates via temporary emigraion (which might be greater for a smaller study area due to larger area to edge ratio).

Initial capture probability estimates for Rufous Fantail were similar between the reduced and full data sets (althoguh slightly higher for the full data set); however, the recapture probability esimate (although small in both cases) was more than twice as high for the full data set compared to the reduced data set. This suggests that the two net arrays may each be sampling largely unique sets of individuals, yet given the overall large decline in capture probability following initial capture, the additional net array may still have a large impact on increasing recaptures.

Overall, we are pleased with the monitoring potential of the study design implemented at Saipan TMAPS stations in 2013. We look forward to future analyses that include additional years of monitoring, which will enable incorporation of greater biological realism into demographic inferences, as well as allow testing hypotheses related to when in the life cycle vital rates may limit populations (e.g., transition from wet-to-dry season v. transition from dry-to-wet season).

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