



Vital Rates of Landbirds on Saipan and Links to Remote-sensed Habitat Data

*A Summary of Five Years (2008-2012) of the Tropical Monitoring Avian
Productivity and Survivorship (TMAPS) program on Saipan, Northern Mariana
Islands*

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Abstract.—We established the Tropical Monitoring Avian Productivity and Survivorship (TMAPS) program, at six sites (stations) on Saipan, Northern Mariana Islands in 2008. Here we provide results of the first five years (2008-2012) of the TMAPS program on Saipan. In particular, we report on the breeding phenology and vital rates of four species: Micronesian Myzomela (*Myzomela rubratra*), Rufous Fantail (*Rhipidura rufifrons saipanensis*), Bridled White-eye (*Zosterops conspiculatus saypani*), and Golden White-eye (*Cleptornis marchei*). We also assessed seasonality of habitats using local (Saipan International Airport) rainfall data and remote-sensed vegetation data (enhanced vegetation index [EVI] from the MODIS instrument of the NASA Terra satellite), and we tested hypotheses relating EVI covariates to avian breeding phenology and vital rates. EVI values varied substantially among stations, between wet (highest in Oct-Nov) and dry (lowest in Mar-May) seasons, and among years. EVI values were positively related to monthly rainfall. We captured individuals in breeding condition in all months with some evidence of breeding peaks in Feb-Jun and to a lesser degree in Oct-Nov (but variable among years). Probability of capturing an individual in breeding condition was positively related to deviation of EVI from monthly mean values (based on multi-species model and single-species models for Bridled White-eye and Golden White-eye). Breeding productivity (probability of capturing a hatching-year bird) in Apr-Jul varied substantially among years (all target species) and stations (Rufous Fantail and Golden White-eye). Productivity of Rufous Fantail, Bridled White-eye, and Golden White-eye was strongly related to wet- and dry-season deviation from year- and station-specific EVI. Annual survival was variable among sites (all species) and years (Rufous Fantail and Bridled White-eye). Both Rufous Fantail and Bridled White-eye had especially low survival in annual interval following especially low dry-season EVI values. These results provide important new insights into spatial and temporal variation in the phenology and vital rates of landbirds on Saipan and their habitats. Continuation of the TMAPS program into the future will help to ensure that information needs critical for guiding the conservation of this insular avifauna continue to be met.

Key words: Barker model, *Cleptornis marchei*, capture-recapture, enhanced vegetation index, mist-netting, *Myzomela rubratra*, *Rhipidura rufifrons*, survival, productivity, *Zosterops conspiculatus*.

Introduction

Oceanic islands are typically characterized by high levels of species endemism and extinction risk (Kier et al. 2009). Island species face a variety of threats, including habitat loss and conversion, exotic invasive species, and climate change (Brooks et al. 2002, Benning et al. 2002). Despite the important role of islands in maintaining global biodiversity, data applicable to the management and conservation of these species are rare, and most research and monitoring has concentrated on a very limited number of islands and species (e.g., de Lima et al. 2011).

The Northern Mariana Islands are home to 23 native landbird species, of which 16 are considered ‘range-restricted’ (range < 50,000 km²) and 10 are endemic to the archipelago (Stattersfield et al. 1998). Birdlife International (2014) suggests that nine of these species are globally threatened; however, few data exist on the status, trends, phenology, and demography of these species. Status and trend data consist mainly of three widely spaced island-wide point-transect distance sampling surveys conducted between 1982 and 2007 (Camp et al. 2009) and from DFW roadside bird surveys (following methods of the North American Breeding Bird Survey or BBS; Sauer et al. 2013) conducted quarterly each year since 1991.

Identifying spatial and temporal patterns of demographic variability can provide insights into proximate causes of population change (Saracco et al. 2008). Furthermore, linking demographic variation to environmental factors can provide additional understanding of the ultimate drivers of population change and can be a critical component for developing realistic projections of population persistence in the face of increasingly variable environments (Boyce et al. 2014). Understanding demography and environmental drivers may be critical for conserving island species for which demographic and environmental stochasticity may play important roles in determining population persistence due to small global populations and limited opportunity for rescue from individuals unaffected by local drivers of population change (Pimm 1991). Despite broad acknowledgement of the need for demographic data in conservation, research and monitoring programs that measure population vital rates are rare.

Application of standardized constant-effort mist netting and modern capture-recapture analytical techniques can be an effective means of monitoring demographic rates of many landbird species (DeSante et al. 2005a). Such efforts have been implemented across broad spatial extents in North America and Europe (Robinson et al. 2009). In 2008 we established the Tropical Avian

Monitoring Productivity and Survivorship (TMAPS) program on Saipan, Northern Mariana Islands, following protocols developed for the Monitoring Avian Productivity and Survivorship (MAPS) program in North America (DeSante and Kaschube 2009), and we have operated this program in each year since that time.

Here we describe the results of the first five years of the Saipan TMAPS monitoring effort (2008 – 2012), highlighting the importance of seasonal and annual variation in this system. In particular, we provide data on the breeding phenology and vital rates (productivity, survival) of four landbird taxa: one species that occurs throughout Micronesia, Micronesian Myzomela (*Myzomela rubratra*); two that are subspecies that occur only on the islands of Saipan and Tinian, Rufous Fantail (*Rhipidura rufifrons saipanensis*) and Bridled White-eye (*Zosterops conspiculatus saypani*); and one species endemic to Saipan and Aguiguan (extirpated from Tinian), Golden White-eye (*Cleptornis marchei*) (Schodde and Mason 1999, Slikas et al. 2000, Pratt 2010). Rufous Fantail and Golden White-eye are of particular conservation concern due to evidence of recent population declines (Camp et al. 2009). In addition to documenting spatial and temporal patterns in avian breeding and vital rates, we examined patterns of vegetation seasonality related to rainfall and links between plant productivity and avian breeding probabilities and vital rates.

Methods

Study areas and field methods

We established six mist-netting stations in typical habitats utilized by landbirds on Saipan (Table 1; Fig. 1). The island is composed of raised, terraced limestone formations culminating in a north-south ridgeline, with flat reefs along shorelines, associated pocket beaches, and a reef enclosed lagoon. Land cover types typical of the island include native limestone evergreen forest, mixed evergreen forest, tanga-tanga (*Leucaena leucocephala*) scrub, coastal scrub or strand vegetation, tropical savannahs, and swordgrass (*Miscanthus floridulus*) thickets. Selection of mist-netting stations was based upon two factors: 1) stations were composed of habitat that is representative of those typical of Saipan and the nearby islands of Tinian and Rota; 2) chosen

stations had a high likelihood of remaining intact during the proposed five year duration of the project.

Each mist-netting station consisted of a sampling area of about 20 ha. Within the central 8 ha of each station, eight to ten 12-m \times 2.5-m, 30-mm mesh, 4-tier nylon mist nets were erected at fixed net sites. We operated each station on one day per 10-day period from 13 April-17 July 2008, 11 April-15 July 2009, 21 February-9 October 2010, 23 March-28 July 2011, and 1 April-13 July 2012 according to the standardized protocol used in the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2009, Desante et al. 2014). During July 2011 through March 2012 we operated stations on a different schedule according to our Monitoreo de Sobrevivencia Invernal (MoSI) program (DeSante et al. 2005b). Under this scheme each station is operated for one pulse of three consecutive days, once per month, in order to be able to analyze survivorship with more precision using mark-recapture analyses between pulses rather than seasons. We intended to operate nets for six morning hours per day of sampling (beginning at 05:30 AST). However, inclement weather (mostly high sun and wind exposure) and high capture rates at some sites resulted in slightly less and variable effort among stations and years. With few exceptions ($< 3\%$ of birds escaped from nets or were otherwise released unbanded), 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.

Remote-sensed Vegetation Data and Relationship to Rainfall

We summarized Enhanced Vegetation Index (EVI) data (Glenn et al. 2008) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite (<http://terra.nasa.gov/>) to calculate covariates for productivity and capture-recapture analyses. We based summaries on monthly EVI values at 1-km² resolution (MODIS product MOD13A2). Prior to summarizing EVI data and extracting station-scale covariates, we removed cloud and aerosol contaminated pixels based on the quality assurance (QA) layer provided with the monthly EVI files (Saleska et al. 2007).

EVI is a composite metric of vegetation greenness. It captures both structural and seasonal components of habitat quality, including primary productivity (leaf chlorophyll content), leaf area, canopy cover, and vegetation complexity. EVI outperforms other vegetation indices (e.g., Normalized Difference Vegetation Index; NDVI) in complex and humid habitats because it exhibits relatively low saturation at high values (Xiao et al. 2004) and is relatively insensitive to clouds and smoke (Miura et al. 1998, Xiao et al. 2003). Relationships between MODIS-derived EVI and local vegetation conditions have not been extensively studied. Case studies, however, have reported strong relationships between EVI and vegetation features measured on the ground, such as leaf area index (Glenn et al. 2008, Park 2009, Potithea et al. 2010). We extracted station-scale values of EVI that represented interpolated monthly EVI values over the four 1-km² pixels closest to station coordinates (using the 'bilinear' option of the 'extract' function in the 'raster' R package; (Hijmans and van Etten 2012)). These monthly values were used to construct covariates for our avian breeding phenology and demographic analyses.

To better understand the relationship between vegetation productivity and rainfall, we modeled the mean EVI values for the six banding stations during each month between July 2007 and December 2012 as a linear function of the log-transformed total monthly rainfall (in mm) during those months. Rainfall data were collected at the Saipan International Airport weather station and were provided by the NOAA National Climate Data Center (<http://www.ncdc.noaa.gov/>). We lagged rainfall data by 1-month to better match acquisition dates of MODIS data (beginning of the month) and the rainfall data (end-of-month sum). To account for temporal autocorrelation, we included autoregressive terms in the linear model with the corARMA option in the “gls” function in the nlme package (Pinheiro et al. 2013) in R (R Core Team 2013). We used a model with five lags in the autoregressive function because a fifth order model was selected as the most parsimonious based on having the lowest Akaike Information Criterion (AIC) value in a model set including models representing the various possible autoregressive orders; model comparison was accomplished with the “ar” function in R. Results were robust to the autoregressive order, as similar parameter estimates and inferences were obtained using both a fifth- and first-order autoregressive model.

Breeding phenology

To provide a broad overview of breeding phenology, we plotted summed numbers of adult (After Hatch Year or AHY) birds in breeding condition and not in breeding condition by month for each year and target species. Birds were determined to be in breeding condition if they had a cloacal protuberance or brood patch of class 2 or 3 (see DeSante et al. 2014 for detail).

To better understand the link between plant phenology and avian breeding phenology, we constructed generalized linear mixed models that modeled the probability of a captured bird being in breeding condition as a function of the deviation of EVI in the month and year of capture from the monthly mean EVI from Jan 2008-Dec 2012. We included random intercepts for species and individuals in this multi-species model. We standardized the EVI covariate to mean zero and unit variance to facilitate estimation and interpretation. We also examined single species models for each target species that included the EVI covariate and a random effect for individuals. Models were estimated with the “glmer” function in the lme4 package (Bates et al. 2014) in R (R Core Team 2013). We report profile 95% confidence intervals for the EVI effects from the confint.merMOD function in lme4 (although for Bridled White-eye, we report Wald’s confidence intervals due to difficulties in estimating profile confidence intervals for this species).

Avian Productivity

Our analyses of productivity derive from the basic method described in Robinson et al. (2007). We assumed a binomial model for the proportion of young (hatching year) birds in the catch:

$$N_{st}^Y / (N_{st}^Y + N_{st}^A) \sim \text{Bin}(N_{st}^Y + N_{st}^A, p[Y]_{st}),$$

where N_{st}^Y is the number of young individuals captured at station s (where $s = 1, \dots, 6$ stations) in year t (where $t = 1, \dots, 5$ years; 2008-2012), N_{st}^A is the number of adult (after-hatching-year) individuals captured at station s in year t , and $p[Y]_{st}$ is the probability of a of an individual bird captured at station s in year t being a young bird. For summarizing N_{st}^Y and N_{st}^A , we only included individuals captured during the ten 10-d sampling periods that were consistent among the three years (11 April-19 July). Sampling effort during this time was similar among years, ranging from a low of 2,897 net-hours in 2008 to a high of 3,095 net-hours in 2010. We did not include a small

proportion ($< 5\%$ for all target species) of individuals in analyses for which we were unable to determine ages.

We used logit-linear models to test hypotheses about spatial and temporal variation in productivity and habitat (EVI) effects on productivity. To assess support for variation among stations and years, we implemented a general (i.e., most parameterized) model that included station (sta_s) and year ($year_t$) effects as fixed factors represented by as many as $s-1=5$ indicator variables for sta_s and $t-1=4$ indicator variables for $year_t$, an intercept representing the value of $\text{logit}(p[Y]_{st})$ for reference station = BICA (see Table 1, Fig. 1), and reference year = 2008, and a continuous covariate, $pr.ef_{st}$, representing the effect of effort prior to the temporal window defined for the productivity analysis. We calculated $pr.ef_{st}$ as the log-transformed (+1) summed net-hours between the end of the previous year's productivity time window and the start of the current year's productivity time window). We included the $pr.ef_{st}$ effect in models to correct for potential sampling variation due to net avoidance that may have been induced by netting prior to the period over which we summed young and adult captures. We expected that p_{st} might have been positively related to $pr.ef_{st}$ due to the likely greater exposure of adults to sampling (young would have likely been entering the population during the sampling period). We also considered intercept-only (no space or time effect) models, models with only spatial effects, and models with only time effects; each combination was considered with and without effort effects included. We did not consider models with $sta_s : year_t$ interaction terms, as data were insufficient to support fully saturated models, and rankings of stations with respect to numbers of adult and young birds were consistent among years (Saracco, Radley, and Pyle, unpubl. data). We assessed support for the general models and all combinations of reduced-parameter sets based on Akaike's Information Criterion adjusted for small sample size (AIC_c) and AIC_c model weights (w_j , where $j = 1, \dots, 8$ models; Burnham and Anderson 2002). Models were implemented using the "glm" function in the R statistical program and (R Core Team 2013) and model selection, model-averaging, and prediction functions in the R package MuMIn (Barton 2013).

We considered a second set of models to test hypotheses about effects of EVI covariates on productivity. Here our most general model was of the form:

$$\text{logit}\left(p[Y]_{st}\right) = \beta_0 + sta_s + \beta_1 \times pr.ef_{st} + \sum_{i=2}^5 \beta_i \times \begin{cases} evi.w_{st-1} \\ evi.d_{st} \\ evi.w.dev_{st-1} + evi.d.dev_{st} + evi.w.dev_{st-1} : evi.d.dev_{st} \\ evi.mn_s \end{cases}$$

where β_0 is the intercept, sta_s is a random station effect, β_1 is the effect of the effort covariate, $pr.ef_{st}$ (as defined above), and the remaining β_i regression coefficients represented effects of one or more EVI covariates. We included 1-3 potential covariates in models that characterized spatial and temporal variation in EVI. The first of these, $evi.w_{st-1}$, was the year- and station-specific monthly mean EVI during the late wet season (Sep-Nov) prior to the temporal window defined for productivity analyses. The second, $evi.d_{st}$, was the year- and station-specific monthly mean EVI during the late dry season (Mar-May; time period overlapping the time window defined for the productivity analysis). Models including these covariates represented hypotheses that variation in productivity resulted from both structural and seasonal (wet or dry) components of vegetation. We only included one of these two covariates in a given model, as they were highly correlated ($r = 0.669$, d.f. = 28; $P < 0.0001$). We also considered covariates representing deviation of the $evi.w_{st-1}$ and $evi.d_{st}$ values from their station-specific wet and dry season averages across the five years of the study (e.g., for the wet season this would be $evi.w.dev_{st-1} - \overline{evi.w.dev_s}$). We denote these as $evi.w.dev_{st-1}$ and $evi.d.dev_{st}$. These covariates represented hypotheses that productivity varied largely as a function of vegetation productivity during the wet and dry seasons, respectively. To represent the hypothesis that productivity varied as a function of overall vegetation structure and productivity, we considered models with a fifth covariate, $evi.mn_s$, which was the average monthly EVI value across all five years of the study. Covariates were standardized to mean zero and unit variance prior to analysis to facilitate estimation and interpretation.

We assessed support for the EVI covariate models based on AIC_c and AIC_c model weights (w_j , where here $j = 1, \dots, 32$ models; Burnham and Anderson 2002). Models were implemented using the “glmer” function of the lme4 package (Bates et al. 2014) in the R statistical program (R Core Team 2013) and model selection and model-averaging using functions in the R package MuMIn (Barton 2013). We report profile 95% confidence intervals for the EVI effects from the confint.merMOD function in lme4 and plots of interaction effects from the ‘plotLMER3d.fnc’ function in the LMERconveniencefunctions package (Tremblay 2013).

Capture-recapture models

We used models developed for the joint analysis of mark-recapture and resighting-recovery data (Barker 1997, 1999) to model capture-recapture data collected between April 11 and July 19 of each year and recaptures of marked birds occurring between these months (our ‘resighting’ data in the context of the Barker model). We included all individuals in analyses for which ages were determined in the field to HY or AHY. The structure of the ‘Barker models’ allowed us to define sampling periods that spanned sampling periods and protocols that were consistent of each year, while also exploiting recaptures outside of these periods as supplemental data to inform estimation of survival and temporary emigration parameters. Despite their flexibility for handling capture-recapture data in the context of irregular annual sampling, Barker models have received little attention in a purely capture-recapture context (Ruiz-Gutiérrez et al. 2012).

The Barker model includes seven estimable parameters, including: (1) S , annual survival rate; (2) p , recapture probability of a marked individual during a regular sampling period (i.e. between Feb and May); (3) F , probability of site fidelity between years, (4) F' , probability of return for a temporary emigrant (i.e., probability of a marked individual not on the study area in time t returning to the study area in time $t + 1$); (5) r , the probability of recovering a dead marked individual between regular sampling periods (i.e., between May and Feb of the following year); (6) R , the probability of recapturing an individual between regular sampling periods given that the individual survives the interval between regular sampling periods; and (7) R' , the probability of recapturing an individual alive between regular sampling periods, given that the individual dies sometime between those regular sampling periods.

The basic Barker model can accommodate grouping structure and covariates to provide insights into factors that affect vital rates and detection parameters (Barker 1999, Slattery and Alisauskas 2002, Barker et al. 2004). We focused most modeling efforts on the survival parameter, S . We interpret this parameter as apparent, rather than true, survival, as we set the fidelity parameter, F , to 1, and the return parameter F' to zero to facilitate estimation. For all models of S , we included an indicator variable, age , to denote the interval after first capture for individuals banded as HY birds. We considered models for which survival was set as spatio-temporally constant (i.e., $S[.]$ models) as well as models that allowed S to vary as a function of group factors representing $year_t$ (where $S(t)$ represents survival between year t and $t + 1$), and station, sta_s . We

also considered models that only allowed adult birds (i.e. birds marked as AHY or older and birds marked as HY birds in years 2+ after initial capture) to vary by station (sta_s^{AHY}) or year ($year_t^{AHY}$). To test hypotheses about EVI, we included continuous covariates in models that represented EVI effects on survival in adult intervals. EVI effects included $evi.d_{st}^{AHY}$ (mean dry-season [Mar-May] EVI at station s and year t) $evi.w_{st}^{AHY}$ (mean wet-season [Sep-Nov] EVI at station s and year t), $evi.d.dev_{st}^{AHY}$ (deviation of dry-season EVI at station s year t from the 5-yr [2008-2012] mean dry-season EVI at station s), $evi.w.dev_{st}^{AHY}$ (deviation of wet-season EVI at station s and year t from the 5-yr [2008-2012] mean wet-season EVI at station s), and $evi.mn_s^{AHY}$, the mean EVI value across the 5-yr of the study. We considered all combinations of models for S including no space-time effects, station-varying survival, time-varying survival, single EVI covariate effect models, and additive and full interaction models including the $evi.d.dev_{st}$ and $evi.w.dev_{st}$ variables. For the sake of simplicity, we focused modeling efforts here on adult survival; however, future efforts might also consider these effects on young birds.

We modeled the remaining model parameters of the Barker model as follows. First, we set r to zero, because no individuals were ever recovered dead, and no effort was expended in searching for dead birds. A very small number of individuals (16) was either found dead in mist nets, or died prior to release, presumably as a result of injury due to mist-netting. We excluded these individuals from our analysis. We modeled p as either time-constant or as a function of year. We modeled R and R' as constant across space and time, with the exception that we fixed these to zero for the interval between 2008 and 2009 (no netting effort between periods) and for the interval after 2012 (again, no effort after July in 2012).

We compared models using AIC corrected for small sample size, AIC_c , and assessed model support using AIC_c model weights (w_i , where $i = 1, \dots, 33$ models; Burnham and Anderson 2002). Models were run in program MARK (White and Burnham 1999) using the R (R Core Team 2013) package RMark (Laake 2013).

Results

Remote-sensed Vegetation Data and Relationship to Rainfall

Enhanced vegetation index (EVI) values varied among stations, between wet and dry seasons, and among years (Fig. 2). Mean monthly EVI values were lowest at the most southerly and lowest elevation station, OBYA (0.41); and highest at the high-elevation sites, MTAP (0.59) and LATA (0.60). EVI values were lowest late in the dry season (Mar-May) and highest during the late wet season (Oct-Nov; Fig. 2A). The pattern of annual variation in EVI during the dry season was similar among stations, with peaks occurring in 2008 and 2011 and lowest values in 2009 (Fig. 2B). Patterns in annual variation in wet-season EVI were less clear, although all stations except OBYA had relatively high EVI in 2011 (Fig. 2C).

Monthly variation in EVI was positively related to rainfall (Fig. 3). Rainfall and EVI were strongly seasonal with marked wet and dry seasons (Fig. 3A). The rainfall covariate (on log-scale) in our regression model with temporal autocorrelation was highly significant ($\hat{\beta} = 0.020$; $SE = 0.006$; $P = 0.001$; Fig. 3B).

Capture summary and breeding phenology

We recorded 8,004 captures (excluding same-day recaptures) of 5,381 individual birds of 13 species. We were able to determine ages HY or (at least) AHY for 92% (4,938) of all individuals. Rufous Fantail was the most commonly captured species (4,083 captures, representing 51% of the total), followed by Bridled White-eye (1,444; 18% of total), Golden White-eye (1,242 captures; 16% of total), and Micronesian Myzomela (521 captures; 7% of total). Capture rates of aged individuals between Apr 11 and Jul 19 (banding period common among years), expressed as mean number of individuals per 100 net-hours, for each species, age class, and station are presented in Table 2.

Timing and extent of reproduction based on captures of adult birds in breeding condition suggested high variability among species and within and among years (Fig. 4). Relatively few adult Rufous Fantails were captured in breeding condition (5% of adult captures) compared to Micronesian Myzomela (17%), Bridled White-eye (19%), or, especially, Golden White-eye (31%).

Based on our multi-species generalized linear mixed model, probability of capturing a bird in breeding condition was positively related to deviation of EVI in the month of capture from the

five year monthly EVI mean ($\hat{\beta} = 0.29; SE = 0.05; 95\% CI: 0.19 - 0.39$). From single species models, Bridled White-eye ($\hat{\beta} = 1.58; SE = 0.47; 95\% CI: 0.66 - 2.51$) and Golden White-eye ($\hat{\beta} = 0.34; SE = 0.09; 95\% CI: 0.16 - 0.53$) also showed significantly positive EVI covariate effects on probability of captured bird being in breeding condition.

Productivity

Our analysis of capture data from the ten sampling periods that were consistent among years showed substantial evidence of spatial and temporal variation in productivity (Table 3; Fig. 5). We found support for annual variation in productivity for all four focal species ($\sum w_j$ for models including $year_t$ effects ranging from 0.57 for Bridled White-eye to 1.00 for the remaining species; Table 3). Productivity was relatively low in 2008 (lowest year for Golden White-eye) and 2009 (lowest year for the rest; Fig. 5). Variation in productivity among stations was supported for Micronesian Myzomela and Rufous Fantail ($\sum w_j = 1.00$ for models with sta_s effects; Table 3). Micronesian Myzomela productivity was highest at the drier low-elevation station OBYA, while Rufous Fantail productivity was highest at the high-elevation (and high-EVI) station MTAP.

We found strong support for effects of deviation of wet and dry season EVI values from their station-specific seasonal means ($evi.w.dev_{st-1}$ and $evi.d.dev_{st}$) for all species except Micronesian Myzomela, for which we found little support for EVI effects ($\sum w_j < 0.20$ for each EVI covariate). The most well-supported model for Micronesian Myzomela included only the prior effort effect ($pr.ef_{st}$), while the best model for the other three species was the full interaction $evi.w.dev_{st-1} \times evi.d.dev_{st}$ model (Table 4). Each of the three species showing effects of EVI deviation from station-specific seasonal means showed unique responses (Fig. 6). Rufous Fantail productivity was highest when EVI was relatively high in both the wet and dry seasons, while the two golden-eye species showed highest productivity when EVI was relatively high in one season and low in the other. Bridled White-eye showed an overall positive response to EVI (Table 4), such that predicted productivity tended to be high when both wet and dry season EVI were high and low when both were low. In contrast, Golden White-eye showed a somewhat negative response overall (Table 4), with predicted productivity tending to be low whenever seasonal deviation in EVI was similar for wet and dry seasons (Fig. 6).

Capture-recapture analyses

Apparent survival.—We found support for spatial variation in survival for all four target species. The top (lowest AIC_c) model for Micronesian Myzomela and Golden White-eye included only station (sta_s) effects (in addition to age effects, which were included in all models; Table 5). For Micronesian Myzomela, we were able to estimate survival at five stations (all but KIFI), among which estimates were highest at SATA and lowest at KIFI (although 95% confidence intervals overlapped for all stations; Fig. 7). Survival estimates for Golden White-eye were also highest at SATA (although precision was low) and lowest at OBYA (Fig. 7). The top survival model for Rufous Fantail and Bridled White-eye included both station and year ($year_t$) effects (Table 5). Survival estimates for Rufous Fantail were highest at KIFI and lowest at MTAP (here too there was broad overlap in confidence intervals) and highest in 2011 (i.e., the 2011-2012 interval) and lowest in 2009 (i.e., 2009-2010; Fig. 8). For Bridled White-eye, we were able to obtain survival estimates for five of the stations (all but KIFI); among these survival was highest at the SATA station and lowest at OBYA (Fig. 8). We were only able to obtain reasonable estimates of Bridled White-eye survival for the 2009-10, 2010-11, and 2011-12 intervals; as for Rufous Fantail, survival was lowest in 2009-10 and increasing through 2011-12. Although we did not find model-selection support for EVI effects on survival, low survival for Rufous Fantail and Bridled White-eye in 2009 coincided with lowest dry-season EVI values (Fig. 2).

Apparent survival rates were considerably lower on average for HY birds than for AHY birds. From best models that only included age effects, differences were greatest for Micronesian Myzomela with HY survival being only about 1/3 of AHY survival ($\hat{\phi} = 0.154$; $SE = 0.112$; $95\%CI = 0.032 - 0.499$ for HY birds v. $\hat{\phi} = 0.464$; $SE = 0.068$; $95\%CI = 0.336 - 0.598$ for AHY birds). Differences were least for Bridled White-eye, for which survival estimates for space-and time-constant survival for HY birds was about 2/3 of AHY birds ($\hat{\phi} = 0.236$; $SE = 0.084$; $95\%CI = 0.109 - 0.437$ for HY birds v. $\hat{\phi} = 0.372$; $SE = 0.050$; $95\%CI = 0.280 - 0.474$ for AHY birds). Differences were intermediate for Rufous Fantail ($\hat{\phi} = 0.322$; $SE = 0.033$; $95\%CI = 0.261 - 0.390$ for HY v. $\hat{\phi} = 0.559$; $SE = 0.016$; $95\%CI = 0.527 - 0.591$ for AHY

birds) and Golden White-eye with HY ($\hat{\phi} = 0.316$; $SE = 0.075$; $95\%CI = 0.189 - 0.478$ for HY v. $\hat{\phi} = 0.569$; $SE = 0.035$; $95\%CI = 0.499 - 0.636$ for AHY birds).

Recapture probability.—Model-selection results suggested that recapture probability was time-constant for Micronesian Myzomela (Table 5; estimate from top model: $\hat{p} = 0.206$; $SE = 0.048$; $95\%CI = 0.127 - 0.314$) and Golden White-eye ($\hat{\phi} = 0.203$; $SE = 0.028$; $95\%CI = 0.154 - 0.263$ for AHY birds). For Rufous Fantail and Bridled White-eye, we found support for time-variation in recapture probability (Table 5; Fig. 9).

Discussion

The first five years of the Tropical Avian Productivity and Survivorship (TMAPS) program on Saipan have provided new insights into the timing and extent of molt (Pyle et al. 2008, Radley et al. 2011, Junda et al. 2012) and breeding, and into the demography of this insular avifauna. For target species examined here, we show the timing and extent of breeding and vital rates to be highly variable among years and sites. Additionally, we show that forested habitats of Saipan are highly seasonal with respect to plant productivity and that this seasonality appears to drive patterns of breeding and productivity for at least some landbird species. Adult survival rates were also highly variable among sites and/or years.

Although we found generally distinct seasons defined by patterns of annual rainfall and vegetation greening, there was also substantial variation among sites and years. Accordingly, the timing of captures of birds in breeding condition appeared to vary among years (although complete annual data not available for all but the 2011-2012 season). There was some indication of two seasonal peaks in breeding, one during the dry season and another smaller peak during the wet season. This pattern was not strong, however, and we recorded individuals of target species in breeding condition in all months (with exception of Bridled White-eye, which was not captured in breeding condition in January). These findings extend inferences about breeding timing described by Craig (1996). Our EVI-breeding analysis suggests that plasticity in breeding timing is likely related to responses in vegetation greenness (particularly for the white-eye species). Bimodal peaks in avian breeding coinciding with biannual peaks in rainfall have been shown in other tropical

systems (e.g., Schondube et al. 2003, Diniz et al. 2013); however, continuous or extended breeding seasons are less well-understood.

Extended or bimodal breeding seasons make assessments of breeding productivity difficult, as does inconsistent annual sampling protocols aimed at meeting multiple objectives. Nevertheless, our analyses of breeding productivity during the April-July period suggested strong annual variation for all target species, as well as differences among stations for Micronesian Myzomela and Rufous Fantail. Variation of three of the species (all but Micronesian Myzomela) appeared related to deviation of EVI from mean values during the dry and wet seasons. Each species showed a unique pattern of productivity response to seasonal EVI deviations, a finding that could reflect unique foraging niches or diets that may be linked to variation in vegetation greenness (e.g., Craig and Beal 2001). However, in general, the three species responded positively to vegetation greenness in at least one season.

Variation in annual sampling protocols (due to variation in annual funding and competing objectives) complicated capture-recapture analyses, however, our implementation of Barker capture-recapture models based on a fixed annual sampling period with supplemental recapture data between periods made efficient use of the extra data provided in years with extended sampling (Ruiz-Gutiérrez et al. 2012). In addition, by allowing recapture probabilities to vary as a function of year, we accounted for the potential influence of net avoidance related to extended sampling in some years in affecting recapture rates (Roche et al. 2013). Indeed, annual declines in recapture probability for Rufous Fantail across years, and declines for Bridled White-eye in the last three years, suggest that net avoidance was an important issue affecting recapture probabilities. Declines in recapture probability for Bridled White-eye are especially problematic because capture probability appears to be generally low for this species (possibly resulting from their tending to forage in vegetation strata above mist-net level Craig 1990).

Capture-recapture analyses showed strong spatial (all species) and temporal (Rufous Fantail and Bridled White-eye) variation in apparent survival rates. Although we did not find strong model support for EVI effects on survival, apparent survival rates for Rufous Fantail (and to some extent Bridled White-eye) were especially low for the 2009-10 survival period following especially low dry-season EVI in 2009. Nevertheless, we have only begun to explore relationships between survival (both adult and young), movement (temporary emigration), and seasonality of habitats. Sampling protocols initiated in 2013 will be more conducive to assessing the importance

of conditions during dry and wet seasons in influencing seasonal survival and movement patterns (Saracco et al. 2014).

Given the dearth of data on Micronesian landbirds (Craig 1990, 1996, 2002, Rodda et al. 1998, Craig and Beal 2001, Mosher and Fancy 2002, Sachtleben et al. 2006, Camp et al. 2009), establishment and implementation of the TMAPS program on Saipan represents a significant advance in informing the conservation of these species. The need for understanding the dynamics of landbird vital rates is pressing given the many threats to the persistence of these populations such as those associated with habitat loss the potential introduction of brown tree snake, *Boiga irregularis* (Rodda et al. 1998; Camp et al. 2009), and the general vulnerability of small endemic island taxa. There is also a critical need to better understand links between climate and phenological and demographic responses of species on the island given projections of warmer, wetter (and potentially more variable) conditions in the coming decades (Collins et al. 2010, van Oldenborgh et al. 2013). Continuation of TMAPS on Saipan in a manner that can efficiently and effectively address information needs into the future will be an important tool for meeting pressing conservation challenges into the future (Saracco et al. 2014).

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Table 1. Station names, codes (see Fig. 1 for locations), major habitat types, geographic coordinates, elevations, and summary of annual effort for the six mist-netting stations operated on Saipan during 2008-2012.

Station	Code	Habitat	Latitude, longitude	Elev. (m)	Effort (net-hours) ^a				
					2008	2009	2010 ^b	2011 ^b	2012 ^b
Bird Island Conservation Area	BICA	Tangantangan (<i>Leucaena</i> <i>leucocephala</i>) forest	15° 15' 45" N, 145° 48' 50" E	30	572.3	574.2	1407.7 (583.7)	1590.0 (567.3)	1066.7 (535.0)
Laderan Tangke	LATA	Lowland tropical rainforest and tangantangan forest	15° 15' 10" N, 145° 47' 54" E	207	520.5	522.2	1379.8 (584.0)	1579.0 (534.7)	1116.7 (537.3)
Sabana Talofofo	SATA	<i>Casuarina</i> savannah with swordgrass thicket	15° 13' 07" N, 145° 45' 44" E	161	414.7	429.0	1102.8 (463.5)	1351.0 (470.7)	957.3 (477.3)
Kingfisher	KIFI	Lowland tropical rainforest with riparian zone	15° 13' 02" N, 145° 46' 37" E	23	406.7	450.0	1033.3 (462.7)	1293.8 (450.5)	893.3 (449.3)
Mount Tapochau	MTAP	Submontane tropical rainforest	15° 11' 01" N, 145° 44' 04" E	274	421.7	454.0	1078.3 (462.7)	1295.3 (468.7)	847.3 (456.8)
Obyan	OBYA	Tangantangan forest	15°06'31"N, 145°43'49"E	1	561.2	543.5	1314.8 (539.0)	1594.3 (574.3)	1077.5 (518.5)

^a 1 net-hour = 1 12-m × 2.5-m mist net open for 1 hr.

^b Numbers in parentheses represent net-hours operated during the 10 sampling periods that were consistent among years (11 April-19 July).

Table. 2. Mean annual capture rates (birds/100 net-hours) of aged birds (young or adult) for all species captured from Apr 11- Jul 19 of each year at the six mist-netting stations operated on Saipan across the five years 2008-2012.

Species	Station											
	BICA		LATA		SATA		KIFI		MTAP		OBYA	
	Young	Adult	Young	Adult	Young	Adult	Young	Adult	Young	Adult	Young	Adult
Yellow Bittern (<i>Ixobrychus sinensis</i>)	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Philippine Turtle-Dove (<i>Streptopelia bitorquata</i>)	0.00	0.10	0.00	0.19	0.00	0.00	0.00	0.09	0.00	0.05	0.04	0.07
White-throated Ground-Dove (<i>Gallicolumba xanthonura</i>)	0.18	0.60	0.07	0.34	0.00	0.17	0.09	1.35	0.04	0.26	0.07	0.11
Mariana Fruit-Dove (<i>Ptilinopus roseicapilla</i>)	0.00	0.11	0.00	0.04	0.00	0.18	0.00	0.00	0.00	0.09	0.04	0.03
Collared Kingfisher (<i>Todiramphus chloris</i>)	0.50	1.31	0.26	1.77	0.00	0.13	0.04	1.20	0.09	0.53	0.22	0.33
Micronesian Myzomela (<i>Myzomela rubratra</i>)	0.40	2.36	0.62	0.89	1.01	3.47	0.09	0.98	0.48	1.23	0.40	0.29

Table 2, continued.

Species	Station											
	BICA		LATA		SATA		KIFI		MTAP		OBYA	
	Young	Adult	Young	Adult	Young	Adult	Young	Adult	Young	Adult	Young	Adult
Rufous Fantail (<i>Rhipidura rufifrons</i>)	4.25	14.95	4.08	19.86	0.35	1.84	1.20	7.44	3.36	5.20	4.81	16.39
Nightingale Reed-Warbler (<i>Acrocephalus luscini</i> a)	0.00	0.39	0.04	0.26	0.09	0.52	0.00	0.00	0.00	0.13	0.00	0.00
Bridled White-eye (<i>Zosterops conspicillatus</i>)	0.64	3.99	1.36	5.18	0.57	1.78	0.13	0.49	0.68	2.77	1.95	7.41
Golden White-eye (<i>Cleptornis marche</i> i)	2.44	9.81	1.32	4.69	0.17	0.58	0.53	3.21	1.05	4.32	0.22	0.76
Micronesian Starling (<i>Aplonis opaca</i>)	0.07	0.28	0.11	0.26	0.04	0.46	0.13	0.19	0.00	0.30	0.00	0.07
Orange-cheeked Waxbill (<i>Estrilda melpoda</i>)	0.04	0.44	0.00	0.07	0.00	0.36	0.00	0.00	0.00	0.04	0.00	0.77
Eurasian Tree Sparrow (<i>Passer montanus</i>)	0.00	0.00	0.00	0.00	0.04	0.54	0.00	0.00	0.00	0.00	0.00	0.00

Table 3. Model selection results for models assessing support for spatial and temporal variation in productivity for four target species captured from Apr 11- Jul 19 of each year at the six mist-netting stations operated on Saipan across the five years 2008-2012. Only lowest AIC_c models and models within 2 AIC_c points of the best model are shown.

Species	Model	No. parameters	ΔAIC_c	AIC_c weight (w_j)
Micronesian Myzomela	$sta_s + pr.ef_{st}$	7	0.00	0.45
	$sta_s + year_t$	10	0.52	0.34
	$sta_s + year_t + pr.ef_{st}$	11	1.56	0.21
Rufous Fantail	$sta_s + year_t$	10	0.00	0.71
	$sta_s + year_t + pr.ef_{st}$	11	1.82	0.29
Bridled White-eye	$year_t$	5	0.00	0.71
	$year_t + pr.ef_{st}$	6	1.92	0.27
Golden White-eye	$year_t$	5	0.00	0.70
	$year_t + pr.ef_{st}$	6	1.91	0.27

Table 4. Model-averaged standardized regression coefficients (95% confidence intervals) for effects included in top models of model sets examining hypotheses relating the enhanced vegetation index (EVI) to productivity. Model sets were run for four target species captured from Apr 11- Jul 19 at the six mist-netting stations operated on Saipan across the five years 2008-2012.

Species	$pr.ef_{st}$	$evi.w.dev_{st-1}$	$evi.d.dev_{st}$	$evi.w.dev_{st-1} : evi.d.dev_{st}$
Micronesian Myzomela	0.87 (0.52, 1.22)			
Rufous Fantail	0.73 (0.56, 0.91)	0.28 (0.12, 0.45)	0.49 (0.35, 0.62)	0.40 (0.26, 0.54)
Bridled White-eye	0.61 (0.36, 0.87)	0.20 (-0.06, 0.45)	0.22 (0.01, 0.43)	-0.26 (-0.47, -0.04)
Golden White-eye	0.48 (0.19, 0.78)	-0.29 (-0.58, 0.00)	-0.16 (-0.38, 0.06)	-0.58 (-0.82, -0.34)

Table 5. Sample sizes and model selection results for the apparent survival (ϕ) and primary recapture (p) probability parameters from Barker capture-recapture models applied to data on four target species from six mist-netting stations on Saipan, 2008-2012. Only top (lowest AIC_c models) are shown; all other models were > 2 AIC_c points of top models. All models also included an age (HY v. AHY) effect for ϕ .

Species	Initial age captures		Recaptures		Model		No. parameters	AIC_c weight (w_j)
	HY	AHY	Primary	Interval	ϕ	p		
Micronesian Myzomela	69	180	26	24	sta_s	.	10	0.89
Rufous Fantail	423	1058	295	400	$sta_s + year_t$	$year_t$	17	1.00
Bridled White-eye	137	515	31	37	$sta_s + year_t$	$year_t$	17	0.73
Golden White-eye	141	457	87	74	sta_s	.	10	0.39

Fig. 1. Locations of six banding stations operated on Saipan, Commonwealth of the Northern Mariana Islands during 2008-2012. Station codes are defined in Table 1. Inset shows Mariana Island chain, excluding northern islands.

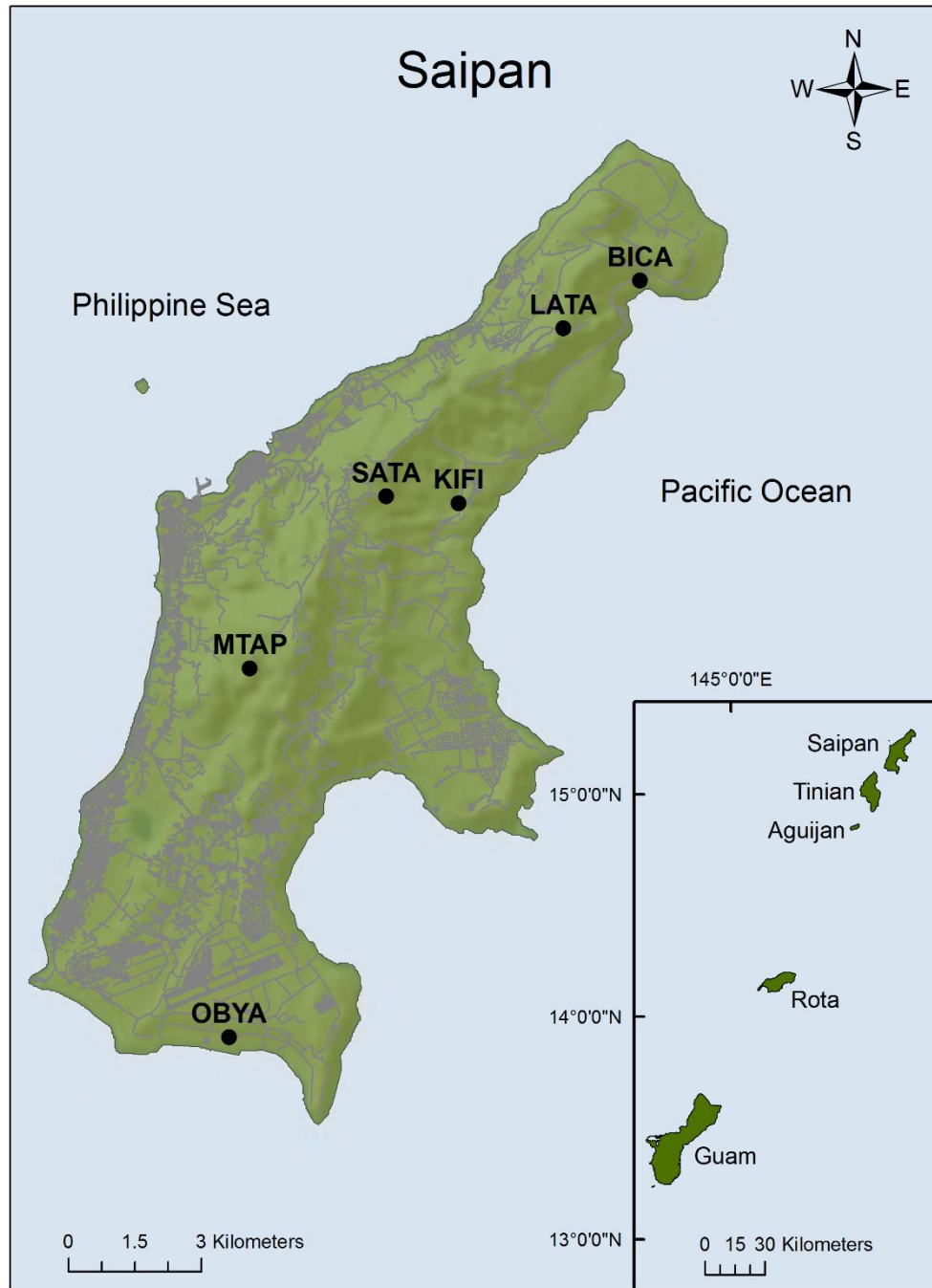


Fig. 2. Distribution of station-scale values of MODIS-derived enhanced vegetation index (EVI) values (A) by month (individual points represent year-specific values for each station; boxplots delineate quartiles with whiskers bounding the 95th percentile) and (B-C) by year during the late dry (B: Mar-May) and wet (C: Sep-Nov) seasons. EVI values represent interpolated monthly EVI values over the four 1-km² pixels closest to station coordinates.

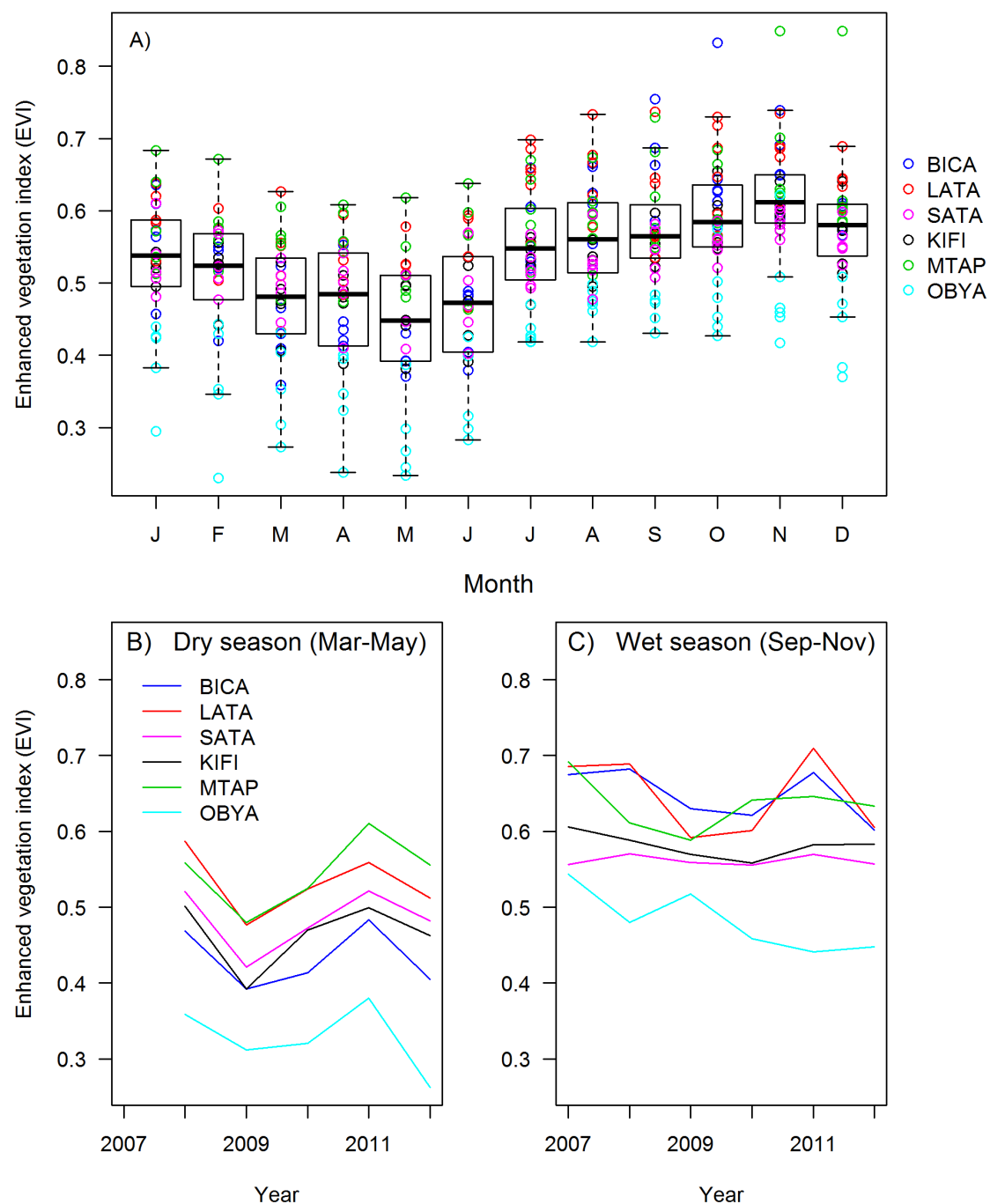


Fig. 3. (A) Time series showing annual and seasonal variation in average monthly enhanced vegetation index values at the six mist-netting stations on Saipan during Jul 2007-Dec 2012 and monthly rainfall recorded at the Saipan International Airport. (B) Relationship between monthly mean EVI and rainfall; curve shows log-linear model fit.

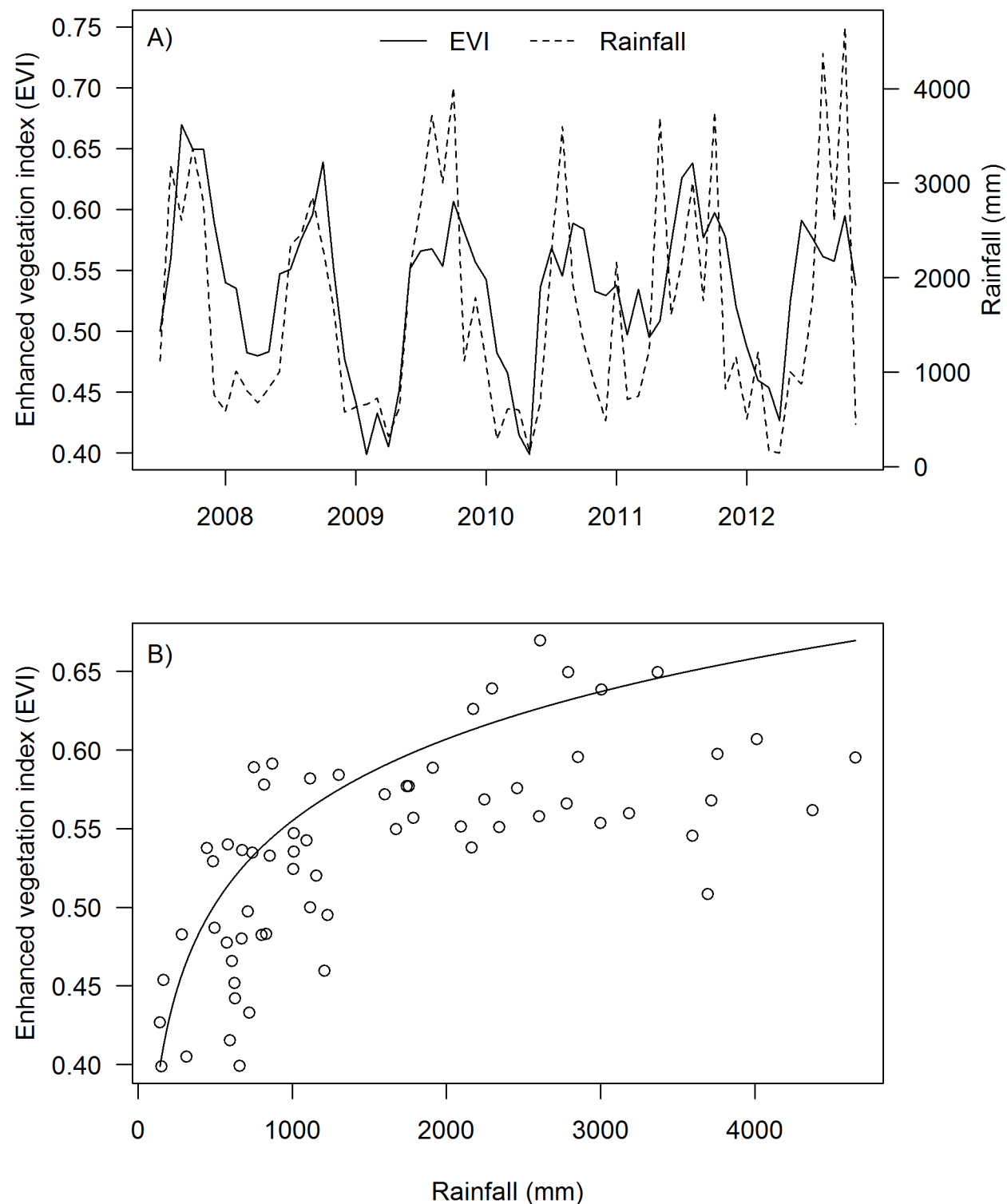


Fig. 4. Numbers of adult captures not in breeding condition (dark shading; "Non-breed") and in breeding condition (light shading; "Breed") by month (typically 3 sampling days/mo) and year at the six mist-netting stations on Saipan during 2008-2012.

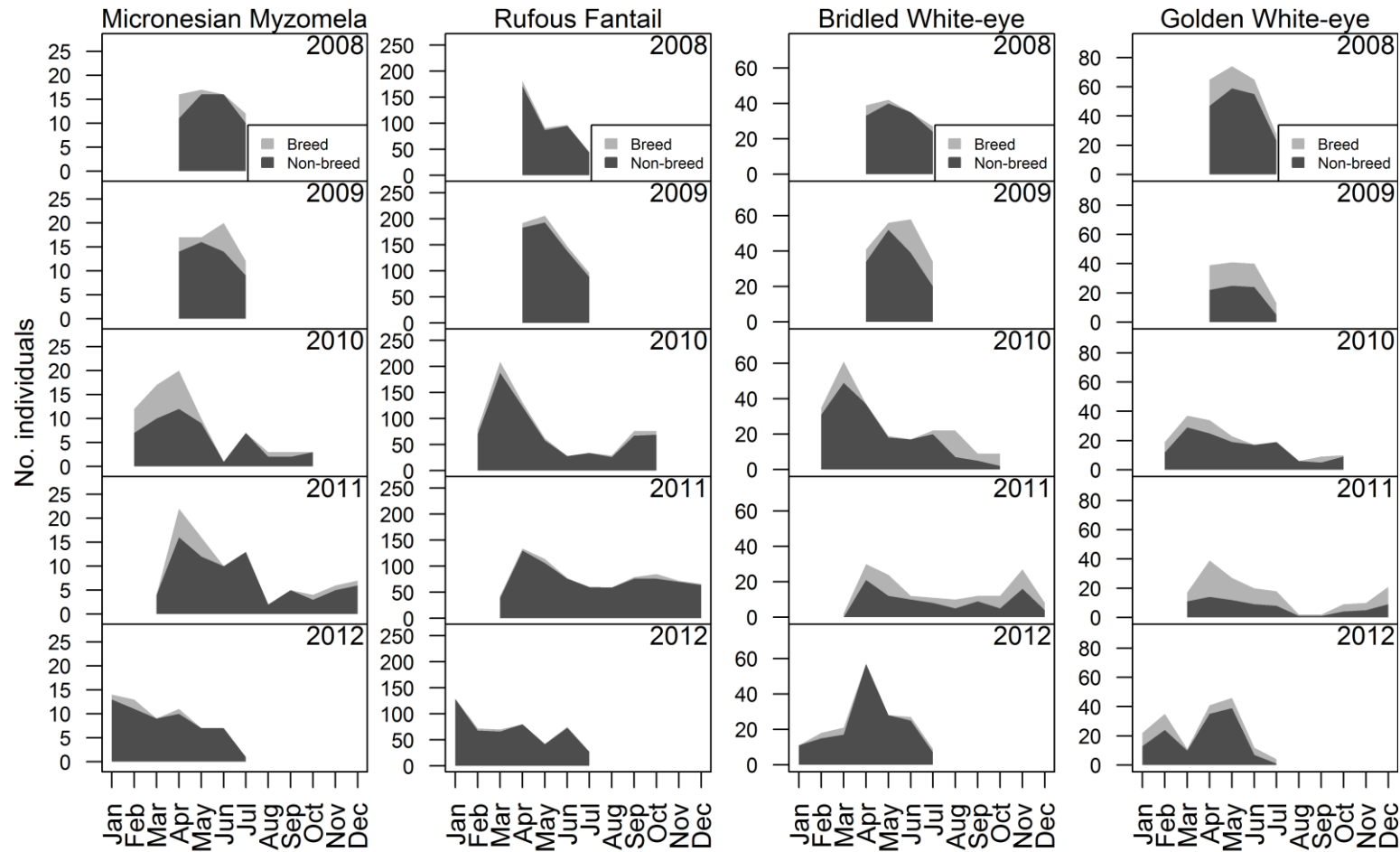


Fig. 5. Estimated productivity index (probability of capturing a young [HY] bird) and 95% confidence intervals derived from model-averaging of 8 logistic regression models assessing spatial and temporal variation in productivity (see Table 3). Models were applied to capture data from 10 sampling periods (11 April-19 July) completed in each of the five years 2008-2012.

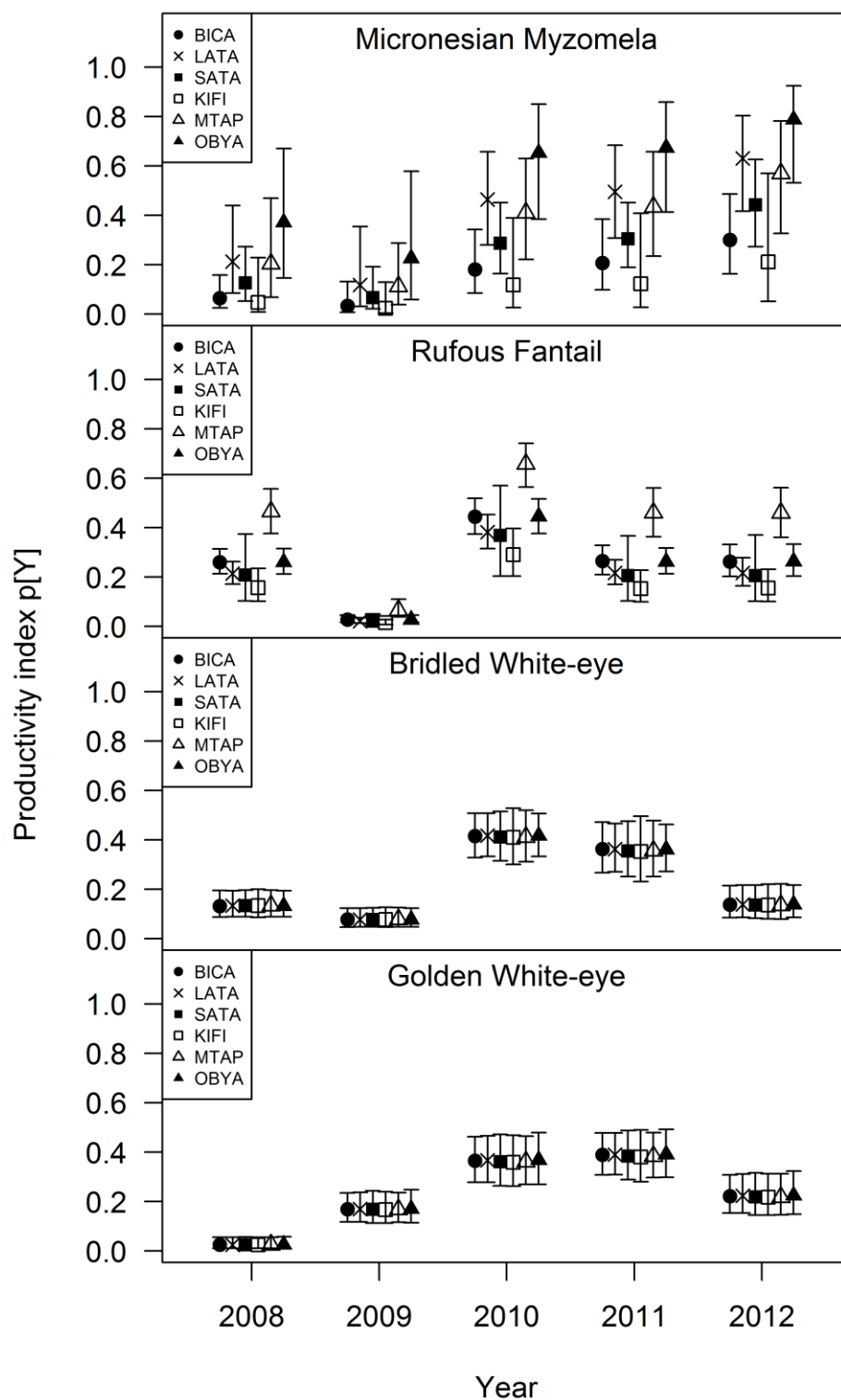


Fig. 6. Predicted productivity in relation to deviation of the enhanced vegetation index (EVI) from 5-year mean values during the late dry (Mar-May; $evi.d.dev_{st}$) and late wet (from previous Sep-Nov; $evi.w.dev_{st-1}$) season from top-performing (lowest AIC_c) models examining EVI effects on productivity for three target species. Predictions are based on capture data collected during the 10 periods (11 April-19 July) sampled in each of the five years (2008-2012).

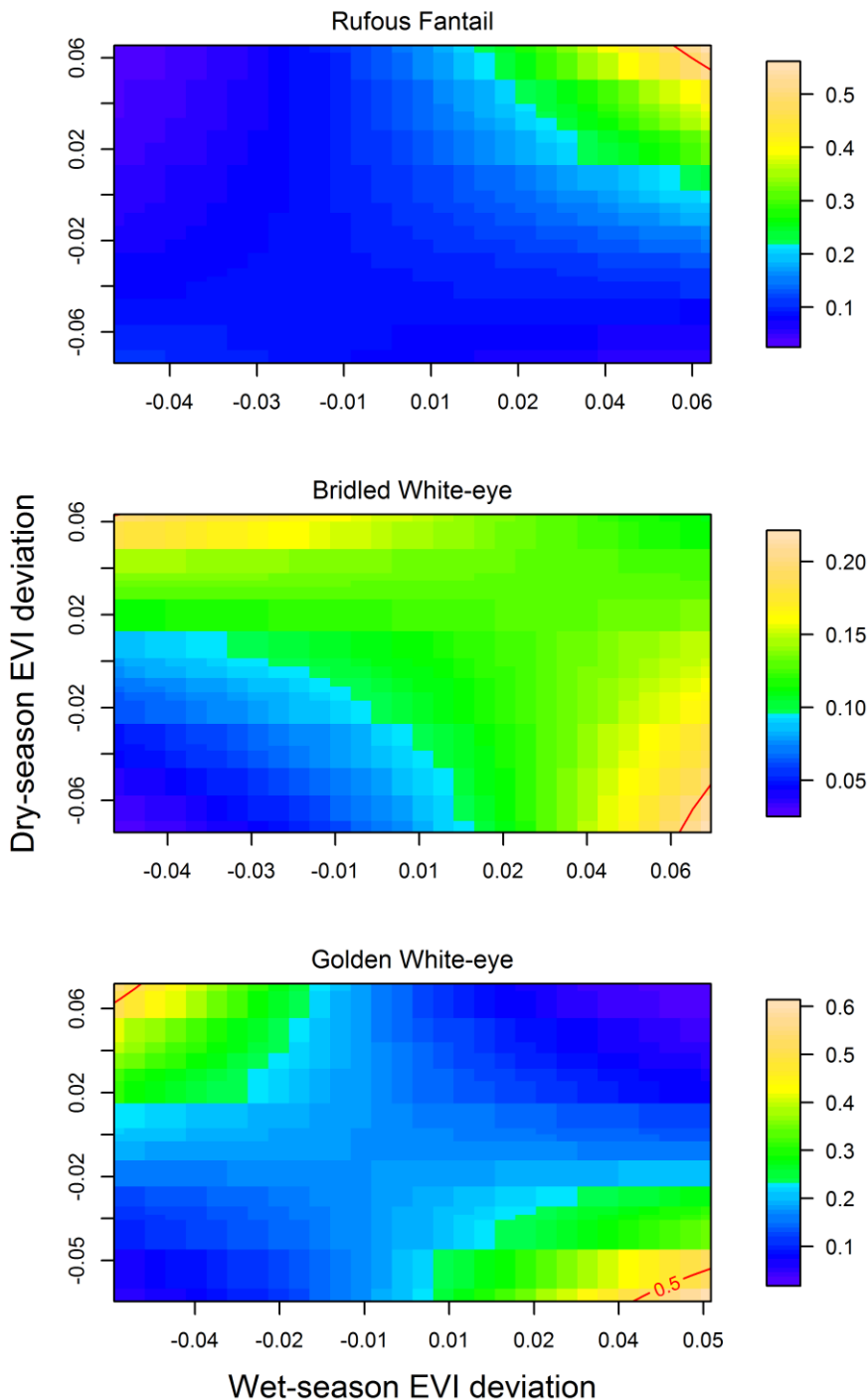


Fig. 7. Estimated annual apparent survival probability ($\hat{\phi}$) for two age classes (HY and AHY) of two target species for which we found support for among-station variation in survival (see Table 4). Estimates were derived from best (lowest AIC_c) Barker capture-recapture models applied to capture-recapture data collected at the six banding stations on Saipan 2008-2012.

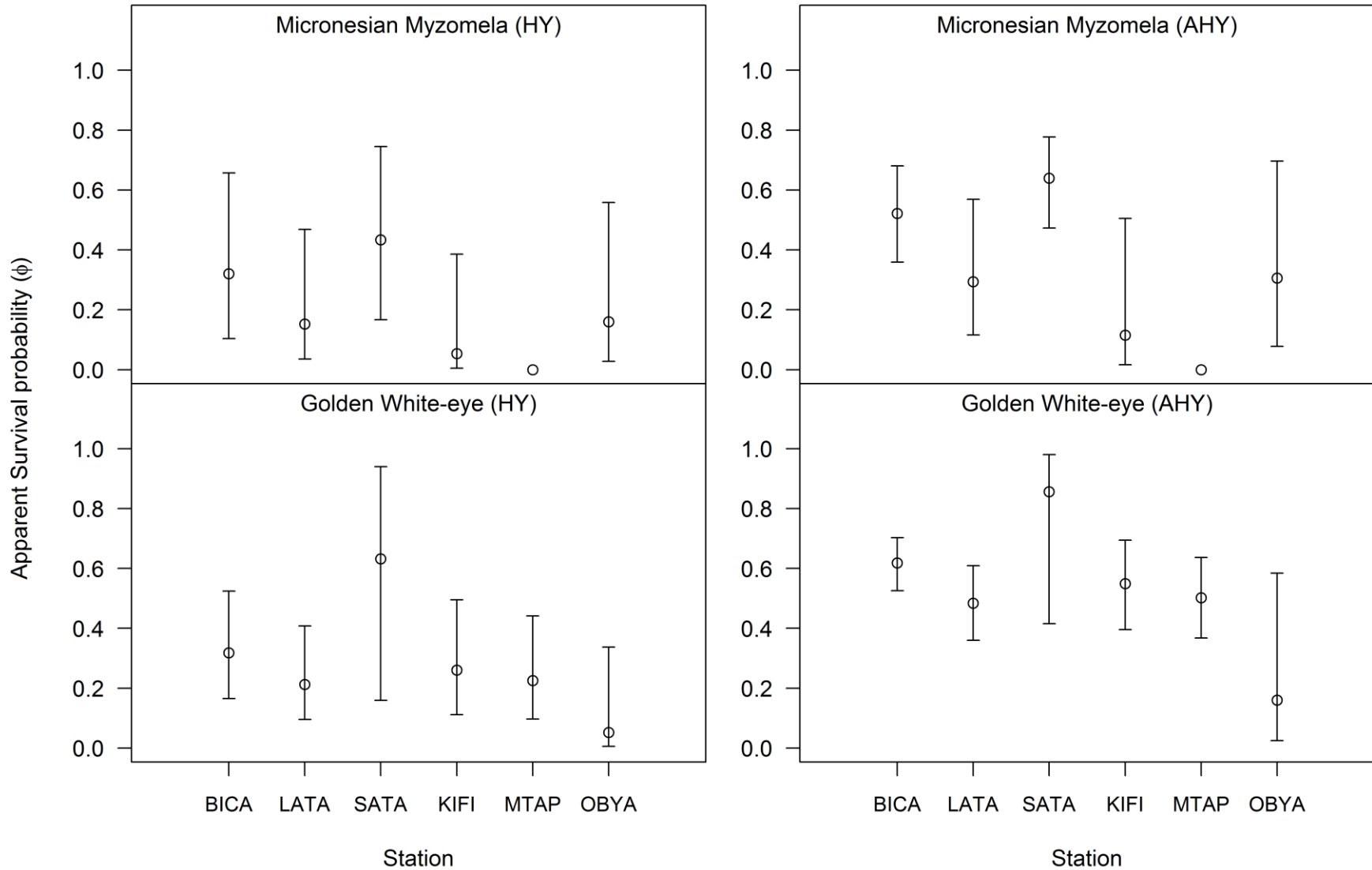


Fig. 8. Estimated annual apparent survival probability ($\hat{\phi}$) for two age classes (HY and AHY) of two target species for which we found support for among-station and among-year variation in survival (see Table 4). Estimates were derived from best (lowest AIC_c) Barker capture-recapture models applied to capture-recapture data collected at the six banding stations on Saipan 2008-2012.

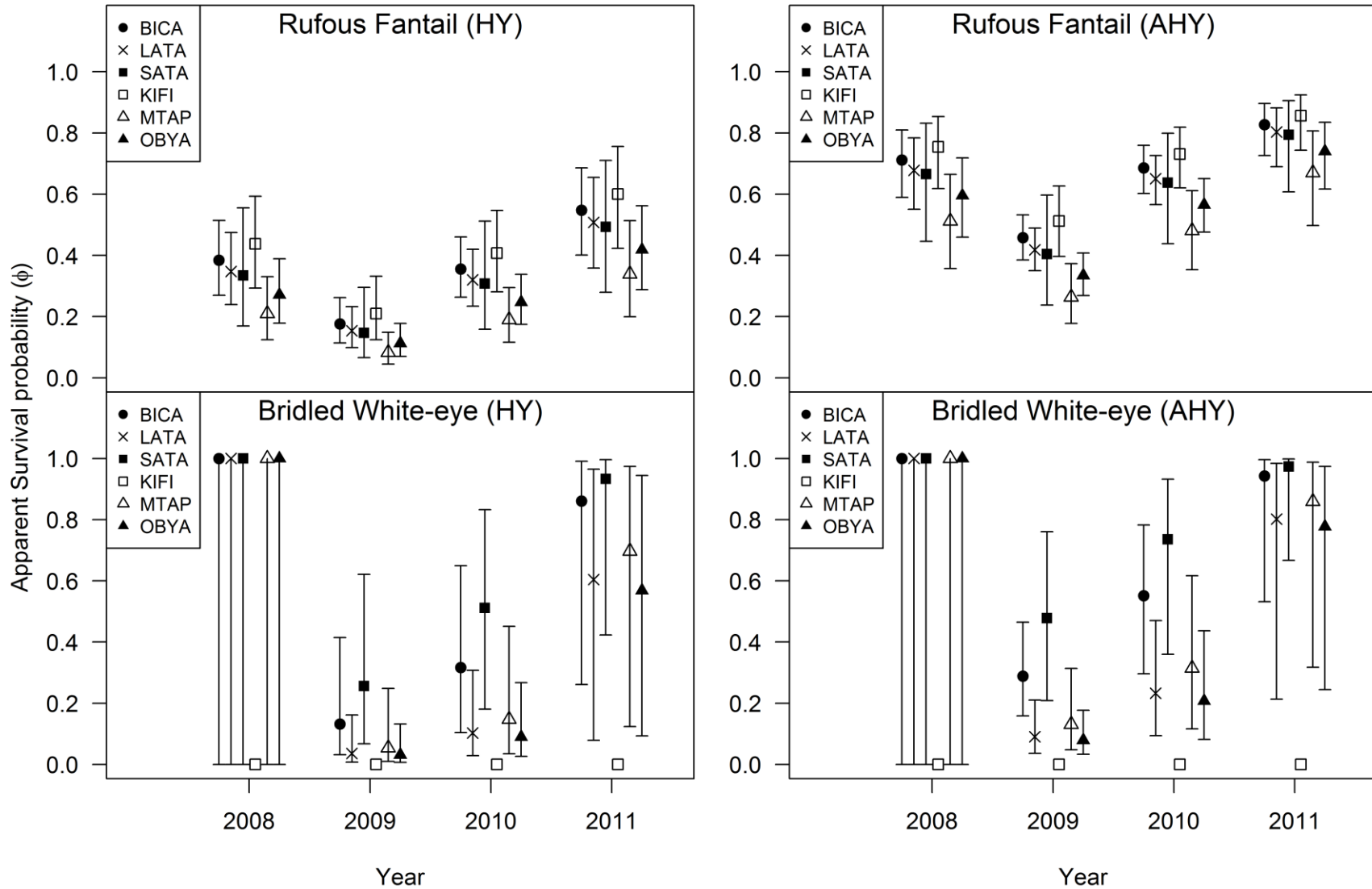


Fig. 9. Estimated recapture probability by year for two species showing evidence of annual variation in recapture probability. Estimates were derived from best (lowest AIC_c) Barker capture-recapture models applied to capture-recapture data collected at the six banding stations on Saipan 2008-2012.

