

# THE IMPORTANCE OF PRODUCTIVITY TO THE DYNAMICS OF A SWAINSON'S THRUSH POPULATION<sup>1</sup>

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**Abstract.** We analyzed the population dynamics of Swainson's Thrushes (*Catharus ustulatus*) breeding at the Palomarin Field Station of the Point Reyes Bird Observatory using 15 years (1980–1994) of long-term, standardized mist-net data. The capture rates of adults and hatching-year birds provided indices of adult abundance and productivity respectively. Annual variation of these indices was high, and linear regression analysis revealed no long-term trends. However, numbers of new and total adults captured in a given year were significantly dependent on the number of hatching-year birds caught the previous year. In addition, per capita productivity was inversely density-dependent and may partially regulate adult abundance. These results suggest that Swainson's Thrushes at Palomarin are most limited by the production of young on the breeding grounds. Return rates of hatching-year birds were exceptionally high compared to other species (18.3%). Strong habitat specificity on the breeding grounds may elevate this return rate and strengthen the link between productivity and adult abundance in this population.

**Key words:** Swainson's Thrush; *Catharus ustulatus*; population; dynamics; limitation; regulation; productivity; constant-effort mist-netting.

## INTRODUCTION

Demographic factors influencing neotropical-nearctic migrant population changes are difficult to investigate due to the distances traversed annually. Also, migrant population limits are poorly understood. Some have suggested that increased over-winter mortality, especially in juvenile birds, due to habitat loss in tropical wintering grounds, is an important factor limiting migrant populations (Morse 1980; Rappole and Warner 1980; Rappole et al. 1989, 1992; Rappole and McDonald 1994). Others have hypothesized that reduced reproductive success resulting from habitat degradation on temperate breeding grounds is important (Wilcove 1985, Hutto 1988, Askins et al. 1990, Sherry and Holmes 1992, Robinson et al. 1995). More recent work has recognized the importance of migration (Moore et al. 1993) and the entire annual cycle (Sherry and Holmes 1993, in press) as potentially limiting periods.

The question, "Where are migrants limited?," is further complicated by the fact that different species may respond differently to land use

changes across their ranges. The potential extinction of the Bachman's Warbler (*Vermivora bachmanii*) has been attributed to the loss of available wintering habitat in Cuban lowlands (Terborgh 1989), while events occurring on the Kirtland's Warbler's (*Dendroica kirtlandii*) breeding range probably led to its declines in the 1970s (Probst 1986). Thus, migrant populations may be limited during a number of periods, and which of these is most important may be species- or site-specific (Sherry and Holmes 1993).

Long-term demographic data for a variety of species throughout their ranges are needed to identify the ecological causes of migrant population limitation, but are rarely available (O'Connor 1991). Most studies of neotropical-nearctic migrant population ecology have been conducted in eastern and central North America (see Keast and Morton 1980, Hagan and Johnston 1992), and demographic data on western populations are especially rare.

Swainson's Thrushes (*Catharus ustulatus*) breed in the northeastern and western United States, and throughout much of Canada. Northeastern populations are declining (Holmes and Sherry 1988, Robbins et al. 1989), while western populations have not shown any trends (Sauer, pers. comm.) and remain poorly understood. We studied a California subspecies (*C. u. oedicus*) which breeds from southern California north through the state's interior and central coast where

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it integrates with the northwest coastal form (*C. u. ustulata*, Phillips 1991). Its winter range is limited to central Mexico south to Nicaragua (Phillips 1991), an area characterized by severe tropical forest loss (Hartshorn 1992).

We investigated the population dynamics of a western Swainson's Thrush population using 15 years (1980–1994) of standardized mist-net data. Specifically, we addressed the hypothesis of summer limitation by investigating the relationship between productivity in one year and adult abundance in the next. We considered potential mechanisms of this relationship by examining hatching-year bird return rates and the influence of adult density on per capita productivity. Lastly, we tested the efficacy of four different indices of adult abundance using capture rates from mist-net data.

## MATERIALS AND METHODS

From 1980–1994, an array of 20 12-m nylon mist nets established at 14 permanent locations operated six to seven days per week, weather permitting, from May to November, and three times per week the remainder of each year as part of ongoing research conducted at the Palomarin Field Station of the Point Reyes Bird Observatory (PRBO), located approximately 28 km NW of San Francisco (Fig. 1). The nets were opened in a standardized manner for six hours per day beginning 15 minutes after local sunrise, thus, 120 net hours were accumulated each full day of netting. Fourteen of the 20 nets were located at eight sites along the edge of a riparian woodland in mixed evergreen forest, while the remaining six nets were located in successional stage coastal scrub adjacent to the riparian woodland (Fig. 1). For a further description of the study site and flora, see DeSante and Geupel (1987).

At Palomarin, Swainson's Thrushes breed almost exclusively in the narrow riparian woodland characterized by California-bay (*Umbellularia californica*), coastal live oak (*Quercus agrifolia*), California buckeye (*Aesculus californicus*), and red alder (*Alnus oregona*). This strong association with riparian woodlands is common in relatively arid regions of the southwestern United States (Grinnell and Miller 1944, Bent 1949, Verner and Boss 1980), and habitats at Palomarin are representative of western Swainson's Thrush breeding habitat.

All birds captured were banded and released

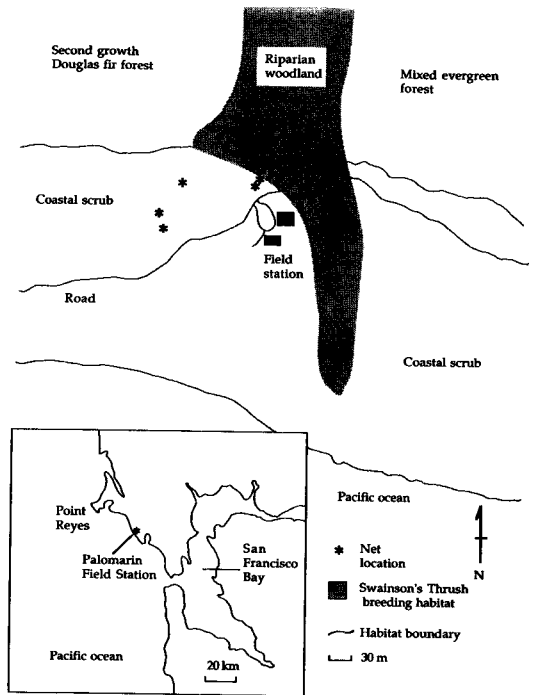


FIGURE 1. Map of study site and net locations.

at the on-site field station. Two age classes were distinguished by the degree of skull pneumatization: juvenile and immature birds in their first calendar years, called hatching-year (HY) birds, and adults in their second or later calendar years, called after-hatching-year (AHY) birds (Pyle et al. 1987). Some new captures (<1.0%) could not be aged because of difficulty in determining the degree of skull pneumatization and were excluded from analyses.

To estimate local productivity, we only included HY birds caught between 15 May and 31 July. The 15 May date was chosen to include the earliest locally produced Swainson's Thrushes, which are first observed in mid-May. The 31 July date was chosen to exclude fall transients. At Palomarin, numbers of summer HY birds peak in mid to late July, rapidly drop in early August, and rise again in late August through September as fall migration begins (Fig. 2). This pattern was consistent between years at Palomarin and a migratory banding station 32 km offshore (Pyle and Henderson 1991). Therefore, we assume most locally produced birds are caught by 31 July, and most fall transients are not. For purposes of comparison, analyses were also conducted with Au-

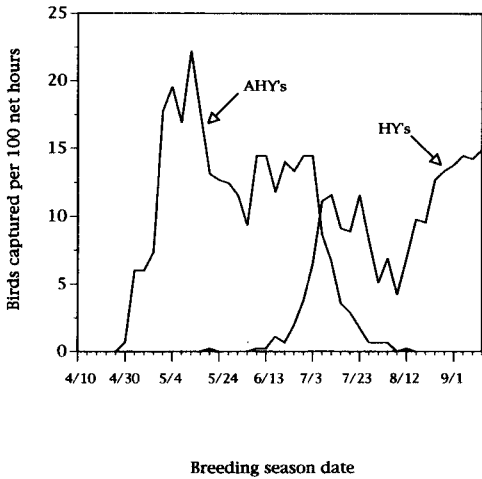


FIGURE 2. Mean number of hatching-year (HY) and after hatching-year (AHY) Swainson's Thrushes captured per 100 net hours from 10 April to 12 September, 1981-1994 (summed over 4-day periods).

gust HY captures included in the index of productivity.

To estimate adult abundance, we attempted to eliminate transients (those birds which pass through Palomarin during their northerly or southerly migrations without staying in the area to breed) and floaters (birds that remain in the general region, but do not establish a persistent territory in which to nest) from the analyses. Adult Swainson's Thrushes typically arrive in late April and capture rates remain relatively high, peaking in early May (Fig. 2). Thus, unlike young birds, a period of predominately transient adults is not evident, prohibiting the elimination of transients based on arrival and departure dates alone. Therefore, we included adults captured between 1 April and 31 July as potentially breeding individuals, and considered four separate indices of adult abundance: (1) total number of adults, (2) number of adults returning between years, (3) number of adults recaptured within a breeding season, and (4) number of adults recaptured within a breeding season over a period of at least seven days. For purposes of comparison, analyses were conducted using all four indices of adult abundance.

To estimate the number of young produced per adult Swainson's Thrush, we divided the total number of HYs by the total number of AHYs captured in a breeding season (DeSante and Geupel 1987, *sensu* Arcese et al. 1992). Lastly, we defined new adults as those birds which were

previously unbanded, and assume they provide an index of the number of one-year-old recruits.

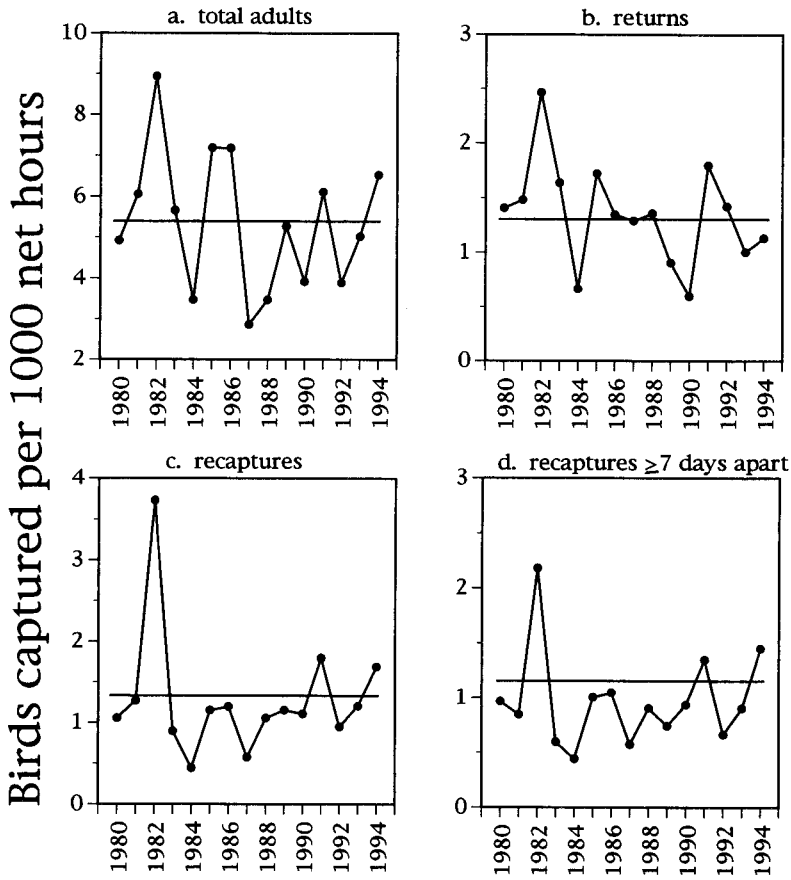
We used standard techniques of parametric statistics (Sokal and Rohlf 1981) and the SYSTAT statistical package (Wilkinson 1989) for our analyses. For linear regressions, we chose independent and dependent variables based on a priori expectations about their relationships from previous research (DeSante and Geupel 1987, Arcese et al. 1992, Sherry and Holmes 1992) and concepts of population biology (Begon and Mortimer 1986, Sinclair 1989).

## RESULTS

For all indices, adult abundance was highly variable over the 15-year study period, and no linear regressions showed significant trends (all  $P > 0.05$ ). However, variability was lower in indices which utilized recapture criteria to index adult abundance (Fig. 3B, C, D; coefficients of variation  $< 0.5$ ) than in the total adults index (Fig. 3A, CV  $> 0.5$ ). Sample sizes were reduced most strongly by using either the number of returns or the number of recaptures over seven or more days (Figure 3B, D). The number of HY birds caught within one breeding season, our index of productivity, was also highly variable, exhibiting no linear trend ( $P > 0.5$ ; Fig. 4).

Although adult abundance varied markedly from year to year, a significant percentage of that variance was attributable to changes in annual productivity. The number of adults captured in a given year was dependent on the number of HYs caught in the previous year for all indices (all  $P < 0.02$ , Table 1, Fig. 5), although the strength of this relationship varied with the index used. The most liberal index, the inclusion of all adults, resulted in the weakest coefficient of determination ( $r^2 = 0.45$ ). Indexing the number of adult breeders as those birds which return between summers (returns) resulted in a slightly higher coefficient ( $r^2 = 0.47$ ), and both indices which used recapture criteria within a summer to estimate adult abundance resulted in the strongest correlations ( $r^2 = 0.62$  and  $0.51$ ; Table 1). Productivity was especially high in 1981 (Fig. 5), but its removal from the analysis did not alter the significance ( $P < 0.05$ ) of any relationship except that between productivity and the number of returns between years ( $P = 0.18$ ).

The relationship of adult abundance to productivity in the previous year was also affected by the capture criterion used to index produc-



### Year

FIGURE 3. Number of AHY Swainson's Thrushes caught per 1,000 net hours as defined by four indices (a-d), 1980-1994: (A) total number of adults, (B) number of recaptures between years, (C) number recaptured within a breeding season, and (D) number recaptured in a breeding season over a period of at least seven days. Horizontal lines indicate 15-year means.

tivity. By including August captures of HY Swainson's Thrushes, the relationship was strengthened only slightly for the "total adults" index, and was weakened for the other three indices (Table 1).

The number of young Swainson's Thrushes produced per adult (per capita productivity) was influenced by the number of adult captures within a given year (Fig. 6). Due to the lack of independence of the axes, we cannot statistically test this relationship. However, approximately two thirds fewer young were produced per adult at peak than at low abundances (Fig. 6).

If density-dependent factors are operating, adult abundance should tend to increase below mean density and decrease when it is above the

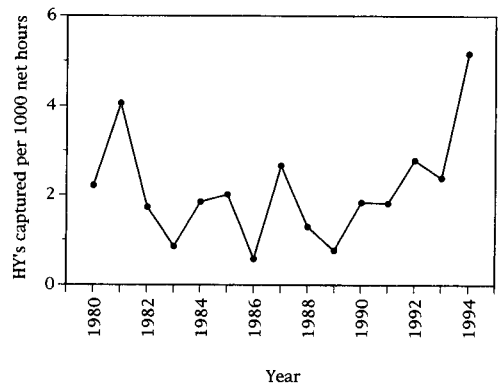


FIGURE 4. Number of HY Swainson's Thrushes captured per 1,000 net hours in a breeding season, 1980-1994.

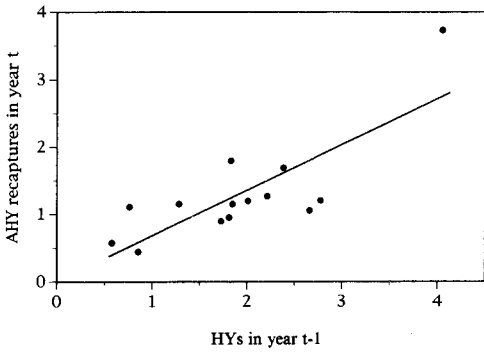


FIGURE 5. Swainson's Thrush adult abundance in year *t* as a function of the number of HYs caught in year *t* - 1 (per 1,000 net hours, 1981-1994). Adult abundance was indexed as the number of recaptures within a breeding season.

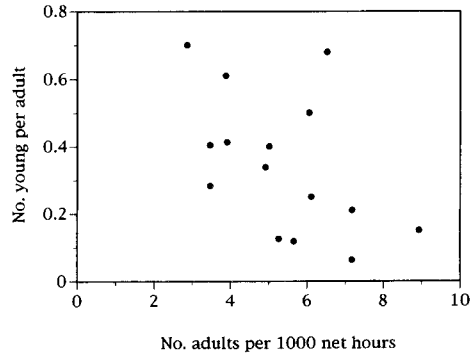


FIGURE 6. Number of young Swainson's Thrushes per adult in relation to the number of adults captured per 1,000 net hours, 1980-1994.

mean (Arcese et al. 1992). Using the number of recaptures to index adult abundance, 11 of the 14 changes in adult abundance were in the predicted direction, that is, toward the 15-year mean (Fig. 3C,  $P = 0.03$ ,  $\chi^2 = 4.57$ , 1 df, chi-square test).

Roth and Johnson (1993) noted that because abundance may affect per capita productivity via density dependence (Fig. 6), a correlation between total productivity and adult abundance is in part an artifact of the total number of breeding adults, and suggest that the relationship between new adults and productivity may be more relevant. The number of new adult Swainson's Thrushes was significantly correlated with the number of HY's captured the previous year (Fig. 7,  $P = 0.03$ ).

From 1981 to 1991, 37 of 202 (18.3%) HY birds banded in a summer were recaptured at Palomarin in a later year (Table 2). The annual return rate values varied from 5.3 to 33.3%, but

were not significantly correlated with year or the number of HYs captured within a year ( $P > 0.05$ ).

DISCUSSION

THE IMPORTANCE OF PRODUCTIVITY

Population limitation results from the sum of density-dependent (regulatory) and density-independent factors that affect rates of production and loss in a population (Begon and Mortimer 1986, Sinclair 1989). Thus, those factors which influence abundance the most strongly may be regarded as limiting factors, and can occur in a specific time (season) or place.

For Swainson's Thrushes breeding at Palomarin, the number of adults in a year was strongly influenced by the number of young produced the previous year (Table 1) and although adult abundance was highly variable (Fig. 3), up to 60% of this variance may be attributed to annual variation in productivity (Fig. 5). This result

TABLE 1. Regression statistics for the relationship between adult abundance in year *t* and productivity in year *t* - 1 (per 1000 net hours, 1981-1994). Four different capture criteria (a-d) were used to index the adult abundance, and the change in the coefficient of determination by including August HY captures in the index of productivity is shown.

Index	Slope	Intercept	F[1, 12]	r <sup>2</sup>	P	Change in r <sup>2</sup>
Total adults <sup>a</sup>	1.27	2.96	9.61	0.45	0.01	+0.08
Returns <sup>b</sup>	0.35	0.67	9.69	0.47	0.01	-0.18
Recaptures <sup>c</sup>	0.68	0.00	19.87	0.62	<0.01	-0.18
Recaptures ≥ 7 days apart <sup>d</sup>	0.31	0.36	12.51	0.51	<0.01	-0.23

<sup>a</sup> Total number of AHYs captured.  
<sup>b</sup> Number of AHYs recaptured between years.  
<sup>c</sup> Number of AHYs recaptured within a breeding season.  
<sup>d</sup> Number of AHYs recaptured within a breeding season over a period of at least seven days.

identifies the relative capacity for productivity to determine abundance and suggests that productivity is the dominant factor influencing this population. In addition, density-dependent per capita productivity (Fig. 6) may regulate the population by acting to return it to mean density. Therefore, we conclude that Swainson's Thrushes at Palomarin are most limited, and at least partially regulated, by the production of young during the summer.

Very few studies of long-distance neotropical-nearctic migrants have investigated the relationship between productivity and adult abundance. Nolan (1978) found that the percentage of adult female Prairie Warblers (*Dendroica discolor*) in a summer population was correlated with productivity in the previous year. Sherry and Holmes (1992) found that fledging success in a year significantly increased yearling recruitment in the next for American Redstarts (*Setophaga ruticilla*), but did not affect the total adult population. Because Swainson's Thrushes lack the delayed plumage maturation present in male redstarts, we cannot as easily detect unbanded one-year-old recruits. However, new adults, which we assume are comprised primarily of one-year-old recruits, were correlated with previous productivity (Fig. 7), suggesting that productivity was affecting the total population by influencing recruitment. Roth and Johnson (1993) found adult abundance to be significantly correlated with the number of local young produced the previous year for Wood Thrushes (*Hylocichla mustelina*), but new adults were not significantly correlated. The Monitoring Avian Productivity and Survivorship (MAPS) program has also shown that adult abundance declined following decreased productivity over a wide range of species and regions (DeSante et al. 1993), although these results are based on only a few years data.

Density-dependence is statistically difficult to demonstrate, except perhaps by using experimental manipulations (Sinclair 1989). However, correlations between indices of reproduction and abundance within years imply density-dependence, and have been found in numerous studies (Nilsson 1987, Arcese and Smith 1988, Torok and Toth 1988), but to our knowledge no such evidence has previously been reported for a neotropical-nearctic migrant. That adult abundance both influenced per capita productivity and changed predictably with respect to the mean, suggests that per capita productivity is negatively

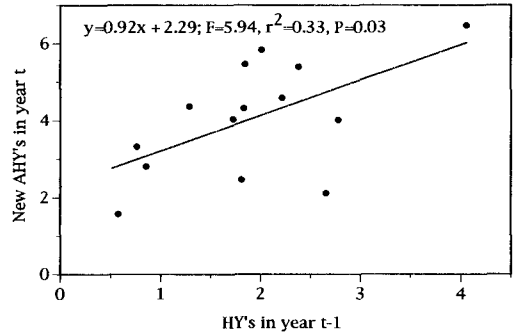


FIGURE 7. Number of new (previously unbanded) adult Swainson's Thrushes captured in year  $t$  as function of the number of HYs produced in year  $t - 1$  (per 1,000 net hours, 1981-1994).

density-dependent (Arcese and Smith 1988, Arcese et al. 1992).

The reasons Swainson's Thrushes breeding at Palomarin are most limited in the summer may be related to their habitat specificity. Sherry and Holmes (in press) stated that a species may be most limited in one season if its habitat use is more restricted in that season relative to other times of the year. Western Swainson's Thrushes are indeed riparian woodland specialists during the breeding season (Grinnell and Miller 1944, Bent 1949, Verner and Boss 1980), but are found in a variety of habitats during migration (Winker et al. 1992), and may be nomadic during the winter (Ramos and Warner 1980, Rappole and Warner 1980). This flexible habitat use in the non-breeding season may lessen the effects of a

TABLE 2. Annual and total Swainson's Thrush HY return rates 1981-1991. Return rate was defined as the percentage of HY birds banded in a summer (May 15-July 31) that returned in a later year.

Year	Number banded	Number returning	Return rate (%)
1981	43	9	20.9
1982	19	1	5.3
1983	9	1	11.1
1984	19	5	26.3
1985	21	2	9.5
1986	6	2	33.3
1987	28	3	10.7
1988	13	3	23.1
1989	8	1	12.5
1990	19	6	31.6
1991	17	4	23.5
Total	202	37	$\bar{x} = 18.3$

severe forest loss occurring in the species' winter range. Thus, Swainson's Thrushes may potentially respond most strongly to annual variation in factors, such as weather or predator density, that influence productivity in temperate breeding habitats.

In addition, it is generally believed that natal dispersal and first-winter mortality combine to result in extremely low HY return rates for migratory passerines (Shields 1984 [Barn Swallow, *Hirundo fulva*, 2%], Payne and Payne 1990 [Indigo Bunting, *Passerina cyanea*, 5.8%], Sherry and Holmes 1992 [American Redstarts 0.6%], Roth and Johnson 1993 [Wood Thrush, 5%]). However, HY Swainson's Thrushes at Palomarin have high return rates (18.3%, Table 2). Our estimates are based on banded young, independent birds rather than nestlings, thus high nesting or dependent fledging mortality may elevate our rates relative to other studies. Nonetheless, identical methodology used on Orange-crowned and Wilson's Warblers (*Vermivora celata* and *Wilsonia pusilla*) at Palomarin have not produced comparable values (PRBO, unpublished data). Swainson's Thrushes in coastal California breed almost exclusively in narrow riparian woodlands (Grinnell and Miller 1944), and the scarcity of this habitat may limit dispersal possibilities, causing young birds to return closer to their fledging sites than other species. As a result, western Swainson's Thrush return rates may more accurately represent recruitment than do return rates of habitat generalists. High HY return rates may be characteristic of other obligatory riparian-nesting species in the west, where riparian forests are patchy and widely distributed. If productivity varies spatially, then this high return rate may strengthen the link between productivity and adult abundance relative to other populations.

#### METHODOLOGICAL CONSIDERATIONS

The results of this study show the importance of careful methodology in the analysis of population dynamics using long-term, standardized mist-net data. First, it is important to understand the seasonal patterns of juvenile captures (see Fig. 2) in establishing capture dates because they may affect comparisons of productivity as it relates to other parameters (Baillie et al. 1986). Although other studies have used later dates in their indices of productivity, such as the inclusion of captures from 1 May to 28 August

(DeSante et al. 1993), inspection of data from Palomarin shows that narrower dates were more effective in the elimination of transient Swainson's Thrushes. An increase in HY captures begins in mid-August and continues into mid-September, indicating the onset of fall migration (Fig. 2). In addition, of 268 Swainson's Thrushes first caught before 1 August of their hatching year, 63 (23.5%) were captured at least once more during the summer. This indicates that these birds were persistent in the area, and were most likely produced locally. In contrast, of 231 birds first captured in August, only 13 (5.6%) were captured again. Thus, HY birds captured in August are probably more transitory and less likely to have been produced locally, and their inclusion in the data set may confound results (Table 1).

We found that the relationship between productivity and adult abundance remained significant for all criteria used to eliminate adult transients and floaters, although the strength of the relationship ( $r^2$ ) was increased by using more effective indices (Table 1). Simply indexing adult abundance with all adults captured undoubtedly includes many transients and floaters. Using either the number of returns or recaptures over a period of at least a week probably eliminates most nonbreeders from the analyses, but these strict criteria greatly reduce sample sizes, may exclude some breeders, and are not practical for small populations or studies with less intensive banding efforts. A study of Swainson's Thrushes migrating through Minnesota showed that mean stop-over durations were less than five days (Winker et al. 1992), and transients are therefore less likely to be recaptured than are breeders. Nur and Geupel (1993) found that most (62%) breeding Wrentits (*Chamaea fasciata*) were caught more than once in a breeding season while most non-breeders (72%) were not, thus, floaters are also effectively removed from the data set by using more liberal recapture criteria. Therefore, we found that using the number of recaptures within a breeding season was the most effective way to index adult abundance using capture rates from mist-net data.

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