Lay Delay in Four Temperate Passerines

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Abstract In many species of birds, the number of days between nest completion and the onset of egg-laying can vary dramatically. This 'lay delay' has been characterized for many species, but reasons for its occurrence are poorly understood. This study examines lay delay in four species of passerines, the western bluebird (*Sialia mexicana*), tree swallow (*Tachycineta bicolor*), violet-green swallow (*Tachycineta thalassina*), and oak titmouse (*Baelophus inornatus*), to determine if temperature, precipitation, wind speed, date of nest completion, or clutch size affect the delay. Nest boxes were checked daily to determine when nest-building ceased and egg-laying commenced. The difference between these two dates was considered to be the lay delay. Daily minimum and maximum temperatures, precipitation, wind speed, and clutch size were also recorded. Minimum temperature had the highest correlation with lay delay, showing very significant correlations for all species except the violet-green swallow. Total precipitation during delay had a significant correlation with lay delay for all species except the oak titmouse. Maximum temperature had a significant correlation with lay delay for the western bluebird and tree swallow, and wind speed correlated significantly with lay delay for the tree swallow and oak titmouse. Date of nest completion correlated significantly with lay delay for three of the species, indicating that individuals who complete their nests earlier in the season have longer delays. Clutch size, however, did not correlate significantly with lay delay for any species, signifying that environmental factors are most likely to affect the timing of onset of egg-laying. However, since 'poor' environmental factors also correlated significantly with date of nest completion, further research is necessary in order to determine whether seasonality in itself or specific environmental factors have the biggest affect on lay delay.

Introduction

Nest-building and egg-laying behaviors of passerines have been studied extensively, but the intervening period is less well known. Once nest-building has been completed, many species wait a number of days before initiating the egg-laying process (e.g., Bent 1942, Stocek 1970, Stutchbury and Robertson 1987). This lay delay is intriguingly variable, and while it has been characterized for some species, reasons for its occurrence remain largely unstudied. This study will examine lay delay in four temperate passerines: the western bluebird (*Sialia mexicana*), tree swallow (*Tachycineta bicolor*), violet-green swallow (*Tachycineta thalassina*), and oak titmouse (*Baeolophus inornatus*). There are two main objectives: first, to characterize the lay delay and its variability in each species; and second, to examine possible correlations between the length of delay and several environmental and biological factors within each individual species. The factors that will be considered are temperature, precipitation, wind speed, date of nest completion, and clutch size.

In order to hypothesize about which processes will most influence lay delay, it is necessary to consider some related aspects of avian biology and behavior. These include but are not limited to: foraging behavior, primary food types, clutch size, number of broods per season, seasonality of egg-laying, and nest-building behavior (Table 1). I will address the expected outcomes related to each factor first in terms of general hypotheses, and then, if differences between species are expected, on a per-species basis.

It is likely that extreme high or low temperatures will, to some extent, affect all species. There are two reasons why this may be true. First, extreme temperatures, especially low temperatures, are known to limit activity and foraging in many species of birds (e.g., Grubb 1978, Clark 1987, Mock 1990). It has been shown that some species' biogeographic distributions are limited by the energy that is needed to survive cold temperatures (Root 1988). Therefore, it seems likely that colder temperatures will slow the process of egg-laying and lengthen lay delay. Also, extreme temperatures may limit availability or quality of food sources. Meijer and Drent (1999) showed that food supplementation "moderately advanced" the timing of egg-laying, probably because egg production requires a substantial nutritional investment. In all four species it is primarily the female who does the nest-building, and she herself must forage for herself during the period of egg-formation. Therefore, if sources of energy are limited by weather, onset of egg-laying may be affected. Since extreme temperatures will likely cause degradation of all food sources, there should be, in all four species, a positive relationship between maximum temperature and length of delay, and a negative relationship between minimum temperature and length of delay. However, species that lay earlier in the season may be less affected by high temperatures, and species that lay later in the season may be less affected by low temperatures and precipitation.

Table 1. Relevant life history aspects of the four study species.

Species	Food	Foraging Behavior	Nest-building Duration	Who Builds the nest	Time of Season	Known Lay Delay	Clutch Size	# Broods/ Season
Western bluebird; WEBL (*Sialia mexicana*)	Breeding season: insects (Guinan et. al 2000).	Takes small arthropods by dropping to ground from low perches; also fly-catches, gleans food from vegetable or tree trunks (Guinan et. al 2000).	Begins mid-mar; first brood: 12.7 days ± -5.9 SD, second brood: 3.6 days ± 3.0 SD (Guinan et. al 2000).	Mostly female; very few instances where male observed nest-building (Guinan et. al 2000).	Nest building begins mid-March in California; egg-laying peaks in late April/early May (Demas 1989).	------	Around 5 eggs (range 2-6).	2
Tree swallow; TRES (*Tachycineta bicolor*)	Mainly flying insects, though vegetable matter is eaten during unfavorable weather conditions (Beal 1918, Hausman 1927).	Forage in open areas over water or ground; pursue prey items in air (Roberts 1932, Tyler 1942).	From a few days to 2 weeks (Cohen 1985a, Stutchbury and Robertson 1987).	Primarily females (Cohen 1985a, Roberts et. al. 1992).	Arrive mid-March to April, nest building usually begins in April (Forbush 1929).	Early-arrivers may wait several weeks to begin laying; late arrivers may begin immediately (Stocek 1970).	4-7	1
Violet-green swallow; VGSW (*Tachycineta thalassina*)	Flying insects exclusively (Brown et. al. 1992).	Aerial foragers. Single report of foraging on ground (Erskine 1984).	A few days to a few weeks (Bent 1942; Edson 1943).	Female gathers most of the nesting material and visits nest box twice as much as male (Comelbellack 1954).	Start nest building around mid-April to mid-May (Edson 1943).	Laying may start before nest is finished, or 1 to 2 days after (Bent 1942; Edson1943)/	4-6	1
Oak titmouse; OATI (*Baeolophus inornatus*)	Plant material and terrestrial invertebrates. 43 % animal and 57 % vegetable (Dixon 1949).	Primary method of capturing insects is gleaning on bark and foliage (Root 1964 and 1967).	4-10 days (Cicero 2000).	Female primarily responsible (Dixon 1949, Roberson and Tenney 1993).	Nest building mid-Mar. through April (Dixon 1949).	------	6-7	1

Precipitation should have a similar effect on all four species: more precipitation following nest-building will correlate with a longer delay, and less (or no) precipitation will correlate with a shorter delay. This is also mainly due to ability to forage and availability of food, and the fact that poor weather limits activity. Because rain may limit the availability of flying arthropods and make aerial feeding difficult, the two species of swallows, which rely on this food source and feed in this manner, will likely be most affected by this factor. The other two species also commonly eat arthropods, but are not aerial predators. Therefore, they will likely be less affected by precipitation. Again, however, seasonality might affect the amount of precipitation, and therefore the early-laying species may be more affected by this variable.

Wind has been shown to limit activity in titmice and other species (Grubb 1978, Wood & Lustick 1989). Therefore, lay delay should correlate positively with wind speed for the oak titmouse. Also, high wind velocities should lengthen lay delay for both species of swallows, since aerial foraging ability will be compromised by wind.

Clutch size should have a positive correlation with lay delay for all four species. The rationale for this is that laying a larger clutch requires more energy and therefore more time spent foraging and recovering after completing the nest-building process. However, in many temperate birds, clutch size is known to decrease throughout the laying season (e.g. Klomp 1970, Winkler & Walters 1983). Therefore, seasonality may have a more important effect on clutch size than lay delay. However, earlier dates of nest completion will likely correlate with longer lay delays. Tree swallow individuals nesting earlier in the season have been shown to have longer lay delays than late-arriving individuals (Table 1). This should also be true for the bluebirds, which lay two clutches in a season. Nest-building duration and lay delay are significantly longer for this species prior to the first clutch, which should remain true in this study (Guinan *et. al.* 2000).

This study aims to characterize lay delay for the four study species and to begin to investigate what factors might affect the duration of the delay. The results will increase understanding of the timing involved in avian nest-building and egg-laying for the four study species.

Methods

Study Site, Study Species, and Materials The study was conducted at the Hopland Research and Extension Center in Hopland, California. The center comprises 5,300 acres of varying topography and vegetation types, including grass, woodland-grass, dense woodland, and chaparral. It is situated in the foothills of the Mayacamas Mountains, and is home to 180 species of wild birds, four of which were used in the study. There are 256 nest boxes situated throughout six pastures, all covering varying topography. The climate during the laying season is fairly temperate, with a cool, rainy early spring, and a hotter, dryer late spring and summer.

The four study species are the western bluebird (*Sialia mexicana),* tree swallow (*Tachycineta bicolor),* violet-green swallow (*Tachycineta thalassina),* and oak titmouse (*Baeolophus inornatus*). All four are temperate, cavity-nesting passerines. The two species of swallows are migratory, while the other species are permanent residents of the area. Information regarding the natural histories of these species can be found in Table 1.

Procedures In order to determine lay delay for the four study species, it was necessary to track the nest-building and egg-laying processes. All nest boxes were checked weekly starting in early March. When nest-building materials began to appear in the nest, the percent completion of the nest was decided according to a pre-determined rubric of the nest-building process. This rubric was different for each species, and was compiled given what is known about the process of and materials involved in nest-building for each species. Once the nest was 75 % complete, it was checked daily. All daily nest activity was recorded after that time, including when the nest reached 100 % completion and the dates on which all eggs were laid. From this data, lay delay was computed (date of first egg - date of 100 % nest completion).

All meteorological data was recorded at two weather stations at the Hopland Research and Extension Center. The first station served three lower pastures, and the second station served three upper pastures. In order to evaluate the effect of extreme temperatures on lay delay, only the maximum and minimum temperature during each individual's delay were used in this study. Precipitation was both averaged and summed during each individual delay, and wind speed was averaged.

Statistical Analyses Analysis of Variance (ANOVA) was used to compare lay delay means between species. Since much of the data were not normally distributed, lay delay data was transformed by taking the $\log_{10}$ of the delay + 1 (to account for many zero values). Regression analyses were performed to look for correlations between that value and the various other variables. To look for differences in the slopes of these regression lines, analyses of covariance (ANCOVAs) were performed on log-transformed lay delay and each variable, with species being the covariate. In addition, stepwise forward multiple regressions were performed for each species to determine which variables accounted for most of the variation in lay delay.

Results

Recorded lay delays ranged between 0 and 25 days for all species (Table 2). The Western bluebird had a longer mean lay delay than the other three species. This difference was significant ($p<0.05$) for the species with the largest sample size of the three, and almost significant ($p=0.08$) for the species with the next largest sample size. There were no other significant differences in mean lay delay between species. Figure 1 shows the distribution of lay delays for all four species.

Table 2. Lay delay in days

Species	**Avg.**	**Min**	**Max**	**N**
Western bluebird	6.07 ± 0.87	0	21	45
Tree swallow	3.84 ± 0.83	0	16	32
Violet-green swallow	2.56 ± 0.90	0	14	16
Oak titmouse	2.90 ± 0.97	0	9	10
All	4.52 ± 0.51	0	21	103

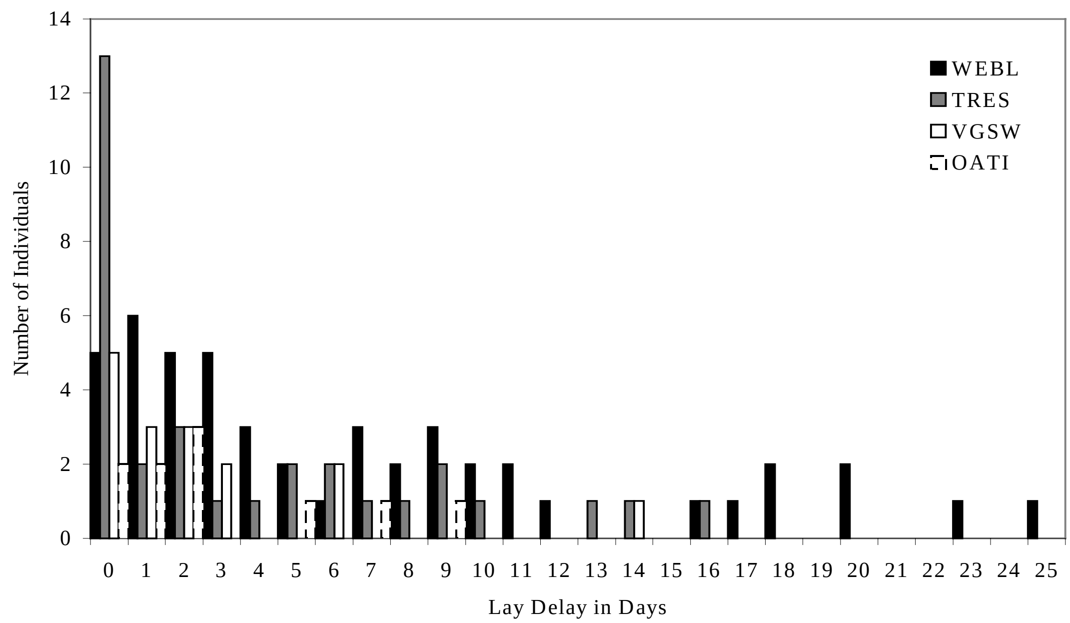

Figure 1. Frequencies of lay delays for all species.

Maximum temperature had a positive correlation with log (lay delay + 1) for both the western bluebird and the tree swallow, and minimum temperature had a negative correlation with log (lay delay + 1) for those two species and also for the oak titmouse (Fig. 2). The sum of precipitation during lay delay had a significant relationship with lay delay for all species except the oak titmouse (Fig. 3). Average wind speed correlated significantly with log (lay delay + 1) for the tree swallow and the oak titmouse (Fig. 4). Average precipitation and clutch size showed no significant correlations for any of the individual species, although clutch size had a nearly significant correlation with log (lay delay + 1) for the tree swallow ($p=0.06$; Figs. 3 & 5). Date of nest completion correlated significantly with log (lay delay + 1) for all species except the violet-green swallow (Fig. 5).

Analyses of covariance performed on significant correlations for each factor revealed few significant differences in regression slopes among species. The western bluebird and tree swallow differed significantly in how log (lay delay + 1) correlated with maximum temperature ($p<0.05$). However, none of the species differed significantly in how log (lay delay + 1) correlated with minimum temperature or sum of precipitation. The oak titmouse and tree swallow differed significantly in the response of lay delay to wind speed, as evidenced by the opposite signs of their slopes and a p-value of <0.01.

Stepwise forward multiple regressions showed that minimum air temperature accounted for 87 % of variation in log-transformed lay delay data for the oak titmouse (Table 3). No other variables were included in the model for that species. Maximum air temperature and sum of precipitation were included in the model for the tree swallow, accounting for 83 % of the variation in lay delay data. Four variables accounted for 74 % of variation for the western bluebird: date of nest completion, maximum air temperature, minimum air temperature, and sum of precipitation. Only sum of precipitation was included in the model for the violet-green swallow, accounting for 50 % of variation in lay delay.

A Pearson correlation test showed several significant correlations among variables. Notably, minimum air temperature correlated significantly with sum of precipitation, date of nest completion, and average wind speed (all $p<0.01$). Both sum of precipitation and maximum temperature showed significant correlations with average precipitation, and date of nest completion correlated significantly with average wind speed (all $p<0.01$). Also important, clutch size correlated significantly with date of nest completion ($r=-0.42$; $p<0.01$).

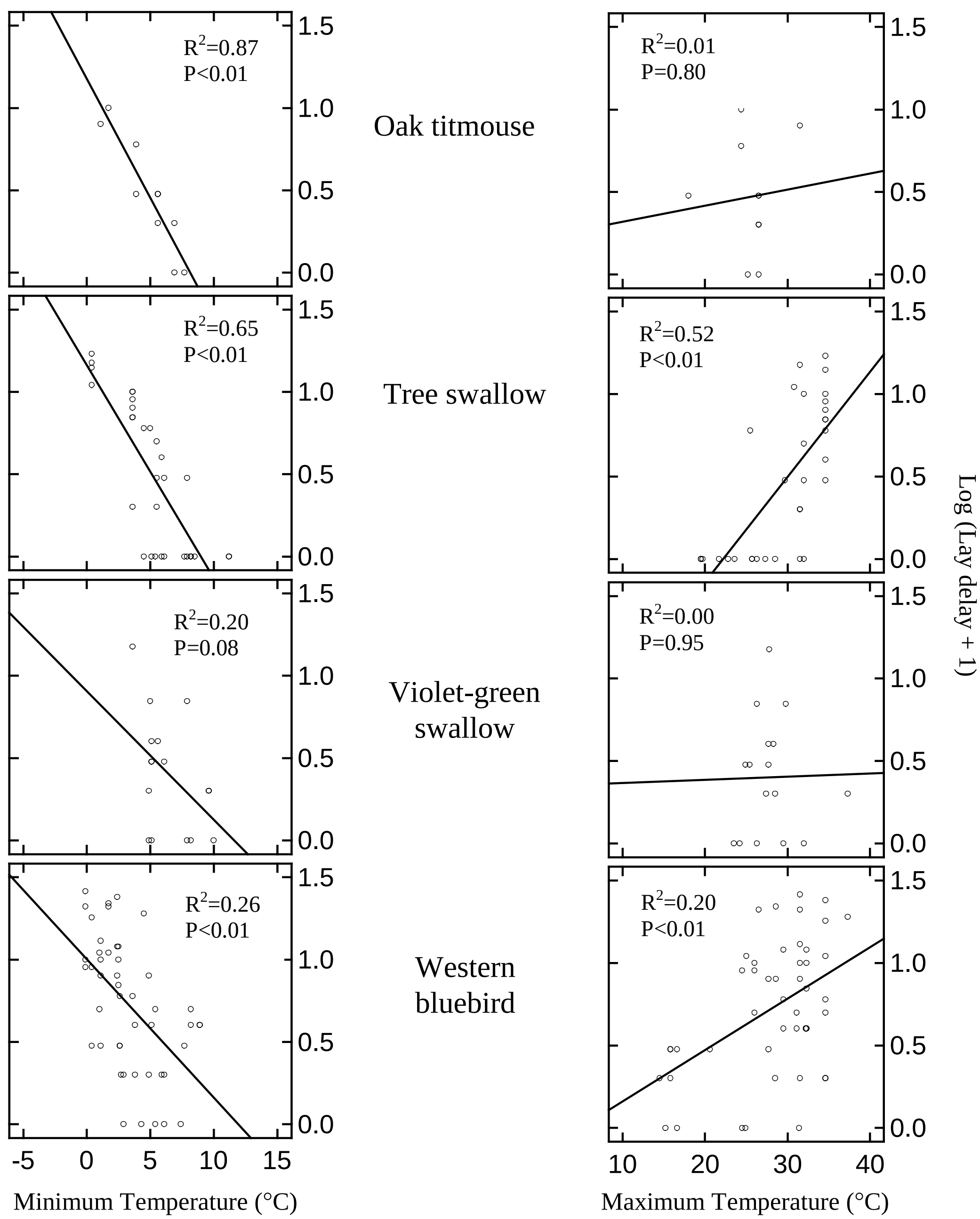

Figure 2. Minimum and maximum temperature vs. log (lay delay + 1) for all species.

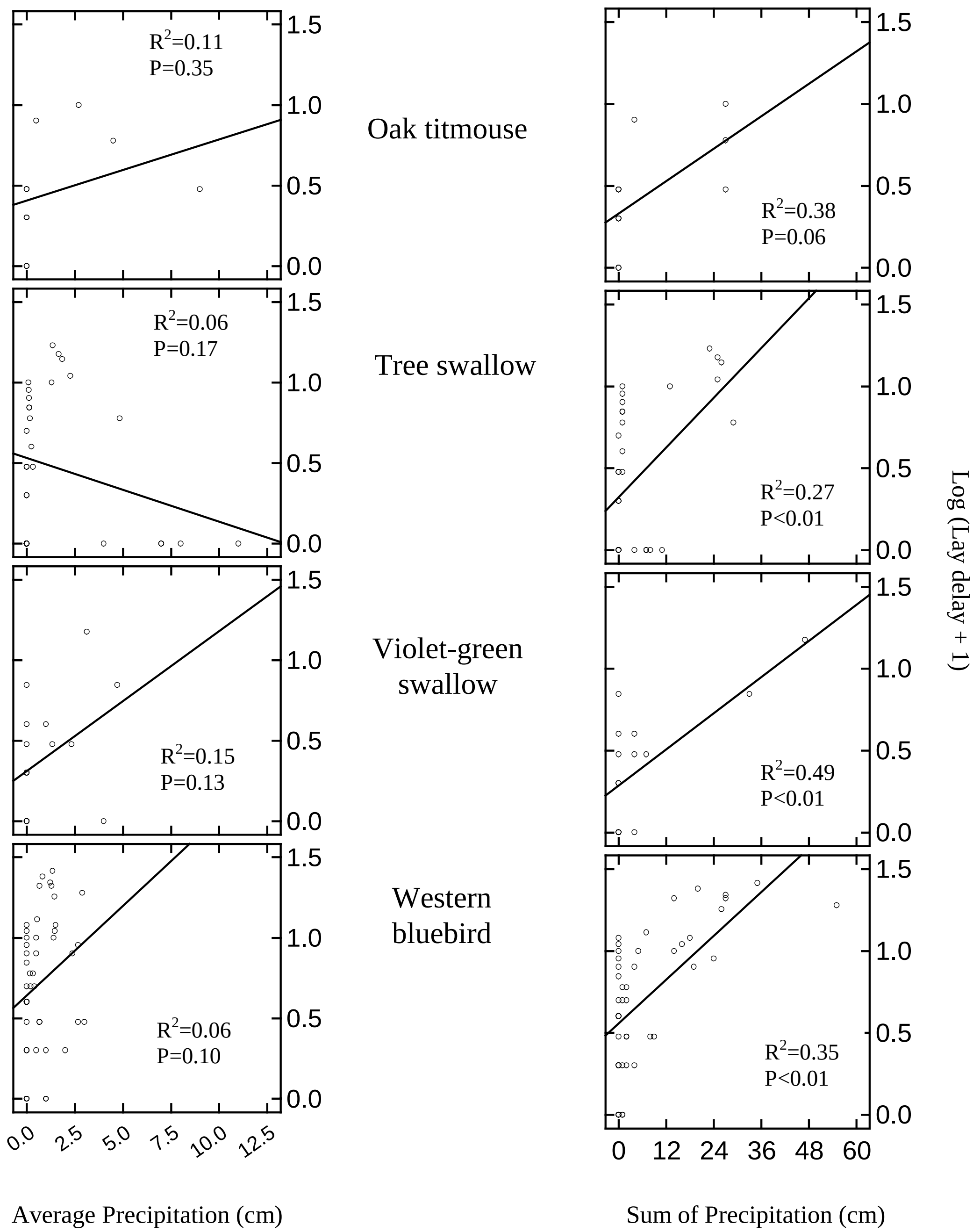

Figure 3. Average precipitation and sum of precipitation vs. log (lay delay + 1).

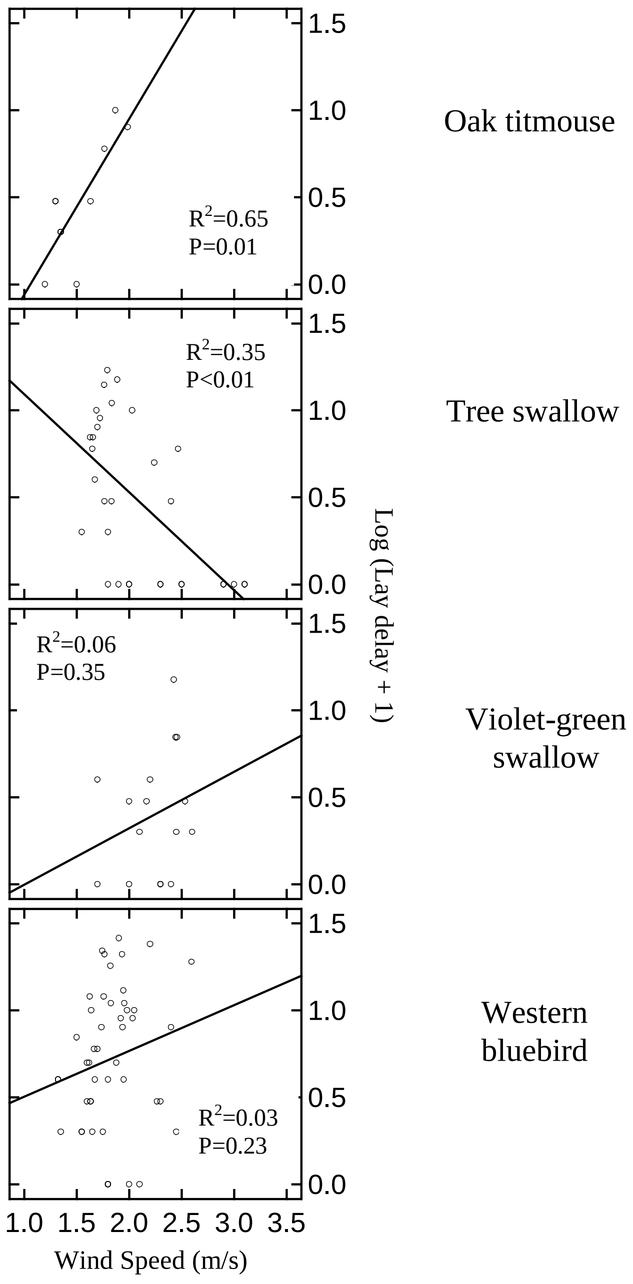

Figure 4. Wind speed vs. Log (lay delay + 1) for all species.

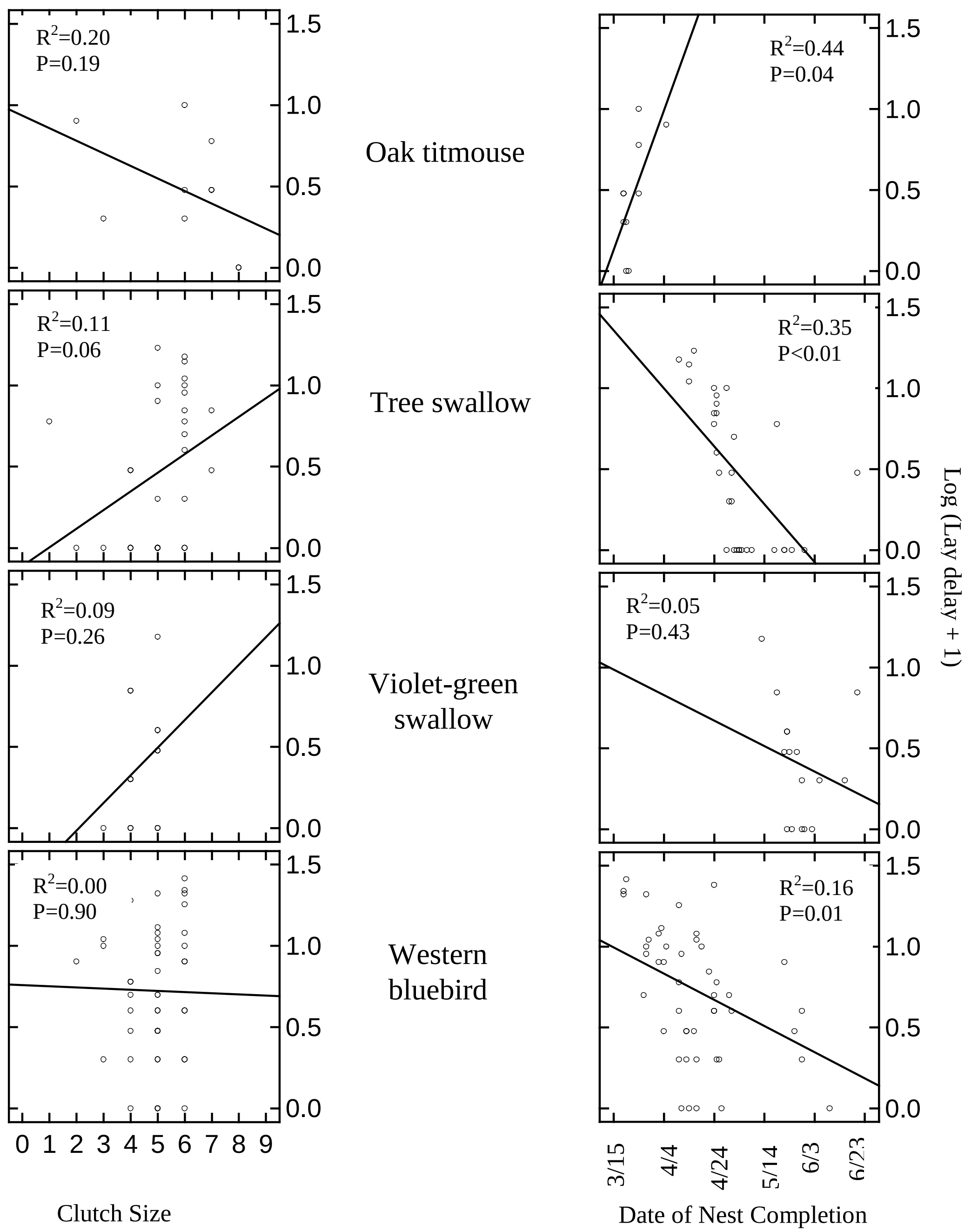

Figure 5. Clutch size and date of nest completion vs. log (lay delay + 1).

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Table 3. Stepwise forward regression for each species using all factors.

Species	**R^2**	**N**	**Effect**	**Coefficient**	**p-value**
Oak titmouse	0.87	10	Constant	1.18	<0.01
			Minimum Temperature	-0.15	<0.01
Tree swallow	0.83	32	Constant	-1.03	0.02
			Maximum Temperature	0.08	<0.01
			Sum of Precipitation	0.02	0.01
Violet-green swallow	0.49	16	Constant	0.29	<0.01
			Sum of Precipitation	0.02	<0.01
Western bluebird	0.74	47	Constant	209.01	0.02
			Date of nest completion	-0.01	0.02
			Maximum temperature	0.03	<0.01
			Minimum temperature	-0.05	0.02
			Sum of precipitation	0.02	<0.01

Discussion

Overall, ‘poor’ environmental factors seem to correlate most significantly and most often with lay delay. Increased precipitation, high and low temperatures, and high wind speeds all corresponded consistently with longer delays. Also, earlier dates of nest completion often correlated with longer delays; however, since earlier dates of nest completion correlated significantly with poorer weather conditions such as minimum temperature and wind speed, it is unclear whether it is time of season or environmental factors that may result in longer lay delays.

Mean lay delay was significantly higher for the western bluebird than for the violet-green swallow, and it was almost significantly higher for the bluebird than for the tree swallow. It is unclear why exactly the western bluebird would have a longer mean lay delay than the other species; however, the mean was greatly affected by several particularly long delays of over 20 days. It is possible that one or more of these long delays occurred as a result of two separate individuals taking part in the nest-building: one beginning the process and then leaving, and another taking up where the first one left off. There were several instances when this happened, and for that reason the data for those individuals was not used in the study. However, if it happened in other cases and was not caught, it would have resulted in erroneously long lay delays.

As predicted, maximum and minimum temperature correlated strongly with lay delay for several of the species. This agrees with previous studies showing that low temperatures, particularly, have an affect on activity and energy levels (Clark 1987, Root 1988). Furthermore, maximum and minimum temperature showed up consistently in models generated by forward multiple regressions that were run on all species, indicating that they have important relationships with lay delay. While it was expected that maximum and minimum temperature would correlate with lay delay for all four species individually, seasonality probably affected the extent of some of these correlations. For example, the titmice lay early in the season compared to the other three species, and their nest-building and egg-laying periods were concentrated mainly in March and April. Cooler weather at this time of the season may explain why lay delay in the titmice showed a significant correlation with minimum temperature, but not maximum temperature. This might also account for some of the scatter in the regression points for the western bluebird. The bluebirds lay two clutches, one in the early, cooler part of the season, and one in summer when it is generally dryer and hotter. For this reason, it would be useful to analyze the bluebird data according to clutch number, which was not done in this case due to inability to characterize some of the mid-season clutches as either first or second clutches. However, it seems likely that first clutches would be affected more by low temperature, and second clutches by high temperatures.

Total precipitation had significant correlations with lay delay for three species, and a nearly significant correlation for the titmice. As expected, the two species of swallows showed significant correlations between lay delay and precipitation; however, it seemed likely that the effect of precipitation on the swallows would be greater than on the other two species, since swallows are aerial feeders, and this was not the case. The violet-green swallow did have the highest correlation, but that of the western bluebird was higher than that of the tree swallow. A possible explanation for this is that western bluebirds often lay two clutches per season, and it has been shown that the nest-building and lay delay periods are shorter for the second clutch than the first (Guinan *et. al.* 2000). Therefore, since the first clutches were laid in the spring (during the rainy season) this very well might be a confounding variable, since we would expect lay delay to be longer for the first clutch and we would also expect more precipitation at that time. This explanation is substantiated by the fact that lay delay did correlate significantly with date of nest completion for the western bluebird. Regardless, higher amounts of precipitation, in general, correlated with longer lay delays for all species, which was expected.

Average wind speed had the highest correlation with lay delay for the tree swallow. However, the correlation was negative, suggesting that higher wind speeds correspond with a shorter lay delay. This goes against the prediction that higher wind speeds would lengthen lay delay for the swallows since it would affect their ability to feed aerially. What likely needs to be considered is the spatial distribution of the nest boxes and weather stations. Since there were only two weather stations serving nest boxes in varying microhabitats, average wind speed is a very broad approximation for what is actually occurring at the microhabitat level. In order to more accurately evaluate the effect of wind speed, we would need to take into account where each individual was nesting, how much cover the location had, and where the individual was going to forage. All of these variables may affect how wind speed influences lay delay, but given the restrictions we had on wind speed data, we cannot determine exactly how each individual was affected. Lay delay for the oak titmouse had a strong positive correlation with average wind speed. This supports the hypothesis that lay delay in oak titmice is lengthened by high wind speeds as a result of a decrease in activity and metabolism, which has been shown to occur in other species of titmice and chickadees (Grubb 1978). Since the oak titmice nested in similar habitats situated only in the upper two plots, they were probably similarly affected by wind speeds, and the wind speed data that is available is more applicable to this species than to the others.

Date of nest completion showed significant correlations with three species. This was expected since previous studies have shown that some early-arriving birds have longer periods of time between nest initiation and onset of egg-laying (e.g. Bent 1942, Stutchbury & Robertson 1987, Guinan *et. al.* 2000). However, there was a positive relationship between lay delay and date of nest completion for the oak titmouse, suggesting that the later-arriving individuals had longer lay delays. This was unexpected, but can probably be explained by the fact that the oak titmice have a very short laying season, so there was little variation in date of nest completion for this species. In general, as mentioned earlier in the discussion, there may be confounding factors for this variable, because date of nest completion also correlates significantly with several of the environmental variables. This relationship must be examined further in order to determine whether it is the timing of the bird's arrival or the seasonal weather variables that are causing longer delays. Since we did not have complete data for date of nest initiation, we could not evaluate what part it might have played (as opposed to date of nest completion).

Interestingly, clutch size showed no significant correlations with lay delay, although it was nearly significant for the tree swallow. However, clutch size did correlate significantly with date of nest completion, which conforms to previous studies which have shown that clutch size decreases throughout the laying season (Klomp 1970, Winkler & Walters 1983). Therefore, it is likely that larger clutch sizes will occur earlier in the season regardless of lay delay or environmental factors.

In short, further research involving manipulation of environmental factors is necessary in order to see if these do indeed *cause* a longer delay regardless of seasonality, and vice versa. This could shed light on whether environmental factors, biological factors, or a combination of the two have the most important effect on lay delay.

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