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THE EFFECTS OF WEATHER AND LUNAR CYCLE ON NOCTURNAL MIGRATION OF LANDBIRDS AT SOUTHEAST FARALLON ISLAND, CALIFORNIA[1]

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Abstract. Proximal climatic and lunar effects on arrival and departure of nocturnal migrant landbirds at Southeast Farallon Island (SEFI), California, were examined using multivariate and univariate statistics. Predictive models including date, weather and lunar variables were developed for both spring and fall, which accounted for 33–40% of variation in arrival totals and 18–21% of variation in departure proportions. Seasonal, regional, and taxonomic variation in weather- and lunar-migration relationships were assessed and, along with comparisons of arrival and departure patterns, used to differentiate proximal effects on arrival to SEFI, from widespread effects resulting in increased migration volume over California. Low wind speeds, low to moderate visibility, full cloud cover and lack of fog were proximal effects increasing arrival to SEFI, while low wind speeds, low but rising barometric pressure, clear and clearing skies, high visibility, and decreased moonlight (in fall) resulted in increased departure proportions and, presumably, caused higher migration volume over the region. Effects of wind direction and air temperature, although related to synoptic weather-migration relationships, generally had obscure or minimal direct influences on arrival and departure at SEFI. Departure proportion in spring increased with decreased departure proportion the day before, but few other delay effects between weather variables and arrival or departure were found. Seasonal, regional, and taxonomic variation in departure effects were relatively small suggesting that selection of weather-migration strategies has evolved convergently in a diverse group of migrants flying over a region the size of California.

Key words: Migration; landbird; nocturnal migrant; weather; lunar cycle; California.

INTRODUCTION

Numerous studies using a variety of techniques have investigated the effects of weather, and to a lesser extent lunar cycle, on nocturnal migration in landbirds (reviewed by Lack 1960; Richardson 1978, 1990). Although optimal weather conditions for migration vary with season, prevailing direction of migration, and local weather patterns, similar synoptic weather-migration relationships have been documented at a wide range of north temperate locations. Conditions that generally favor migration include clear or clearing skies, reduced or following winds, warmer or cooler temperatures (according to season), increased visibility, and lack of fog or precipitation. Variables with marginal, varying or little-understood effects include humidity, barometric pressure and pressure trend, and lunar phase and timing. As weather variables are strongly intercorrelated, it is difficult to pinpoint causal effects, even with complex statistical analyses.

Most studies on weather and landbird migration have been conducted in Europe and eastern North America. Commonly used censusing techniques include counts of grounded migrants, surveys of visible diurnal migration or nocturnal migration against a full moon, and detection of migrants with radar. Censusing biases exist with each method (Richardson 1978), and most counts detect birds in the process of migrating or following completion of passage, hence observed weather conditions may not represent those that had elicited migration. Ideally, investigations of causal effects should be based on departure proportions from a single location (Rabol 1978, Bolshakov 1981, Richardson 1990), but this has been practical only in a few, limited analyses (Gauthreaux 1971, Rabol and Hansen 1978, Bolshakov and Rezvyi 1982, Mehlum 1983). It has also been proposed that the number of elapsed days since the preceding migratory flight, as correlated with previous weather conditions, may be a confounding factor; but again, few studies have examined this influence (Alerstam 1978,

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Richardson 1990). Further work in a variety of areas is needed to better understand migration-weather relationships (Richardson 1990).

Daily landbird censuses conducted by the Point Reyes Bird Observatory (PRBO) since 1968 on Southeast Farallon Island (SEFI), California, provide a unique opportunity to examine the effects of weather on landbird migration. Located 48 km west of San Francisco and 30 km south of Point Reyes, the island is close enough to the coast that it is regularly used as a stopover by nocturnal migrants, yet far enough from shore that little daytime passage to or from the coast occurs. SEFI is small and devoid of dense vegetation such that daily censuses are virtually complete and unbiased, and by banding most landbirds and carefully noting the plumage of those not banded, accurate daily arrival totals and departure proportions for each species can be estimated (DeSante 1983). Weather data have been recorded by PRBO five times daily since 1971.

The number of arriving landbirds that reach SEFI daily is influenced by both "proximal" weather variables, those which affect the westward drift of migrants over the ocean and to the island, and "widespread" weather variables which affect the volume of nocturnal migrants aloft over California, where most SEFI arrivals presumably originate (DeSante and Ainley 1980). Although proximal factors may obscure true weather-migration relationships at coastal locations (Richardson 1978), by determining seasonal, regional, and taxonomic differences in weather-arrival patterns and by comparing these patterns with those for departure, widespread weather-migration relationships can be inferred. Assuming regional consistency in weather effects on migration (see Mewaldt and Kaiser 1988), we expect widespread factors over California to be similar to those which affect departure from SEFI. If different species have evolved similar migration strategies with respect to synoptic weather patterns, we would also expect widespread weather-arrival relationships to show relatively little variation between seasons and among migrants from different regions and taxa. The effects of proximal weather variables, on the other hand, should be more sensitive to such factors as exact direction of flight and specific migratory properties; consequently, relationships between arrival and proximal weather variables should show more variation between seasons and among regional and taxonomic subgroups. In addition, weather-departure patterns at SEFI would not be expected to correspond as well with proximal as with widespread weather-arrival relationships.

Using both multivariate and univariate statistics, we examine the effects of local weather and lunar cycle on arrival and departure of nocturnal migrant landbirds at SEFI. Weather-arrival models for SEFI are developed that will be used to refine estimates of trends in landbird occurrence (Pyle et al., in press). Effects of weather, lunar cycle, and delay since previous migratory flight on propensity to migrate are described and assessed using extensive data on departure proportions from SEFI. Differences in arrival and departure patterns between seasons and among regional and taxonomic subgroups are examined to infer nocturnal migration-weather relationships along the Pacific North American coast, where few similar studies have occurred. Our results, when compared to those of other studies, provide insights into both general weather-migration relationships, and the evolution of migratory strategies.

STUDY AREA AND METHODS

The topographical features of Southeast Farallon Island and methods of censusing landbirds there were described by DeSante and Ainley (1980), DeSante (1983), and Pyle and Henderson (1991). Each day PRBO biologists thoroughly censused all landbird migrants and banded as many as possible. For each species the total number present and the number of arrivals were calculated at the end of each day using all available information from banding and observations of plumage variation. If similar unmarked landbirds were encountered on successive days we assumed that a minimum number of individuals was involved; because most landbirds were either banded or were individually recognizable by plumage, this assumption resulted in <5% underestimation of arrival totals (DeSante and Ainley 1980). Nightly departure proportions were calculated for each species as $(\text{total}_n - \text{arrivals}_n)/\text{total}_{n-1}$ where n denotes the following day. Marked individuals were occasionally missed between days of observed presence; totals were adjusted in these cases to reflect the presence of the missed individuals before departure proportions were calculated. The great majority of nocturnal migrants recorded on SEFI were observed throughout days of presence, and 37% remained for more than one day (PRBO, unpubl. data).

We restricted present analyses to nocturnal migrant landbirds because sample sizes of diurnal migrants were small and weather-occurrence relationships of these species at SEFI differ from those of nocturnal migrants (PRBO, unpubl. data). Diurnal migrant landbirds excluded from the analyses include all diurnal raptors, swifts, hummingbirds, kingfishers, swallows, corvids, starlings, cardueline finches, Rock Dove (*Columba livia*) and House Sparrow (*Passer domesticus*). We excluded owls from the analyses because their day-to-day occurrence patterns at SEFI were difficult to determine and their nocturnal habits may have caused unique migratory strategies at SEFI. Rock Wrens (*Salpinctes obsoletus*) were also excluded from departure analyses because they tend to reside on SEFI (see DeSante and Ainley 1980).

Arrival analyses were restricted to the seasonal periods 1 March–30 June (spring) and 1 August–30 November (fall) and departure analyses to 15 March–30 June (spring) and 1 August–15 November (fall). Departure seasons were shortened to exclude winter residents or migrants with a tendency to winter (see DeSante and Ainley 1980) that might bias these analyses. Winter residents (as defined by Pyle and Henderson 1991) that arrived before 15 November or departed after 15 March (*n* = 143 individuals) were excluded from departure analyses, as were 316 landbirds known to have perished on the island. Otherwise, the analyses include all individuals of the 175 species of nocturnal migrant landbirds that occurred on SEFI, within the spring and fall seasons, during the 20-year period 1971 through 1990.

DeSante (1983) categorized landbird taxa into 12 subgroups according to their seasonality and presumed geographic origin of populations occurring at SEFI (see also DeSante and Ainley 1980). We compared migration patterns between the four subgroups with the largest sample sizes, as defined by DeSante (1983): coastal wintering (CW) and coastal summering (CS; species that primarily winter and breed, respectively, in coastal California), interior summering (IS; noncoastal, western breeding species—to increase sample size we pooled DeSante's interior, montane, and basin summering groups), and northern vagrants (NV; species that breed in northern and northeastern North America and winter in eastern Mexico, the Caribbean, or South America). DeSante and Ainley (1980) and DeSante (1983) list regional subgroups for species that had occurred at SEFI through 1979. Subgroups for additional species used in regional comparisons, first recorded on SEFI from 1979 to 1990, are: Black-billed Cuckoo (*Coccyzus erythropthalmus*) NV, Yellow-bellied Sapsucker (*Sphyrapicus varius*) NV, Cassin's Kingbird (*Tyrannus vociferans*) IS, Bewick's Wren (*Thryomanes bewickii*) CW, Western Bluebird (*Sialia mexicana*) CW, Sprague's Pipit (*Anthus spragueii*) NV, and Sharp-tailed Sparrow (*Ammodramus caudacutus*) NV. We also compared weather-migration relationships between the four taxonomic subgroups with the largest sample sizes, tyrannid flycatchers (21 species), thrushes (11 species), wood-warblers (41 species), and emberizid sparrows (27 species). See Pyle and Henderson (1991) for a list of species and totals (through 1989) within each taxonomic subgroup.

Weather data were collected at 06:00, 09:00, 12:00, 15:00, and 20:00 P.s.t. Meteorological instruments were periodically calibrated by the National Weather Service, for whom we recorded these observations. Proximal variables considered in the present analyses were surface wind direction (measured to the nearest 10 compass degrees) and speed (m/sec), visibility (km), air temperature (nearest 0.1°C), barometric pressure (millibars), cloud cover (measured in 10ths of the sky obscured), fog (presence or absence) and precipitation (presence or absence). Arrival analyses use weather data recorded at 06:00 the day of arrival and departure analyses used data recorded at 20:00 the night of departure. Differentials in temperature, pressure, and cloud cover were also examined; for arrival analyses these were defined as differences recorded between 20:00 the previous night and 06:00 that morning, and for departure analyses two sets of differentials were examined, afternoon differences between 12:00 and 20:00 the day before departure and overnight differences between 20:00 and 06:00 the following morning. Wind direction was scored as east (E; 30–140), south (S; 150–260), and northwest (NW; 270–20), reflecting the three prevailing wind directions recorded on the island (Parrish et al. 1982, Ainley and Boekelheide 1990; Fig. 1), and indicating three synoptic weather patterns that we define, as based on examination of daily weather maps of the region (National Oceanic and Atmospheric Administration 1986–

1990; see Discussion). Lunar variables considered were illumination and sequence. Illumination (hereafter "moonlight") was scored 0–100 according to the proportion of full the moon was at midnight, and sequence was categorized as either waxing (therefore, moonlit predominately in the evening) or waning (moonlit predominately in the morning).

The results of both univariate and multivariate analyses are presented to help differentiate true effects from those confounded by other independent variables (see Richardson 1978). Variables with significant multivariate effects are likely true influences whereas stronger univariate than multivariate effects indicate confounding. In both arrival and departure analyses the terms date and date^2 were highly significant covariates within our defined seasons and were thus included as factors in both multivariate and "univariate" analyses. This procedure (hereafter referred to as a "date-adjusted" analysis) has the advantage that it controls for seasonal variation in weather variables as well as date effects on arrival and departure patterns of migrants. For multivariate analyses we used linear multiple regression to estimate the effects of weather and lunar variables on arrival, and grouped logistic regression (or "empirical logistic regression"; Cox 1970) to produce least-square estimates of these effects on departure probability (STATA 1990).

Landbird occurrence at SEFI is highly variable (DeSante 1983); to reduce skew and to facilitate regional and taxonomic comparisons, arrival analyses were based on the dependent variable $ln(\text{arrivals} + 0.5)$. The analyses of departure probability weighted the proportion of birds departing in a day (the dependent variable) = X/N = p, where X = the number departing, N = total number of birds of a species or set of species present on the island, and p = proportion departing, according to N and according to $p(1 - p)$ as is appropriate for a binomial process (Cox and Snell 1989). Unlike the more common form of logistic regression (maximum likelihood method), grouped logistic regression does not assume that each bird departs or stays independently of every other bird, but instead treats the proportion departing in a day as the unit of observation. Because ratios can become unstable and highly variable when the denominator is small, we excluded days ($n = 509$) where $N < 3$.

Our objective with multiple regression was to determine single predictive arrival and departure models based on date and the above defined weather and lunar variables. Linear and quadratic terms were fitted in a stepwise manner by (1) examining the date-adjusted effects of all variables independently and simultaneously; (2) refitting the models after eliminating variables that had insignificant effects in all analyses of both spring and fall; (3) eliminating quadratic terms that were significant in neither season; and (4) re-examining the effects of each previously dropped variable within final models. Terms were omitted from final models if they had insignificant effects during both seasons. Linear effects and interactions of variables with significant quadratic terms were determined by refitting the models without their quadratic terms. We examined the final models for robustness by comparing significance levels of all variables before and after replacement of other terms; adding or dropping single weather terms had little effect on either the adjusted R^2 or on the estimated effects of the other variables.

To further clarify the inter-relationships among weather variables, we performed Pearson product-moment correlation analyses on weather recorded at 06:00 and 20:00 and we looked for significant statistical interactions between all pairs of weather variables, by examining the effects of interaction terms as additions to arrival and departure models. Differences between seasons and among regional or taxonomic subgroups were analyzed by testing for interactions between each variable (linear term only) and season or subgroup, after adjustments for other variables based on the final models. For seasonal comparisons we standardized the date terms and included date-season and date^2-season interaction terms to minimize the effects of seasonal differences in occurrence patterns and weather effects. To investigate the effects of previous weather and delay since prior migratory flight on migration at SEFI, we substituted weather terms or added delay terms of the previous 1–3 days individually to current arrival and departure models, and we also examined the simultaneous effects of weather and lunar variables during the previous 1–3 days on current arrival totals and departure proportions.

Significance was assumed when $P < 0.05$ in tests of within-season effects; for analyses of differences among regional or taxonomic subgroups (four groups, therefore six possible pairwise comparisons) we used $P < 0.0083$ according to the Bonferroni inequality (Seber 1977). Arrival analyses use a total of 78,026 migrants (16,132 in spring and 61,894 in fall) arriving on 4,880 nights (2,440 each in spring and fall), and departure analyses include 153,485 "migrant-days" (32,647 in spring, 120,838 in fall) departing during 3,771 nights (1,707 in spring, 2,064 in fall).

RESULTS

WEATHER AND LUNAR COVARIATION

Overall, we found unexpectedly low correlations among weather variables recorded at SEFI. Examination of weather observations taken at 06:00 and 20:00 indicates very similar distributions and correlations among all variables between these two observation times; data relative to wind direction, based on observations taken at 06:00, are shown in Table 1. The greatest associations, besides those involving wind direction, are between cloud cover and the three variables wind speed (Pearson product-moment correlation = −0.33 in spring, −0.16 in fall), visibility (−0.43, −0.41) and fog (0.35, 0.38). Other high correlations, between visibility and fog (−0.55, −0.61), pressure and rain (−0.48, −0.44), and each differential variable with its antecedent (0.29–0.54), were expected. All other correlations, including those between lunar and weather variables, had absolute Pearson product-moment values <0.20. Differences in most variables were evident when examined by wind direction (Table 1), an indicator of synoptic pattern (Fig. 1), especially in comparisons of conditions during NW winds with those of the other two directions, S and E.

ARRIVAL AT SEFI

The effects of weather and lunar conditions on arrival of nocturnal migrants at SEFI, as determined with multivariate analysis, are shown in Table 2. Overnight temperature differential, cloud cover differential, and lunar sequence had no significant linear or quadratic effects on arrival in either season and thus were dropped as components from the final model and further arrival analyses. Low surface wind speed, low but increasing barometric pressure, lack of fog, and increased cloud cover at SEFI were variables resulting in significantly heavier arrival in both seasons. In spring, arrival increased significantly with south or east winds but decreased when

TABLE 1. Mean ± SD weather and lunar variables recorded at 06:00 at SEFI, summarized in relation to three synoptic weather patterns, as defined by wind direction (Fig. 1). Fog and precipitation were scored as 1 (present) or 0 (absent). See text for other units of measurement.

	Spring			Fall		
Weather condition	East	South	Northwest	East	South	Northwest
Wind speed	4.20 ± 2.39	3.80 ± 2.18	6.30 ± 2.83	4.11 ± 2.49	3.22 ± 1.97	5.10 ± 2.43
Visibility	21.6 ± 15.6	17.7 ± 14.8	23.0 ± 13.6	21.1 ± 15.9	16.1 ± 13.8	20.0 ± 15.5
Air temperature	11.8 ± 1.70	11.5 ± 1.22	10.8 ± 1.22	13.5 ± 2.09	13.5 ± 1.54	13.0 ± 1.45
Overnight difference	0.07 ± 0.78	−0.14 ± 0.78	−0.07 ± 0.60	−0.05 ± 0.74	−0.12 ± 0.79	−0.11 ± 0.71
Barometric pressure[a]	15.4 ± 5.42	14.8 ± 5.04	16.9 ± 4.03	16.8 ± 5.08	14.6 ± 5.94	16.1 ± 4.07
Overnight difference	−0.01 ± 2.21	0.15 ± 2.65	0.37 ± 1.99	0.47 ± 2.46	0.60 ± 2.47	0.56 ± 1.95
Cloud cover	5.43 ± 3.64	8.62 ± 2.80	4.84 ± 4.24	6.35 ± 4.14	8.70 ± 2.84	4.85 ± 4.35
Overnight difference	0.45 ± 4.65	0.50 ± 3.50	0.64 ± 4.77	0.19 ± 4.42	0.64 ± 3.69	0.39 ± 4.66
Fog	0.17 ± 0.38	0.24 ± 0.43	0.10 ± 0.30	0.15 ± 0.35	0.24 ± 0.43	0.21 ± 0.40
Precipitation	0.08 ± 0.27	0.08 ± 0.27	0.02 ± 0.13	0.06 ± 0.23	0.07 ± 0.25	0.03 ± 0.17

[a] Pressure expressed as millibars − 1,000 to save space.

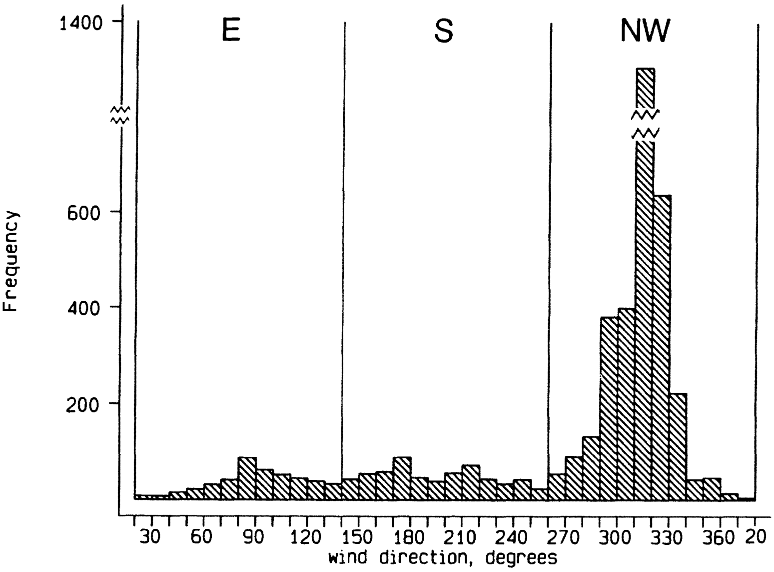

FIGURE 1. Frequency of wind directions recorded at 06:00 on SEFI during 2,107 days of spring and fall, 1970–1991. Distributions were similar during the two seasonal periods (see Table 1). Divisions between the three categories (east, south and northwest), indicators of synoptic patterns (see Fig. 2), were based on examination of the data.

winds were from the northwest; these tendencies were also apparent in fall although only the positive effect of east winds was significant. Decreased air temperature resulted in higher arrival in fall but not spring. Arrival increased significantly with decreased moonlight in fall whereas in spring this relationship was positive.

Linear effects of visibility on arrival were insignificant when the fog term was included in the model but positive in both seasons when it was excluded ($t = 4.67$, $P < 0.001$ in spring; $t = 9.94$, $P < 0.001$ in fall). In contrast, fog had similar significant negative effects with or without the inclusion of visibility terms and the variation explained by the model decreased during both seasons when fog was replaced by visibility (adj. $r^2 = 0.3174$ in spring, 0.3719 in fall; see Table 2). A significant interaction occurred between the effects of fog and visibility ($t = 6.29$, $P < 0.001$ in spring; $t = 9.15$, $P < 0.001$ in fall when visibility and interaction terms were added to the model). When foggy days were excluded visibility had a negative effect on arrival in spring ($n = 2{,}009$, $t = -3.24$, $P = 0.001$) but an insignificant effect in fall ($n = 1{,}803$, $t = 0.79$, $P = 0.433$); all other variables had similar effects and levels of significance with and without foggy days. A significant interaction between the effects of visibility and cloud cover (with fog excluded from the model) was found in spring ($t = 2.62$, $P = 0.009$) but not fall ($t = 0.44$, $P = 0.664$). No other significant interactions between any weather and/or lunar variables on arrival were found.

The effects of pressure differential and moonlight on arrival were primarily linear, whereas significant positive curvilinear effects occurred with wind speed in spring but not fall, temperature in spring but not fall and cloud cover in both seasons, and significant negative curvilinear effects occurred with visibility (when the fog term was removed: $t = -4.66$, $P < 0.001$ in spring, $t = -6.95$, $P < 0.001$ in fall), pressure differential in fall, and moonlight in fall (Table 2). Variables with significantly stonger effects in fall were temperature, visibility (estimated without the term fog; $t = 5.86$, $P = 0.000$), fog, and moonlight; whereas cloud cover was a stronger factor in spring. The effects of wind direction also varied seasonally ($F_{21,4583}) = 4.30$, $P = 0.005$), the result primarily of a stronger positive effect in spring vs. fall of east winds. Wind speed, pressure and pressure differential showed no seasonal variation.

A comparison of multivariate (Table 2) with univariate (date-adjusted only; Table 3) analyses reveals similar directions and levels of signifi-

TABLE 2. Multiple regression model of weather variables affecting arrival of nocturnal migrants to SEFI. See text for stepwise procedures. Shows are effects of each variable after adjusting for effects of all other variables in the table. Linear and seasonal effects on weather variables where quadratic terms are also included (wind speed, air temperature, pressure change, cloud cover, and moonlight) were estimated by refitting the model without the respective quadratic term. For spring: $n = 2{,}321$, adjusted $r^2 = 0.3261$, $F_{(17,2303)} = 67.05$, $P = 0.000$. For fall: $n = 2{,}284$, adjusted $r^2 = 0.3982$, $F_{(17,2266)} = 89.85$, $P = 0.000$.

Variable	Spring		Fall		Seasonal comparison
	t	*P*	*t*	*P*	*P*
Date	21.48	0.000	25.85	0.000	—
Date^2	−20.69	0.000	−25.37	0.000	—
Wind direction					
East	4.96	0.000	2.46	0.014	0.035
South	3.67	0.000	1.26	0.209	0.119
Northwest	−2.85	0.004	−0.69	0.489	0.884
Wind speed	−14.07	0.000	−14.35	0.000	0.415
Wind speed^2	3.49	0.000	−0.74	0.459	—
Air temperature	1.16	0.283	−5.98	0.000	0.000
Air temperature^2	2.98	0.003	1.22	0.225	—
Barometric pressure	−4.10	0.000	−3.73	0.000	0.942
Overnight difference	3.72	0.000	2.50	0.013	0.977
Overnight difference^2	−0.40	0.691	−2.09	0.037	—
Cloud cover	10.86	0.000	6.89	0.000	0.000
Cloud cover^2	7.41	0.000	9.65	0.000	—
Fog	−7.20	0.000	−15.16	0.000	0.000
Moonlight	2.40	0.016	−3.66	0.000	0.000
Moonlight^2	−1.76	0.079	−2.01	0.048	—

cance for most weather and lunar effects. Effects of wind speed on arrival, although in the same directions, were stronger in the univariate than in the multivariate analyses, particularly in fall. The effects of air temperature were also stronger in the univariate analyses in both seasons; in fall this effect was significantly positive vs. significantly negative in the multivariate analysis.

Most arrival effects showed significant regional and taxonomic variation in both seasons (Table 4), although it should be noted that the directions of slopes of all effects were the same among

TABLE 3. "Univariate" linear and curvilinear effects of weather variables (recorded at 06:00 P.s.t.) on arrival of nocturnal migrant landbirds. Effects were determined with regression on each term (linear) or the term plus its quadratic (curvilinear) after adjustment for date and date^2. Fog, rain and each wind direction were scored as either present (1) or absent (0). Moon sequence was scored as waxing (0) or waning (1).

Weather condition	Spring				Fall			
	Linear		Curvilinear		Linear		Curvilinear	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Wind direction								
East	6.8	0.000	—	—	3.3	0.000	—	—
South	16.7	0.000	—	—	4.2	0.000	—	—
Northwest	−14.9	0.000	—	—	−9.2	0.000	—	—
Wind speed	−20.7	0.000	2.1	0.034	−16.5	0.000	−1.3	0.209
Visibility	−5.8	0.000	1.9	0.054	3.0	0.003	−2.2	0.027
Air temperature	5.9	0.000	4.3	0.000	2.9	0.004	2.4	0.016
Overnight difference	0.8	0.403	1.1	0.262	0.3	0.792	−1.9	0.056
Barometric pressure	−4.8	0.000	3.2	0.001	−2.1	0.038	−9.4	0.000
Overnight difference	1.7	0.088	0.2	0.867	3.4	0.001	−1.2	0.246
Cloud cover	15.9	0.000	5.4	0.000	6.0	0.000	6.4	0.000
Overnight difference	0.0	0.982	0.6	0.545	0.2	0.837	−0.6	0.532
Fog	−1.1	0.277	—	—	−8.4	0.000	—	—
Rain	−1.6	0.104	—	—	−0.2	0.859	—	—
Moonlight	0.8	0.454	−2.2	0.029	−4.3	0.000	−0.9	0.367
Moon sequence	−0.2	0.820	—	—	−0.9	0.388	—	—

TABLE 4. Differences between regional and taxonomic groups in arrival patterns of nocturnal migrant landbirds at SEFI, as determined by covariate analyses of linear trends after adjusting for weather effects by fitting the arrival model (Table 2). Individual differences are indicated by the symbol between adjacent groups: = indicates $P > 0.05$, < indicates $0.05 < P < 0.0083$, and ≪ indicates $P < 0.0083$ according to Bonferroni inequality; groups are ordered by value of t (negative to positive). Regional groups are: CW—coastal winterer, CS—coastal summerer, IS—interior western summerer, NV—northern vagrant; taxonomic groups are: FLY—flycatchers, THR—thrushes, WAR—warblers, SPA—sparrows. For both regional and taxonomic comparisons, n = 9,372 "subgroup-days" in spring and n = 9,192 "subgroups-days" in fall.

Variable	Spring			Fall		
	F	*P*	Group differences	*F*	*P*	Group differences
Date						
Regional	117.81	0.000	CW ≪ IS ≪ NV = CS	363.46	0.000	CS ≪ IS ≪ NV ≪ CW
Taxonomic	76.88	0.000	SPA = THR ≪ FLY = WAR	49.55	0.000	FLY< WAR ≪ SPA < THR
Wind direction						
Regional	6.16	0.000	See text	8.43	0.000	See text
Taxonomic	9.12	0.000	See text	6.46	0.000	See text
Wind speed						
Regional	25.20	0.000	CW = CS ≪ IS = NV	4.72	0.003	CS = CW < IS = NV
Taxonomic	42.30	0.000	WAR ≪ SPA = FLY ≪ THR	38.87	0.000	WAR ≪ SPA ≪ FLY < THR
Visibility						
Regional	14.75	0.000	CS ≪ NV = IS < CW	47.69	0.000	CS < IS < NV ≪ CW
Taxonomic	23.09	0.000	WAR < FLY ≪ SPA = THR	10.71	0.000	WAR = FLY ≪ SPA = THR
Temperature						
Regional	14.68	0.000	IS = NV ≪ CS = CW	6.04	0.001	NV = IS < CW < CS
Taxonomic	30.24	0.000	THR < SPA ≪ FLY ≪ WAR	18.33	0.000	THR = FLY ≪ SPA ≪ WAR
Barometric pressure						
Regional	11.27	0.000	CS < NV = IS < CW	58.49	0.000	CS < IS ≪ NV ≪ CW
Taxonomic	9.74	0.000	WAR = FLY ≪ THR = SPA	13.52	0.000	WAR < FLY = SPA ≪ THR
Overnight difference						
Regional	0.24	0.866	CS = IS = NV = CW	3.85	0.008	CS = IS = NV < CW
Taxonomic	1.25	0.290	WAR = THR = FLY = SPA	1.94	0.119	FLY = WAR = THR = SPA
Cloud cover						
Regional	15.85	0.000	IS = NV = CW ≪ CS	55.11	0.000	CW ≪ NV ≪ IS < CS
Taxonomic	43.10	0.000	THR = SPA ≪ FLY ≪ WAR	23.34	0.000	THR = SPA ≪ FLY < WAR

TABLE 4. Continued.

Variable	Spring			Fall		
	F	P	Group differences	F	P	Group differences
Fog						
Regional	11.95	0.000	CS = NV = IS $\ll$ CW	20.37	0.000	CS < NV = IS $\ll$ CW
Taxonomic	11.92	0.000	FLY = WAR $\ll$ THR = SPA	6.06	0.001	FLY < WAR = THR < SPA
Moonlight						
Regional	0.50	0.684	CW = IS = CS = NV	3.95	0.008	CW < NV = CS = IS
Taxonomic	1.42	0.233	WAR = SPA = THR = FLY	5.08	0.002	WAR < THR = SPA = FLY

groups, indicating generally similar weather-arrival patterns of all nocturnal migrants. Relatively uniform effects included those of pressure differential, with little variation in either season, and moonlight, which showed no differences in spring and significant but relatively weak variation in fall. Significant regional differences in wind direction during spring resulted from increased arrival of coastal winterers during east winds as compared with the other three subgroups (CS = IS = NV < CW; see Table 4 for codes and terminology), and significantly reduced arrival of coastal summerers and coastal winterers during northwest winds as compared with the other two subgroups (CS = CW $\ll$ NV = IS). In fall, a significantly weaker effect of east winds on arrival of coastal summerers was evident as compared with the other three subgroups (CS $\ll$ IS = NV = CW). Taxonomic differences included significantly fewer warblers arriving than other subgroups during northwest winds in both seasons (WAR $\ll$ SPA = FLY = THR in spring, WAR $\ll$ SPA = THR = FLY in fall) and significantly more arrival of warblers with east winds in fall (SPA = THR = FLY $\ll$ WAR). Interestingly, no regional or taxonomic variation was found in either season during south winds.

DEPARTURE FROM SEFI

The effects of weather and lunar conditions on departure of nocturnal migrants at SEFI, as determined with multivariate analysis on departure proportion, are shown in Table 5. Temperature differential, the presence or absence of rain and, surprisingly, wind direction had no significant linear or quadratic effects on departure during either season and thus these variables were dropped from final models and subsequent comparisons. Conditions resulting in increased departure in both seasons were low wind speed, high visibility, warmer temperature, and clear and clearing skies; wind speed and cloud cover had significant negative curvilinear correlations with departure in fall but not spring. Higher proportions of migrants departed in fall but not spring during lower absolute pressure, dropping afternoon pressure differential, and rising overnight pressure differential. A weak correlation between afternoon clearing and departure was evident in spring while in fall there was no linear but a positive curvilinear effect. Departure increased significantly with decreasing moonlight in fall, but there was no effect of sequence. In spring,

TABLE 5. Multiple grouped logistic regression model of weather variables affecting departure of nocturnal migrants from SEFI. Shown are the effects of each variable after adjustment for all other variables in the model. Linear and seasonal effects of variables where quadratic terms are also included (wind speed, afternoon pressure change, cloud cover, afternoon and overnight cloud cover change, and moonlight) were derived by refitting the model without the quadratic terms. For spring: $n = 1{,}288$, adjusted $r^2 = 0.2096$, $F_{(19,1268)} = 13.53$, $P = 0.000$. For fall: $n = 1{,}457$, adjusted $r^2 = 0.1806$, $F_{(19,1437)} = 15.57$, $P = 0.000$.

	Spring		Fall		Seasonal comparison
Variable	*t*	*P*	*t*	*P*	*P*
Date	5.76	0.000	6.88	0.000	–
Date^2	−4.93	0.000	−6.74	0.000	–
Wind speed	−4.76	0.000	−3.85	0.000	0.971
Wind speed^2	−0.49	0.626	−2.36	0.018	–
Visibility	3.88	0.000	2.73	0.006	0.749
Temperature	1.58	0.113	3.72	0.000	0.306
Barometric pressure	−1.23	0.218	−3.99	0.000	0.176
Afternoon difference	−1.00	0.318	−4.95	0.000	0.051
Afternoon difference^2	−2.07	0.039	2.41	0.016	–
Overnight difference	1.15	0.252	4.07	0.000	0.147
Cloud cover	−4.10	0.000	−4.34	0.000	0.639
Cloud cover^2	−1.94	0.053	−3.22	0.001	–
Afternoon difference	−1.93	0.047	−1.04	0.299	0.074
Afternoon difference^2	−0.62	0.535	3.50	0.000	–
Overnight difference	−2.28	0.023	−0.80	0.426	0.023
Overnight difference^2	3.69	0.000	1.30	0.194	–
Moonlight	−0.83	0.407	−2.22	0.027	0.153
Moonlight^2	3.32	0.001	0.97	0.335	–
Moon sequence	2.73	0.007	0.74	0.427	0.210

higher proportions of migrants departed during partial moons than during either full or new moons, and departure was significantly higher during waning than it was during waxing moon periods. Fog had no effect regardless of whether the visibility and cloud cover terms were included or excluded ($t < 1.74$, $P > 0.080$). A significant interaction between the effects of visibility and fog occurred in fall ($t = -2.42$, $P = 0.016$) but not spring ($t = -1.861$, $P = 0.063$); no other significant interactions between weather and/or lunar variables were found.

Univariate analyses of weather and lunar variables on departure (Table 6), as with arrival, indicated similar levels of significance and directions for most weather and lunar effects. The significant negative effects of fog in both seasons according to univariate analysis, absent in the multivariate analysis, likely resulted from confounding of the variable fog with those of cloud cover and visibility. Other significant linear effects according to univariate but not multivariate analyses included those of overnight cloud cover differential in fall (negative), precipitation in spring (negative), moonlight in spring (negative), and moon sequence in fall (positive).

In contrast to results of arrival analyses, there were very few significant differences in departure-weather relationships between seasons (Table 5) and among regional and taxonomic subgroups (Table 7). The only significant seasonal difference observed was a stronger effect of overnight cloud cover differential on departure in spring than in fall. The correlation between low pressure and higher departure in fall (Table 5) was significantly stronger for northern vagrants than for the other groups (Table 7). Weaker (insignificant according to Bonferroni inequality) subregional variation occurred with the effects of wind speed in spring, and weaker taxonomic variation occurred with the effects of temperature, cloud cover, and moon sequence in fall.

EFFECTS OF PREVIOUS WEATHER, MOONLIGHT AND DELAY

No effects of any previous weather variables or of delay since previous migration during the previous one, two, and/or three days, were found on arrival patterns to SEFI during either season ($t < 1.79$, $P > 0.073$ when terms were either added to or substituted with those of the same day in the arrival model; Table 2). As with its

TABLE 6. "Univariate" linear and curvilinear effects of weather variables on departure of nocturnal migrant landbirds. Effects were determined with grouped logistic regression on each variable (linear) and with its quadratic (curvilinear) after adjustment for date and date^2. Fog, rain, and each wind direction were scored as either present (1) or absent (0). Moon sequence were scored as waxing (0) or waning (1).

	Spring				Fall			
	Linear		Curvilinear		Linear		Curvilinear	
Weather condition	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Wind direction								
East	0.67	0.505	—	—	0.93	0.354	—	—
South	−1.69	0.092	—	—	−0.07	0.941	—	—
Northwest	−1.64	0.101	—	—	−1.54	0.123	—	—
Wind speed	−5.42	0.000	1.20	0.230	−4.00	0.000	0.43	0.669
Visibility	7.35	0.000	3.07	0.002	9.48	0.000	−1.33	0.183
Temperature	5.02	0.000	−2.93	0.003	6.43	0.000	−1.93	0.054
Barometric pressure	−0.48	0.633	0.10	0.921	0.04	0.705	4.49	0.000
Afternoon difference	−1.43	0.154	−2.13	0.034	−1.48	0.140	0.38	0.706
Overnight difference	−0.12	0.904	1.25	0.212	1.68	0.093	1.96	0.050
Cloud cover	−5.30	0.000	−4.41	0.000	−8.32	0.000	−4.77	0.000
Afternoon difference	1.17	0.242	1.97	0.049	1.02	0.306	4.60	0.000
Overnight difference	−3.47	0.001	2.96	0.003	−3.59	0.000	3.68	0.000
Fog	−4.80	0.000	—	—	−7.11	0.000	—	—
Rain	−2.21	0.028	—	—	1.54	0.125	—	—
Moonlight	−2.16	0.031	0.94	0.347	−2.55	0.011	−0.66	0.511
Moon sequence	2.00	0.045	—	—	2.35	0.019	—	—

same-day effect (Table 2) the effects on arrival of moonlight the previous one ($t = -2.74$, $P = 0.006$) and two ($t = 2.19$, $P = 0.029$) days were negative in fall but not spring, when the moonlight terms were substituted for that of the same day in the model. Moonlight three days before had a nearly-significant effect in fall as well ($t = -1.93$, $P = 0.054$).

For departure, barometric pressure the day before had a significant negative effect in fall, both as an independent addition to the current, weather-adjusted model ($t = -4.99$, $P < 0.001$), and as a component of all weather variables affecting the next day's departure ($t = -4.16$, $P < 0.001$). Moonlight the previous day also significantly affected departure in fall ($t = -2.04$, $P = 0.041$), when its term was substituted for the current term. Otherwise, weather or lunar variables during the previous three days, substituted or added either singly or simultaneously, did not significantly affect departure ($t < 1.68$, $P > 0.094$).

In spring, departure increased significantly with lower departure proportion the day before ($t = -3.839$, $P < 0.001$) when the previous day's departure term (square-root transformed) was added to the current model, indicating a significant effect of delay, i.e., lower departure proportions the day before resulted in higher proportions on a given night. The addition of this term to the departure model in spring increased the power of the model ($F_{(20,1141)} = 13.76$, adjusted $r^2 = 0.2151$); however, significance levels of all weather and lunar terms remained unaffected. This delay factor was not present for the day before in fall ($t = 0.98$, $P = 0.325$) or for the two or three previous days in either season ($t < 1.33$, $P < 0.184$), when previous departure terms were added to, or substituted for, those in the current departure model.

DISCUSSION

WEATHER AT SEFI

Weather conditions at SEFI, as with elsewhere at north temperate locations, are strongly influenced by the eastward passage of high and low pressure systems and associated wind circulation (Lamb 1975). Unlike many other locations where bird migration has been studied, however, the climate at SEFI and adjacent California coast is equally affected by the marine environment, including large scale air-sea interactions (Namais 1969, Ainley and Boekelheide 1990). Generally, the marine influence tempers weather conditions at SEFI, especially during the spring and fall. The Aleutian Low and the Pacific High pressure systems, which dominate northeastern Pacific weather in winter and early summer, respectively, weaken during spring and fall, resulting in relatively little pressure fluctuation at these times.

TABLE 7. Differences between regional and taxonomic groups in departure patterns of nocturnal migrant landbirds from SEFI, as determined by covariate analyses of linear trends after adjusting for weather effects by fitting the departure model (Table 5). See Table 4 for terminology and regional and taxonomic codes. For regional comparisons, $n = 3{,}934$ "subgroup-days" in spring and $n = 6{,}201$ in fall; for taxonomic comparisons, $n = 3{,}642$ in spring and $n = 5{,}426$ "subgroup days" in fall.

	Spring			Fall		
Variable	*F*	*P*	Group differences	*F*	*P*	Group differences
Date						
Regional	3.97	0.008	CS = NV = IS < CW	17.11	0.000	NW = CW < IS ≪ CS
Taxonomic	2.18	0.087	WAR = FLY = THR = SPA	1.78	0.148	THR = FLY = SPA = WAR
Wind speed						
Regional	3.34	0.019	CW = IS < NV = CS	0.82	0.483	CW = IS = CS = NV
Taxonomic	1.06	0.367	FLY = WAR = THR = SPA	2.06	0.102	THR = WAR = FLY = SPA
Visibility						
Regional	0.52	0.671	NV = CW = IS = CS	1.24	0.292	IS = NV = CS = CW
Taxonomic	0.97	0.409	SPA = WAR = THR = FLY	2.32	0.072	WAR = THR = FLY = SPA
Temperature						
Regional	0.20	0.895	NV = CS = CW = IS	1.07	0.359	IS = CS = NV = CW
Taxonomic	1.29	0.275	THR = WAR = FLY = SPA	5.22	0.002	THR = WAR = FLY < SPA
Barometric pressure						
Regional	0.79	0.503	CW = IS = NV = CS	7.52	0.000	NV < CW = CS = IS
Taxonomic	1.07	0.364	SPA = THR = FLY = WAR	0.38	0.768	SPA = FLY = WAR = THR
Afternoon difference						
Regional	0.56	0.648	NV = IS = CS = CW	1.38	0.245	NV = IS = CS = CW
Taxonomic	1.49	0.214	SPA = THR = WAR = FLY	1.87	0.131	THR = FLY = WAR = SPA
Overnight difference						
Regional	0.97	0.409	CS = NV = CW = IS	1.25	0.289	CS = NV = CW = IS
Taxonomic	0.20	0.898	WAR = THR = SPA = FLY	0.98	0.404	THR = WAR = SPA = FLY
Cloud cover						
Regional	0.81	0.489	NV = CW = CS = IS	1.90	0.126	CS = CW = IS = NV
Taxonomic	0.57	0.642	WAR = FLY = SPA = THR	4.43	0.004	SPA = FLY < THR = WAR
Afternoon difference						
Regional	0.43	0.735	NV = CW = CS = IS	0.29	0.831	CS = IS = CW = NV
Taxonomic	1.06	0.366	WAR = THR = FLY = SPA	1.53	0.204	WAR = SPA = THR = FLY

TABLE 7. Continued.

Variable	Spring			Fall		
	F	P	Group differences	F	P	Group differences
Overnight difference						
Regional	1.07	0.361	CW = IS = CW = NV	0.45	0.719	IS = NV = CW = CS
Taxonomic	1.74	0.156	WAR = THR = FLY = SPA	0.04	0.982	THR = WAR = FLY = SPA
Moonlight						
Regional	0.31	0.821	IS = CW = NV = CS	0.09	0.958	NV = CW = IS = CS
Taxonomic	0.44	0.727	SPA = WAR = FLY = THR	1.04	0.375	FLY = SPA = THR = WAR
Moon sequence						
Regional	0.04	0.984	NV = CW = IS = CS	1.03	0.379	CW = CS = IS = NV
Taxonomic	0.47	0.707	WAR = SPA = THR = FLY	2.86	0.035	SPA < WAR = THR = SPA

Air temperature fluctuation is also moderated substantially by the ocean.

The marine environment is highly variable, however, resulting in much interseasonal and interannual variation in prevailing conditions and their interactions (Bolin and Abbott 1963, Ainley and Boekelheide 1990). Weather variability increases during El Ninos or other warm-water years, whereas colder ocean temperatures are correlated with stronger northwest winds, fewer high clouds but more fog and low clouds, and better-defined synoptic patterns (National Oceanic and Atmospheric Administration 1986–1990; PRBO, unpubl. data). The influence of highly variable marine conditions is probably the main reason that correlations between most weather variables are smaller at SEFI than at localities of other migration studies (e.g., Nisbet and Drury 1968, Alerstam 1978, Richardson 1982). Although these smaller correlations should strengthen the power of our arrival and departure models, other correlations with untested variables (e.g., weather in central California) may confound the results of multiple regression (Nisbet and Drury 1968, Richardson 1974), and we interpret our results accordingly.

Despite the variable marine influence, three short-term synoptic weather patterns can be defined at SEFI, as generally indicated by wind direction (Figs. 1, 2, Table 1). The first pattern results from the eastward approach of weak low-pressure systems, which typically generate relatively light and southerly winds, moderate air temperatures, cloudiness occasionally with fog, and moderate to low visibility at SEFI (Fig. 2a); these south-wind conditions typically last for 1–4 days. Rain occasionally results from these systems, especially in early spring and late fall. As low-pressure troughs pass through, high pressure builds in the northeastern Pacific, the wind shifts to northwest and strengthens, and air temperature drops at SEFI (Fig. 2b). Skies are initially clear and visibility high; toward the culmination of these periods fog or low clouds often move over the coastal region. Skies are clear and temperatures are warm over most of central California. Because high pressure systems can become stationary to the west of SEFI for days or even weeks on end, this is the most common synoptic pattern (Fig. 1). The third pattern occurs when relatively weak high pressure stablizes over western North America, resulting in light to moderate easterly winds, warm temperatures,

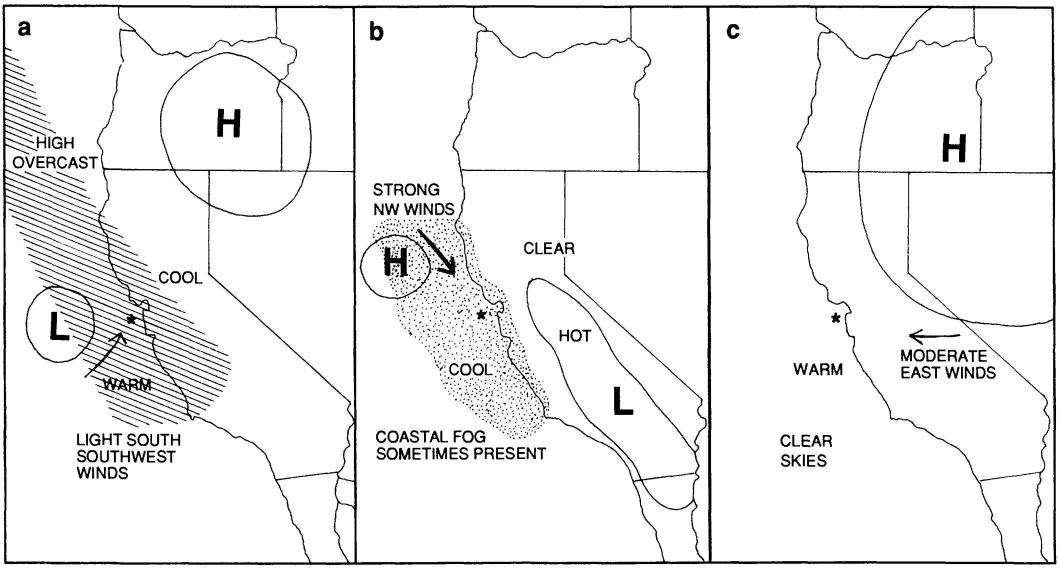

FIGURE 2. Location of Southeast Farallon Island (*) relative to western North America, and diagrammatic representation of three synoptic weather patterns that influence migration to SEFI (see text).

moderately clear skies, high visibility, and lack of fog at SEFI (Fig. 2c). These conditions are most common in late fall and early spring, between passing low-pressure systems.

WEATHER AND LUNAR EFFECTS ON MIGRATION

We synthesize seasonal, regional, and taxonomic differences in arrival and departure proportion to help differentiate proximal from widespread weather effects on migration at SEFI. Potential causes for seasonal differences in weather-arrival relationships include differences in direction of flight, coastal topography north vs. south of SEFI, and migratory experience. Most fall arrivals to SEFI are birds of the year (Ralph 1971, Stewart et al. 1974, DeSante 1983); the orientational responses to weather of these first-time migrants likely differ from the navigational responses of birds in spring (DeSante 1973, Emlen 1975, Gauthreaux 1982). Variation in effects among regional subgroups may result from direction of flight and site-specific migrational strategies, while variation in body size, flight strength, flight characteristics (as related to, e.g., long- vs. short-distance migrancy), and divergent evolution of migratory strategies could explain differences in weather-migration relationships among different taxa. Based on our results and these considerations, we evaluate the effects of each weather variable on arrival and departure patterns at SEFI.

Wind direction. Nocturnal migrants may alternately use to their benefit, compensate for, or become displaced by the effects of wind drift on flight direction (Alerstam 1979, Williams 1985, Richardson 1991). At SEFI, surface wind direction significantly influenced landbird arrival but had no effect on departure. Based on the lack of an effect on departure, the differences in effects on arrival among taxonomic and regional subgroups, and differences between univariate and multivariate results, we conclude that the influence of wind direction on arrival to SEFI results from a combination of uncompensated wind drift, a proximal effect, and the intercorrelation of wind direction over central California with other weather variables.

Our results suggest that the course of both spring and fall migrants is shifted eastward away from the coast and SEFI during northwest winds, is shifted westward toward the coast and SEFI during east winds, and is relatively unaffected by south winds; these effects are present after adjustment for other weather variables (Table 2). As suggested by DeSante (1983), this wind drift affects the coastal subgroups to a greater extent than the more misoriented inland or eastern subgroups. Taxonomic variation can be explained by body size and consequent flight strength, with east and northwest winds causing more and less westward drift, respectively, in the smaller warblers than in the other taxonomic groups.

Intercorrelation of wind direction with other weather variables over California, however, may confound the exact nature of wind direction-migration relationships. This point is supported by the much greater univariate (Table 3) than multivariate (Table 2) effects of wind direction on arrival at SEFI. The lack of season-specific variation in the effect of northwest winds on arrival is interesting, however, as these winds are the strongest (Table 1) and differences between following (fall) and head (spring) winds should be apparent. This supports our conclusions based on the lack of an effect of wind direction on departure (see below), that observed wind direction-migration relationships on the Pacific coast of North America may be confounded by other causal effects.

Wind speed. Both arrival to and departure from SEFI increased strongly and consistently with lower wind velocity, an effect that has been found in most other studies of nocturnal migrants (Richardson 1978, 1990). Wind speed generally accounted for more variation in arrival than the other weather factors, and was a relatively more important influence on arrival than departure. These results suggest that both numbers aloft over central California and the proportion of migrants reaching SEFI, especially in fall, increases with lower wind speeds. As with wind direction (see above), the effect of velocity on arrival is stronger in the two coastal subgroups, and decreases with the increasing size and/or flight strength of warblers, sparrows, flycatchers and thrushes (Table 4).

Air temperature. Air temperature effects on both arrival and departure were relatively stronger in univariate than in multivariate analyses, suggesting substantial intercorrelation of the effects of air temperature at SEFI with those of other weather variables. Greater arrival with cooler temperature in the fall is an expected result (Richardson 1990), however, other effects of temperature at SEFI are more difficult to infer from our data. Because of the marine influence, air temperature is relatively low at SEFI during northwest winds and high during south winds (Table 1), whereas the converse is often true over central California away from the immediate coast (National Oceanic and Atmospheric Administration 1986–1990; see Fig. 2). Covariation of air temperature at SEFI with other weather variables such as wind direction, cloud cover and visibility, both at SEFI and over California, may account for our varied arrival and departure results in both seasons. The positive correlations between temperature and departure from SEFI in the fall, an unexpected result (Richardson 1990), may also result from confounding with a food availability factor, as suggested by Rabol and Hansen (1978). Higher temperatures may result in more insect availability, increasing fat reserves and the likelihood of migration.

Barometric pressure. Similar effects of pressure on arrival and departure suggest that increased migration with lower but rising air pressures is a widespread effect, especially in fall. Similar correlations have been found in other migration studies, especially those conducted in fall on birds headed to the southeast (Richardson 1978, 1990), the intended direction of most SEFI migrants at this time. The stronger effect of pressure on departure of northern vagrants than of the other regional subgroups in fall (Table 7) may indicate that lower pressure results in more migration in eastern North America, where synoptic relationships between pressure and favorable flying conditions may be stronger than those along the Pacific coast. The significant regional-, and taxonomic-specific effects of pressure per se on arrival (Tables 3 and 4) are interesting; these may result from differences in strategies relative to varying synoptic weather relationships. Conversely, the linear effect of increasing overnight pressure on arrival shows no variation between subgroups and is generally consistent with departure results (Tables 5 and 6), indicating that this may be a more widespread factor.

Cloud cover. The positive effects of cloud cover on arrival varied widely between seasons, regional and taxonomic subgroups and differed substantially from the negative effects of cloud cover and cloud cover differential on departure (Tables 2–6). We conclude that a strong positive effect of proximal cloud cover on arrival (perhaps relatively stronger with more experienced spring birds) offsets a negative effect of widespread cloud cover on departure and migration volume. The positive quadratic (accelerating) relationships further suggest that this proximal effect is strongest when cloud cover is complete or virtually so.

We conclude that cloud cover along the coast not only causes disorientation by removing or reducing the effectiveness of celestial cues (Griffin 1973, Able 1982), but may also preclude migrants from detecting the coast, thereby increasing the probability of drift over the ocean (Bellrose 1971; but see Williams and Williams 1990). The marine influence often causes the presence of coastal low cloudiness over SEFI and the immediate coast while at the same time clear skies prevail over most of California (Fig. 2b); thus, both widespread and proximal cloud cover effects, although opposite, can simultaneously contribute to arrival. These conflicting factors may explain the lack of a cloud cover differential effect on arrival to SEFI; given the above a positive effect might be expected.

Fog and visibility. Our findings indicate that a strong negative relationship between fog and arrival is a proximal effect, and that greater visibility otherwise results in more departure from SEFI (and migration over California) but has a curvilinear (decelerating) proximal relationship to arrival at SEFI. The presence of fog (hence low visibility) at SEFI prevents migrants from locating the island and thus negatively affects arrival. This correlation is relatively strong (Table 2), swamping any other visibility-arrival effects. Otherwise, arrival is highest with low to moderate visibility and decreases rapidly as visibility increases. This pattern in spring may be the result of the significant visibility-cloud cover interaction, as low to moderate visibility tends to occur more with complete cloud cover. The decrease in arrival during high visibility further suggests that migrants bypass SEFI in favor of the coast, if visible (see DeSante and Ainley 1980). Effects of fog and visibility are stronger with shorter-distance migrants, the sparrows, coastal winterers, and fall migrants in general, as would be expected. Longer-distance migrants and spring migrants, which potentially move farther off the coast during the night, often arrive later in the day, after the fog has cleared (PRBO, unpubl. data). That fog had no effect on departure may indicate that migrants can distinguish between a thin layer of fog and complete cloud cover.

Precipitation. The presence or absence of rain has been strongly correlated with migration in other studies (Richardson 1978, 1990), and would be expected to affect arrival and departure of nocturnal migrants at SEFI. The lack of significant effects of precipitation in this study may have resulted from the relatively small number of days with rain, i.e., insufficient variation in this variable to detect significant effects. Alternatively, it is possible that precipitation may not strongly influence migration on the Pacific North American coast, where rain is generally less prevalent and milder during spring and fall, than in eastern North America and Europe.

Lunar cycle. Interestingly, both arrival and departure increased linearly with decreased moonlight in fall, whereas in spring this effect was weakly positive. Previous studies have suggested several possible influences of varying moon phase on nocturnal migration (see Moore 1987), including effects of gravitational changes (Larkin and Keeton 1982); of mistaking the moon for the sun by inexperienced birds (Brown and Mewaldt 1968); and of the selection by migrants of darker nights to fly in order to better use the stars in bicoordinate navigation (Vleugel 1954, Nisbet and Drury 1968, Richardson 1978). The presence of a lighthouse at SEFI could also be biasing true lunar-arrival patterns at the island (Richardson 1978); however, the similar results we obtained in analyses of arrival vs. departure, and the lack of regional and taxonomic variation in lunar relationships, suggest a widespread lunar effect rather than a proximal one.

The most likely explanation for our results may be that fewer inexperienced birds in fall migrate during moonlit nights, because bright moonlight hinders their ability to orient according to the stars. More experienced birds in the spring may rely less on the stars for navigation, and may even be selecting for moonlit nights with greater visibility of terrestrial landmarks. As such, slightly increased volume in spring over California during moonlit nights could account for the weakly positive correlation at SEFI at this time. An additional lunar effect on arrival at SEFI may be that decreased moonlight in fall hinders the ability of inexperienced birds to detect the coast (see Bellrose 1971), thereby increasing the probability for drift over the ocean. If spring migrants are mistaking the moon for the setting sun as Brown and Mewaldt (1968) suggest, northbound migrants would deflect westward, and a negative rather than positive correlation of moonlight and arrival would be expected at SEFI at this time.

Synoptic patterns. Although individual weather variables may serve as cues to nocturnal migrants, adaptive responses overall are probably related to synoptic weather patterns or, at least, to a combination of weather factors (Nisbet and Drury 1968, Alerstam 1978, Richardson 1990).

At SEFI, synoptic patterns, as indicated by wind direction (Figs. 1, 2, Table 1), play an important role in proximal effects on arrival. Eastward drift, stronger winds, either high or low visibility (depending on the presence of fog), clearer skies, and perhaps higher barometric pressure during northwest winds all act to reduce arrival to SEFI during this synoptic weather pattern. On the other hand, the reduced wind drift, lighter winds, low to moderate visibility, cloudier skies, and lower barometric pressure associated with south winds all result in increased arrival. Our results (Table 3) quantitatively confirm this long-recognized difference in synoptic weather effects on arrival to SEFI (DeSante and Ainley 1980). The combination of favorable (westward wind drift, light winds) and unfavorable (clear skies, high visibility) conditions during the east wind synoptic pattern results in moderate arrival of nocturnal migrants.

The effects of synoptic weather on departure from SEFI, and presumably migration volume over California, are less clear from our data. The lack of a wind direction effect on departure (Table 6) is surprising, especially given the strong relationships between wind direction and migration found in other studies (Alerstam 1978, 1979; Richardson 1991). Interestingly, weather conditions that appear (according to our inferences) to result in increased migration over California (low but rising pressure, lighter winds, and clearer skies), occur during different synoptic patterns; low pressure and lighter wind velocities occur during south winds whereas clear skies and rising pressure are associated with northwest winds (see Fig. 2). This might suggest that a complex or weak relationship exists between synoptic weather conditions and migration on the Pacific North American coast, perhaps related to the fact that synoptic patterns themselves are generally weaker in California than in locations of other studies. Alternatively, because flying over the ocean is not selectively advantageous to migrants, more migration during the northwest wind pattern, especially in fall, might be expected over California as a whole. Radar or other studies of migration patterns over California would help elucidate these relationships.

WEATHER ASSOCIATED WITH DEPARTURE

Although departure proportion is likely the best indicator of the causal components of migration, only four studies have considered the effects of weather on departure of nocturnal migrants. Gauthreaux (1971) censused woodlots in coastal Louisiana on consecutive days to evaluate departure relative to previous migrations over the Gulf of Mexico, and the other three studies occurred in Europe and were based on a single species, the European Robin (*Erithacus rubecula*; Rabol and Hansen 1978, Bolshakov and Rezvyi 1982, Mehlum 1983); most of the data concerns spring migration only. Our results (based on 153,485 "migrant-days" on 3,771 nights in both seasons), represent a unique opportunity to infer causal weather and lunar components of nocturnal migration. As such, some additional remarks (to those presented on departure in the above section) are warranted here.

As found in the other studies on emigration, and in most studies of migration using radar and other techniques (Richardson 1978, 1990), our results (Tables 5 and 6) indicate that the weather and lunar conditions associated with the greatest volume of departure are clear skies, low wind velocity, high visibility, low but rising overnight pressure (in fall), and little moonlight (in fall). All of these effects logically result in favorable weather both for flying and for the ability to orient and/or navigate. That our departure results generally support those of other migration studies implies that techniques such as radar and direct censuses are valid measures of factors eliciting migration.

The one exception to the above concerns the effects of surface wind direction; in contrast to most studies on migration we found no relationships between wind direction and departure from SEFI. Interestingly, the two other studies of departure that considered wind direction (Rabol and Hansen 1978, Bolshakov and Rezvyi 1982) also indicated that its influence on departure was absent, or at best obscure. Much theory surrounds the adaptation of migrants to wind direction (Alerstam 1979, Richardson 1991), and selection for wind direction has been documented for trans-Atlantic migrants (Williams and Williams 1978, Stoddard et al. 1983). Although wind direction and adaptations to it may be important once migrants are aloft, our results coupled with those of the other studies of departure suggest that its unconfounded effects on departure are minimal.

The effect of the previous day's migration on departure in spring but not fall indicates that experienced birds (spring migrants) are more inclined to wait for favorable weather than inexperienced first-time migrants in fall. These results support previous evidence and speculation that a delay effect exists (Blokpoel 1973, Alerstam 1978, Richardson 1990), at least in spring, although how it is implemented (i.e., which weather variables are important) is unclear from our data.

Finally, the general lack of seasonal-, regional-, and especially taxonomic-specific differences in the effects of weather on departure suggests that selection of weather-migration strategies has evolved convergently in a diverse group of migrants flying over a region as large as California. Concurrence of our results with those of eastern North American and European studies further suggests that these parallel strategies extend at least throughout the Northern Hemisphere.

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