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Research Papers

Sea Surface Temperatures Mediated by the El Niño-Southern Oscillation Affect Birds Breeding in Temperate Coastal Rain Forests

Les températures de surface de la mer liées au phénomène El Niño-oscillation australe affectent la nidification des oiseaux des forêts ombrophiles tempérées côtières

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ABSTRACT. We studied the timing of breeding and juvenile/adult ratios among songbirds in temperate rain forests over four years on the Haida Gwaii (Queen Charlotte Islands) archipelago, British Columbia. In May 1998, air temperatures in Haida Gwaii were above average, whereas in 1999 they were the lowest in 20 yr: temperatures in the other two years were closer to normal, although 2001 was almost as cold as 1999. Temperatures closely followed the patterns of sea surface temperatures created by the 1997–1998 El Niño, i.e., warm, event and the subsequent strong La Niña, i.e., cool, event. Timing of breeding, as measured by the first capture of juveniles or by direct observations of hatching, varied by approximately 19 d between the earliest (1998) and latest (1999) years. In 1998, the proportion of juveniles among birds trapped increased steeply as soon as young birds began to appear. In other years, the rate of increase was slower. In 1999, the peak proportions of hatching-year individuals among the foliage-gleaning insectivores, i.e., the Orange-crowned Warbler (*Vermivora celata*), Townsend's Warbler (*Dendroica townsendi*), and the Golden-crowned Kinglet (*Regulus satrapa*), were lower than in other years, with almost no young Orange-crowned Warblers captured at all. The pattern of variation in the timing of breeding and in the proportion of hatching-year individuals trapped fitted the temperature data well, although rainfall may also have contributed. We concluded that changes mediated by El Niño-Southern Oscillation (ENSO) in sea surface temperatures off northern British Columbia, through their effects on air temperatures, had a strong effect on the breeding of forest birds, to the point of causing nearly complete reproductive failure for one species in 1999. An intensification of the ENSO cycle could lead to more erratic reproduction for some species.

RÉSUMÉ. Nous avons étudié la phénologie de nidification et les rapports juvéniles:adultes chez les oiseaux chanteurs sur une période de quatre ans dans les forêts ombrophiles tempérées de l'archipel Haida Gwaii (îles de la Reine-Charlotte), en Colombie-Britannique. En mai 1998, les températures de l'air à Haida Gwaii ont été plus élevées que la moyenne tandis qu'en 1999, elles étaient les plus froides des 20 dernières années; les températures des deux autres années étaient plus proches de la normale, quoique 2001 a été presque aussi froide que 1999. Les températures ont suivi de près les tendances des températures de la surface de la mer liées au phénomène El Nino 1997-1998 (c.-à-d., chaudes) et à l'intense phénomène La Nina subséquent (c.-à-d., froides). La phénologie de la nidification, telle que déterminée par la première capture de juvéniles ou par des observations directes d'éclosion, a varié d'environ 19 jours entre l'année la plus hâtive (1998) et la plus tardive (1999). En 1998, la proportion de juvéniles parmi les oiseaux capturés a augmenté très rapidement aussitôt que les jeunes oiseaux ont commencé à apparaître. Au cours des autres

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années, le taux de captures de juvéniles n'a pas augmenté aussi rapidement. En 1999, la proportion maximale de juvéniles parmi les insectivores s'alimentant dans le feuillage, c.-à-d., la Paruline verdâtre (Vermivora celata), la Paruline de Townsend (Dendroica townsendi) et le Roitelet à couronne dorée (Regulus satrapa) était plus faible que durant les autres années, avec la quasi-absence de captures de Parulines verdâtres juvéniles. Les variations de la phénologie de nidification et de la proportion de juvéniles capturés correspondaient bien aux données de température, quoique les précipitations pourraient aussi avoir joué un rôle. Nous concluons que les changements de température de la surface de la mer au large de la portion nord de la Colombie-Britannique, par l'entremise de leurs effets sur la température de l'air, ont eu une influence majeure sur la nidification des oiseaux forestiers, au point de causer un échec quasi total de la nidification d'une espèce en 1999. Une intensification du cycle ENSO pourrait entraîner des patrons de nidification encore plus erratiques chez certaines espèces.

Key Words: *El Niño-Southern Oscillation; oceanography; reproductive success; songbirds; temperate rain forest; temperature;* Vermivora celata*;* Dendroica townsendi*;* Regulus satrapa*; timing of breeding*

INTRODUCTION

The effects of climate on the timing of breeding and reproductive success in birds have often been described on the basis of the effects of year-to-year variation on particular populations (Järvinen and Väisänen 1984, Järvinen 1994, Veistola et al. 1997, Winkel and Hudde 1997, Meijer et al. 1999, Chase et al. 2005). Recently, several studies have described the effects on terrestrial biota of oceanographic cycles, especially the El Niño-Southern Oscillation (ENSO) cycle, which affects large areas of the Pacific Ocean every three to five years (Francis et al. 1998, Freeland and Whitney 2000). This oceanographic cycle has strong effects on wind patterns, resulting in marked changes in rainfall on adjacent coasts (Castello and Shelton 2004). Some regions receive above-average rainfall, which is usually associated with increased avian productivity (Gibbs et al. 1984, DeSante and Geupel 1987, Polis et al. 1997, Jaksic and Lazo 1999, Grant et al. 2000, Coe and Rotenberry 2003). Other regions may experience drought (Wright et al. 1999), causing reduced avian breeding success (Lindsey et al. 1997).

The predominant vegetation of islands and coasts in the northeastern Pacific is temperate rain forest. Although years of strong El Niño events tend to bring increased rainfall to these areas, the ENSO cycle has little impact on rainfall patterns otherwise. However, sea surface temperatures (SST) in the eastern and central Pacific fluctuate in parallel with the ENSO cycle, and these effects extend as far north as the waters off British Columbia and the Gulf of Alaska (Hatch 1987, Piatt et al. 1989, Gaston and Smith 2001), having a marked effect on air temperatures in coastal regions.

For small, isolated islands, climate is controlled rather closely by the influence of the surrounding ocean. The air temperatures experienced by such islands fluctuate in parallel with changes in the temperature of adjacent waters. Such islands therefore provide good opportunities to study the relationships between songbird biology and year-to-year weather fluctuations. This understanding can be especially valuable in predicting the consequences of climate changes that are increasingly affecting the phenology and success of avian reproduction worldwide (e.g., Visser et al. 2004, Both and Visser 2005, Torti and Dunn 2005). We can only understand these consequences if we understand the climatic context in which they occur. This study is designed to highlight the impact of one specific climate process, the ENSO cycle, on the biology of forest birds in northwestern North America.

We studied the biology of terrestrial birds on several small islands in the coastal rain-forest biogeographic zone of British Columbia. We examined the timing and success of reproduction among these island avifaunas in relation to weather variables, the sea surface temperatures of surrounding waters, and the ENSO cycle. Our results should give an indication of the impacts that may occur throughout the coastal temperate rain forests of the region.

STUDY AREA AND METHODS

The study was carried out in Laskeek Bay, on the east side of the Haida Gwaii (Queen Charlotte Islands) archipelago, British Columbia (Fig. 1), during the breeding seasons of 1998–2001. Observers were at the field site from early May through late July in all years. Birds were captured with mist nets at East Limestone Island, Vertical Point, Louise Island, two locations on Reef Island, and Low Island in each of the study years and at West Skedans Island in 2000 and 2001 only. The sites were selected for a study of the effect of deer browsing (Allombert et al. 2005) and were therefore spread among islands with different browsing histories. All the birds captured were marked with numbered aluminum bands from the U.S. Fish and Wildlife Service as well as age- and island-specific color bands.

Determination of post-fledging period

We aimed to carry out mist-netting during the immediate post-fledging period, before family parties broke up and dispersed. To do this, the timing of intensive netting was adjusted on the basis of independent evidence obtained by searching for nests on the ground and in shrubs from May to July, especially in 1998 and 1999, when three people searched intensively during May and June (see Martin and Joron 2001), and by recording observations of fledged broods. We visited nests at intervals of 4 d and occasionally 3 or 5 d until failure or fledging. Dates of hatching were estimated on the basis of nestling size at the first visit after hatching ($N = 74$).

Mist-netting protocol

At each location, 6–12 12-m five-panel mist nets were set in prepared sites kept constant for each netting session and from year to year. Nets were opened from 0700 to 1200 once every 4 d, on a rotational basis. The spread of this systematic mist-net effort varied among years, from 30 to 40 d from the expected start of fledging, predicted in advance as detailed above. Because some locations had to be accessed by boat and because nets were not opened in rain or high wind, it was impossible to follow the schedule exactly. However, a minimum of seven catching sessions were carried out over the systematic netting period at all locations each year, except for Low Island in 1998, which was visited only five times. Because netting stations varied in numbers of nets and sessions varied somewhat in duration because of weather, capture rates were calculated in terms of birds captured per 100 net-hours (DeSante and Geupel 1987). In addition to the scheduled netting described above, some exploratory netting sessions were carried out earlier in the season in 1998 and 2000. The results of these training sessions have been excluded, except for the capture, in 2000, of one hatching-year (HY) Golden-crowned Kinglet (*Regulus satrapa*) and one HY Brown Creeper (*Certhia americana*); those were used as the dates of first capture for that year. No other HY birds were captured in preliminary sessions.

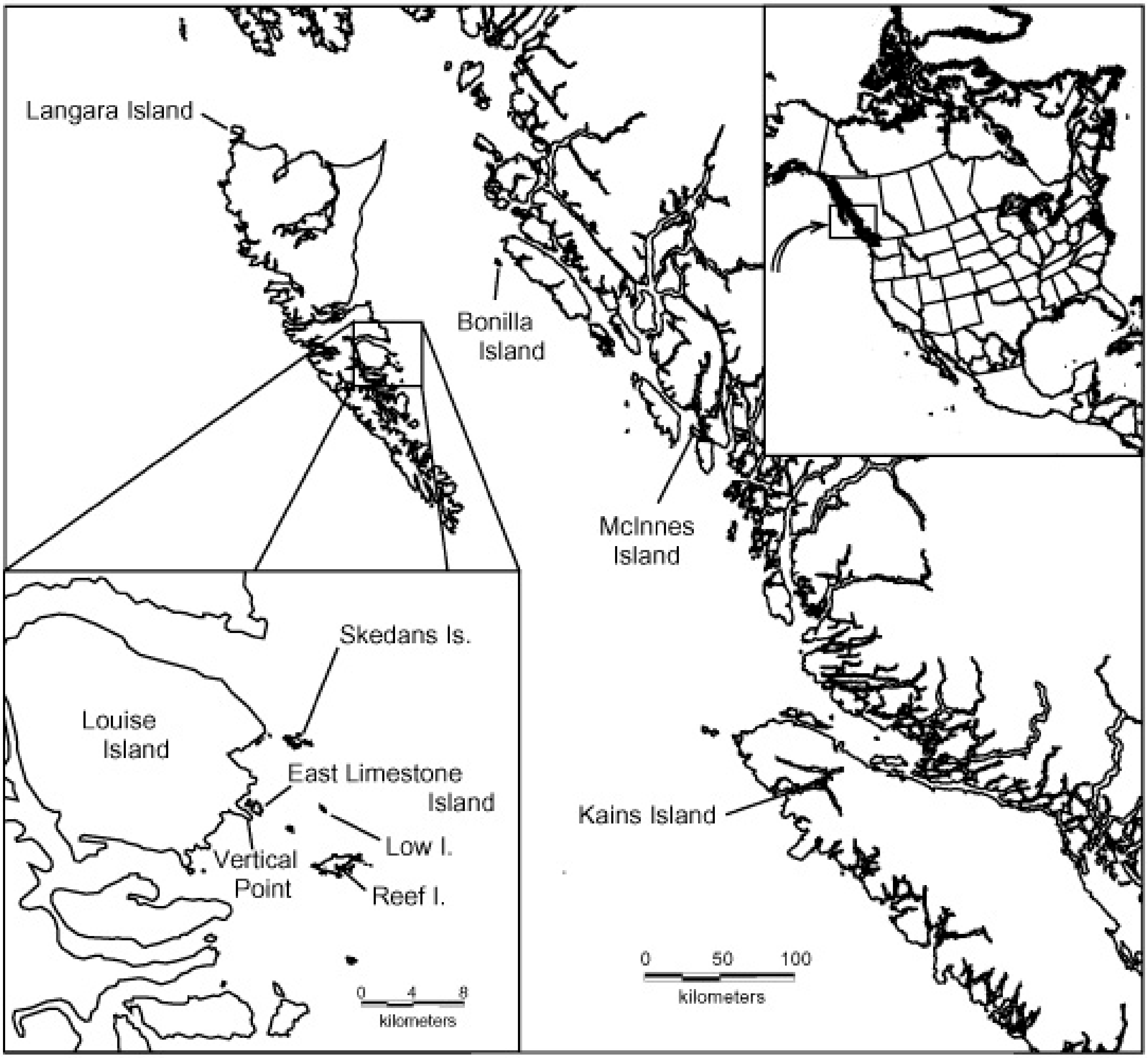
All birds captured were identified, aged, and sexed using the criteria of Pyle (1997). Most birds were examined by more than one person. Where plumage characteristics or brood patch did not provide decisive information on age, the skull was examined for degree of pneumatization.

Analysis

Timing of breeding was examined on the basis of the date on which HY birds were first captured and by plotting the proportion of HY birds among all captures, by 10-d periods, for species captured in adequate numbers, i.e., > 14/yr during the period of systematic mist-netting. The slope of the increase between consecutive 10-d periods is an indication of the degree of synchrony of fledging within species.

To adjust interyear comparisons for variation in timing of breeding, we defined retrospectively a “core period” of mist-netting, starting 5 d before the mean date of capture of the first HY individuals for the six species for which we had annual samples containing more than 14 individuals each. These included Golden-crowned Kinglet, Hermit Thrush (*Catharus guttatus*), Orange-crowned Warbler (*Vermivora celata*), Song Sparrow (*Melospiza melodia*), Townsend’s Warbler (*Dendroica townsendi*), and Winter Wren (*Troglodytes troglodytes*). The duration of the core period was the maximum period of intensive mist-netting available for all years after the starting date, i.e., 30 d. For exact dates, see the *Results* section. Numbers of mist-net sessions within the core period at

Fig. 1. Map of Haida Gwaii and adjacent coasts showing the position of light stations providing sea surface temperatue data at Innes Point, Bonilla, Kains, and Langara islands. The inset of the study area indicates the position of mist net locations at East Limestone Island, Vertical Point, Louise Island, Reef Island (points 13 and 16), Low Island, and West Skedans Island.



different sites averaged 7 in 1998, 8 in 1999, 6 in 2000, and 6.5 in 2001.

Indices of overall success of reproduction were then determined as the proportion of HY birds among those trapped each year during the core period. The proportion of HY birds during the immediate post-fledging period is believed to be a good indicator of year-to-year variation in reproductive success when applied to a particular population (DeSante and Geupel 1987, Nott et al. 2002).

Sea surface and air temperatures

Analyses of sea surface temperature (SST) were based on the period 1980–2001, which included two major events related to the El Niño-Southern Oscillation in 1982–1983 and 1997–1998 and three weaker events in 1986–1987, 1991–1992, and 1994 (Freeland 1998). We restricted the analysis to this period, because a major regime shift occurred in the North Pacific in the late 1970s, causing a general warming of surface temperatures compared with earlier decades (Trenberth and Hurrell 1995, Sugimoto and Tadokoro 1997, Beamish et al. 1999). Interyear comparisons of temperature were based on data for May, because this was the month in which egg-laying was initiated for practically all species in most years. We examined precipitation for May and June, because heavy precipitation in June might have affected the ability of parents to provision their young. As an index of the state of the Southern Oscillation, we used the mean of monthly Southern Oscillation Indices (SOI) for the period January–March and as an overall index of regional SST, we used the mean of SST values reported for the four stations closest to the study site: Langara Island, Bonilla Island, McInnes Point, and Kains Island (Fig. 1). SST values were expressed as the mean of deviations from the 20-yr average, 1980–1999, for the month of May. We obtained the SST and SOI data from the Institute of Ocean Sciences Lightstation Data Web site.

Nott et al. (2002) demonstrated significant effects of the Northern Atlantic Oscillation (NAO) on forest birds in Pacific coastal regions of North America. To assess the effect of additional large-scale climate indices, we analyzed our data in relation to the NAO, Northern Oscillation Index (NOI), Pacific Decadal Oscillation (PDO), and Arctic Oscillation (AO), using May values obtained from the sources given in Table 1.

Air temperatures in May were recorded daily at midnight at East Limestone Island, and information on maximum and minimum daily temperatures and total daily precipitation was obtained from the meteorological station at Sandspit, approximately 25 km north of the study area. The Sandspit data are expressed as deviations from the mean value for 1980–1999.

Statistical analysis

Statistical tests were performed using STATISTICA 6.0 (Statsoft 2001). All distributions involved in parametric tests were tested for departure from normality; no significant departures were found among the results included. Means are given ±1 SD.

RESULTS

Sea surface temperature, Southern Oscillation Index, Northern Oscillation Index, air temperature, and precipitation

As expected, sea surface temprature (SST) values during 1980–2001 were positively correlated with the January–March Southern Oscillation Index ($r_{20} = 0.70$, $P < 0.01$) and with air temperatures at Sandspit ($r_{20} = 0.64$, $P < 0.01$). The fit was particularly close during the four years of the study (Fig. 2), when deviation in mean May air temperature fell from +0.7°C in 1998 to -1.9°C in 1999, in concert with a decline in SST deviation from +1.1°C to -0.8°C over the same period. May 1999 was the coldest May recorded during the period considered, and May 2001 the second coldest, whereas May 1998 was the sixth warmest. Two of the five warmer years, 1983 and 1992, also followed El Niño-Southern Oscillation (ENSO) events. Among other atmospheric indices, only the Northern Oscillation Index (NOI) was correlated with SST, and none of them were correlated with air temperature when analyzed individually (Table 1). In a backward stepwise multiple regression analysis of SST with the Southern Oscillation Index (SOI), NOI, North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), and Arctic Oscillation (AO) as independent variables, only SOI entered as significant. We concluded that the SOI

Table 1. Pearson correlations coefficients among atmospheric indices and air and sea surface temperatures (SST) and precipitation in Haida Gwaii.

	Correlation with Sandspit			
Index	SST			Source
		May rainfall	Air temperature	
Southern Oscillation	-0.62†	-.15	-0.55†	Web site
Northern Oscillation	-0.50‡	0.22	-0.28	Web site
North Atlantic Oscillation	-0.09	0.38	-0.12	Web site
Pacific Decedal Oscillation	0.17	0.20	-0.06	Web site
Artic Oscillation	-0.23	0.38	0.10	Web site

†$P < 0.001$
‡$P < 0.05$

was the dominant climatic index affecting May SST and air temperatures in our study area.

For the years of the study, mean May temperatures at East Limestone Island were 0.3-0.7°C above the daily mean at Sandspit. Mean May temperatures at the two sites ranked in the same order and were closely correlated ($r_3 = 0.98$, $P < 0.01$).

There was no correlation between precipitation in May and SST over the period since 1980 (SST: $r_{20} = -0.35$, $P = 0.15$), nor was it correlated with any of the atmospheric indices considered (all $P > 0.1$). However, precipitation in May was negatively correlated with mean air temperature, $r_{20} = -0.61$, $P < 0.01$. Rainfall at Sandspit in May 1998 was the lowest in any year since 1980 (-30.9 mm from normal), and in 1999 and 2001 it was above normal (+30.4 and +38.3 mm from normal, the fourth and third highest since 1980). Rainfall in May 2000 was close to normal (+2.1 mm). Rainfall in June was not correlated with May rainfall, May temperatures, or SSTs. June rainfall was below average in 1998, 1999, and 2000 (-21.5, -15.2, and -10.6 mm) and close to normal in 2001 (+3.5 mm).

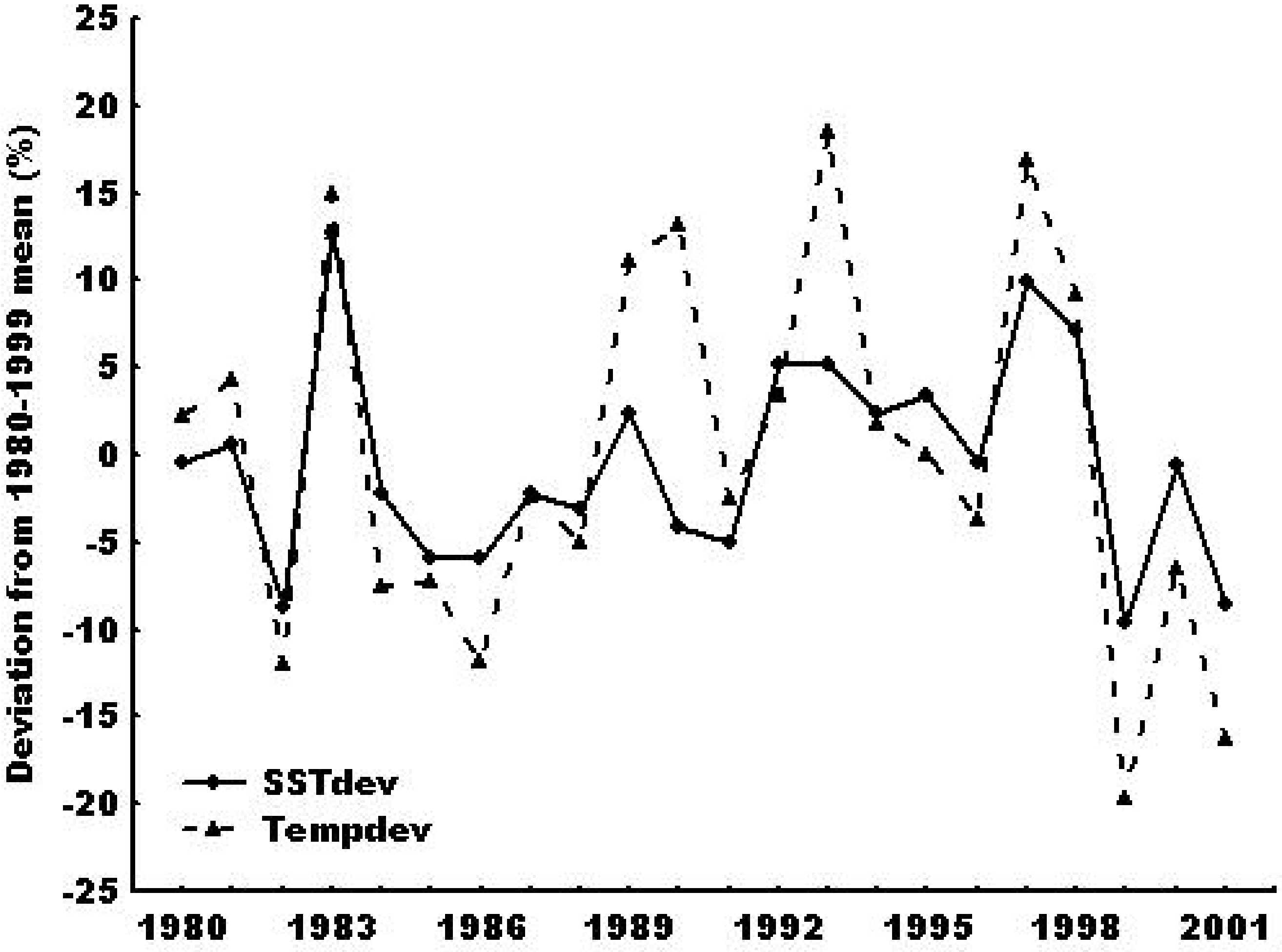
Rainfall during the 15 d prior to mean date of first hatching-year (HY) captures varied little during 1998–2000 (total precipitation 19.1, 16.5, and 21.8 mm, respectively), but was somewhat higher in 2001 (30.7 mm). During these periods, rainfall accumulation exceeded 5 mm on one day in 1998–2000 and on three days in 2001.

Timing of breeding based on the first capture of hatching-year birds

Dates of starting for the intensive mist-netting periods were 12 June 1998, 28 June 1999, 18 June 2000, and 20 June 2001. The dates of capture of the first HY individuals during these periods were relatively synchronous for all the species considered, with two exceptions. One was Swainson’s Thrush (*Catharsus ustulatus*), which in most years arrives in Haida Gwaii in early June rather than April, like the other migrants. The other was the Pacific Slope Flycatcher (*Empidonax difficilis*), for which no HY individuals were trapped among 21 captures in 2001 (Table 2). For the six species with qualifying sample sizes in all four years, the dates of first trapping of HYs fell between 4 and 21 June in 1998, 29 June and 14 July in 1999, 8 and 27 June in 2000, and 21 and 29 June in 2001.

Mean dates of first HY capture for the six species that qualified in all four years with > 14 individuals trapped were 15 June 1998, 4 July 1999, 21 June 2000, and 23 June 2001 (Table 2). Hence, core periods were set at: 10 June–9 July 1998, 29 June–

Fig. 2. Mean May deviations in sea surface temperature (SSTdev) for Bonilla Island, Innes Point, Kains Island and Langara Island, and mean May air temperature deviations (Tempdev) at Sandspit, British Columbia, for 1980–2001. Both data sets are expressed as % deviations from the 1980–1999 mean.



28 July 1999, 16 June–15 July 2000, and 18 June–17 July 2001.

There was significant variation among years in the mean dates of first captures for the six species qualifying in all years ($F_{3,17} = 13.1$, $P < 0.001$). As seen in Fig. 3, variation among years did not differ significantly in magnitude between migrant and resident species (ANOVA, $F_{1,23} = 2.27$, $P = 0.14$).

Overall, the differences in timing of breeding between 1998 and 1999 determined from the first trapping of HY individuals were very similar to those determined by direct nest observations. Mean dates of actual hatching were later in 1999 than in 1998 for all species by an average of 18 d (Table 3). The Orange-crowned Warbler (*Vermivora celata*) had the greatest difference of 27 d, compared with a difference of 26 d in the dates on which HYs were first caught, and the Hermit Thrush (*Catharus guttatus*) had the smallest difference of 11 d, compared with 13 d based on HY trapped. Estimates of mean fledging dates, based on observed hatch dates and known fledging periods for the species in

Table 2. Dates of first capture of hatching-year birds at Laskeek Bay. Sample sizes in parentheses are the numbers of individuals trapped and aged during systematic mist-netting sessions.

Species	1998	1999	2000	2001	Mean
Brown Creeper (*Certhia americana*)	...	30 June (17)	8 June (36)	...	19 June
Chestnut-backed Chickadee (*Parus rufescens*)	...	17 July (17)	24 June (25)	28 June (22)	03 July
Fox Sparrow (*Passerella iliaca*)	...	07 July (18)	22 June (89)	21 June (54)	27 June
Golden-crowned Kinglet (*Regulus satrapa*)	16 June (48)	01 July (16)	08 June1 (89)	25 June (26)	20 June
Hermit Thrush (*Catharus guttatus*)	16 June (63)	29 June (49)	18 June (96)	21 June (110)	21 June
Orange-crowned Warbler (*Vermivora celata*)	12 June (131)	08 July (33)	25 June (131)	29 June (81)	26 June
Pacific Slope Flycatcher (*Empidonax difficilis*)	...	...	28 June (26)	... (21)	...
Red-breasted Sapsucker (*Sphyrapicus ruber*)	...	...	...	29 June (22)	...
Song Sparrow (*Melospiza melodia*)	18 June (36)	03 July (32)	27 June (89)	21 June (43)	25 June
Swainson's Thrush (*Catharus ustulatus*)	... (23)	... (20)	26 July (38)	22 July (53)	24 July
Townsend's Warbler (*Dendroica townsendi*)	21 June (66)	14 July (34)	24 June (57)	21 June (57)	30 June
Varied Thrush (*Ixoreus naevius*)	17 June (18)	...	...	...	...
Winter Wren (*Troglodytes troglodytes*)	4 June (45)	01 July (18)	22 June (80)	21 June (49)	20 June

[1] Two hatchling-year individuals were trapped in a preliminary netting session on 8 June 2000: one Brown Creeper and one Golden-crowned Kinglet.

Fig. 3. Median dates of capture of hatching-years for six species qualifying in all years, separated into migrants and nonmigrants. The symbols represent the median, the boxes contain a range of 25–75%, and the whiskers illustrate the extremes.

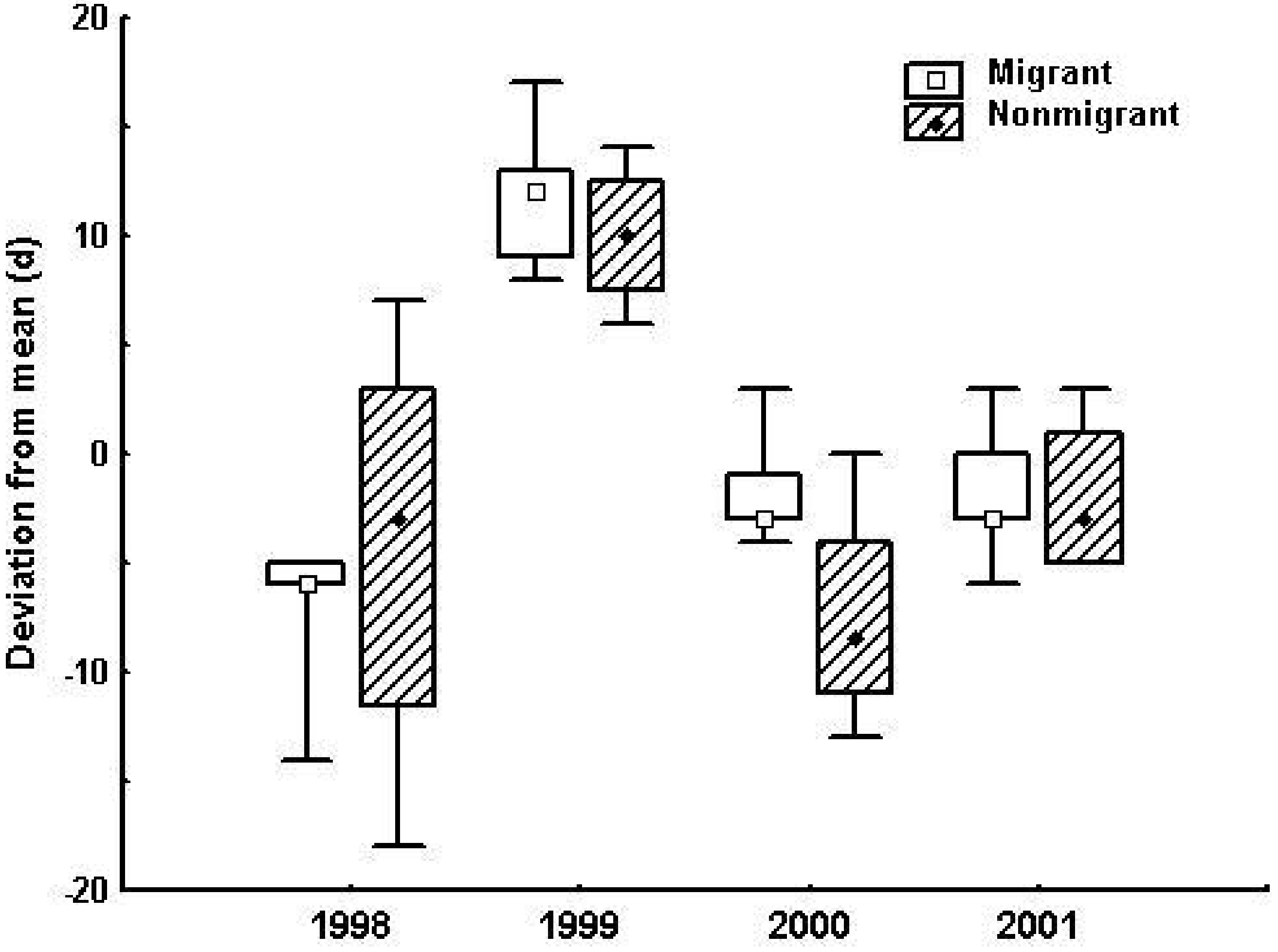


Table 3, all fell either within the core period or within the preceding 5 d.

Bird abundance as expressed by capture rates

Interyear comparisons of capture rates were based on the core period. For all sites combined, the rates were highest in 1998 at 50 birds/100 net-hours (net-h), falling to 18 birds/100 net-h in 1999, then rising to 29 birds/100 net-h in 2000 and 37 birds/100 net-h in 2001. The trends for individual sites were similar, except for East Limestone Island, where capture rates fell from 61 to 24 birds/100 net-h between 2000 and 2001. Details of the numbers trapped at each locality in all years are given by Gaston et al. (2002).

Evidence for post-breeding dispersal

Recaptures of birds banded previously in the same year made up 48% (*N* = 3789) of all trapping events. Despite this and despite the fact that some localities were < 1 km apart, e.g., sites 13 and 16 on Reef Island, Vertical Point and East Limestone Island,

Table 3. Information on hatching dates based on nests found with eggs. Sample sizes are given in parentheses.

Species	Mean dates of hatch 1998 1999		Mean	First date
Hermit Thrush (*Catharus guttatus*)	7 June (3)	18 June (3)	11	13
Orange-crowned Warbler (*Vermivora celata*)	31 May (4)	27 June (2)	27	26
Song Sparrow (*Melospiza melodia*)	25 May (8)	13 June (5)	19	15
Winter Wren (*Troglodytes troglodytes*)	21 May (10)	7 June (3)	17	14

we had no cases of birds captured at one locality recaptured at another during the same year. General observations of behavior suggested that some mist-net samples involved whole family parties, e.g., male and female adults with 4–5 HY captured simultaneously. The mix of species captured at different localities remained stable throughout the core period. We concluded that no significant dispersal took place either within or from outside of our study area before the end of trapping each year.

Timing of breeding as expressed by changes in proportion of hatching-year with date

Seven species qualified for inclusion in at least three years (Fig. 4). In 1998, HY proportions exceeded 50% for five species in the first 10-d period in which HYs were trapped. This relatively abrupt increase in numbers of HY birds was otherwise seen only for Golden-crowned Kinglets (*Regulus satrapa*) in 2000.

When the date on which the proportion of HY for each species exceeded 30% was ranked by year, the order for all species except Fox Sparrow (*Passerella iliaca*), for which 1998 and 1999 samples were very small, was 1998 > 2000 > 2001 > 1999. Likewise, in Orange-crowned Warbler and Hermit Thrush, the timing was very similar in 1999 and 2001: for all other species, the timing was later in 1999.

Proportion of hatching-years during the core period

The mean proportion of HYs trapped during the core period for the six species qualifying with > 14 trapped in all years varied significantly among years (ANOVA, $F_{3,33}$ = 8.00, $P < 0.01$), the lowest being 26% (+/-17%, $n = 9$) in 2001 and the highest 63% (+/-16%, $n = 8$) in 1998. Neither the early 1998 and 2000, nor the late 1999 and 2001, years differed significantly in proportion of HY birds, but both pairs differed from one another, with a higher proportion of HY birds in 1998 and 2000 (Duncan and LSD post-hoc comparisons, $P < 0.05$).

All species with adequate sample sizes in all four years showed positive correlations between proportion of HY and May temperatures (Fig. 5), SST, and SOI, and negative correlations with May rainfall. The relationships were significant for Orange-crowned Warbler (temperature: $r_3 = 0.998$, $P = 0.002$; SST: $r_3 = 0.998$, $P = 0.002$; rainfall: $r_3 = -0.984$, $P = 0.016$) and Hermit Thrush (temperature: , $r_3 = 0.95$, $P = 0.048$). There was a significant positive correlation between SOI and proportion of HY for Hermit Thrush ($r_3 = 0.964$, $P = 0.036$), and for Townsend’s Warbler (*Dendroica townsendi*) as well ($r_3 = 0.994$, $P = 0.007$).

When migrants, i.e., Hermit Thrush, Orange-crowned Warbler, Townsend’s Warbler, Pacific Slope Flycatcher, Fox Sparrow, and Song Sparrow

Fig. 4. Trends in the proportions of hatching-year birds captured by 10-d periods. Only species with *n* > 14 are shown. The year 1998 is represented by diamonds; 1999, by solid squares; 2000, by triangles; and 2001, by open squares.

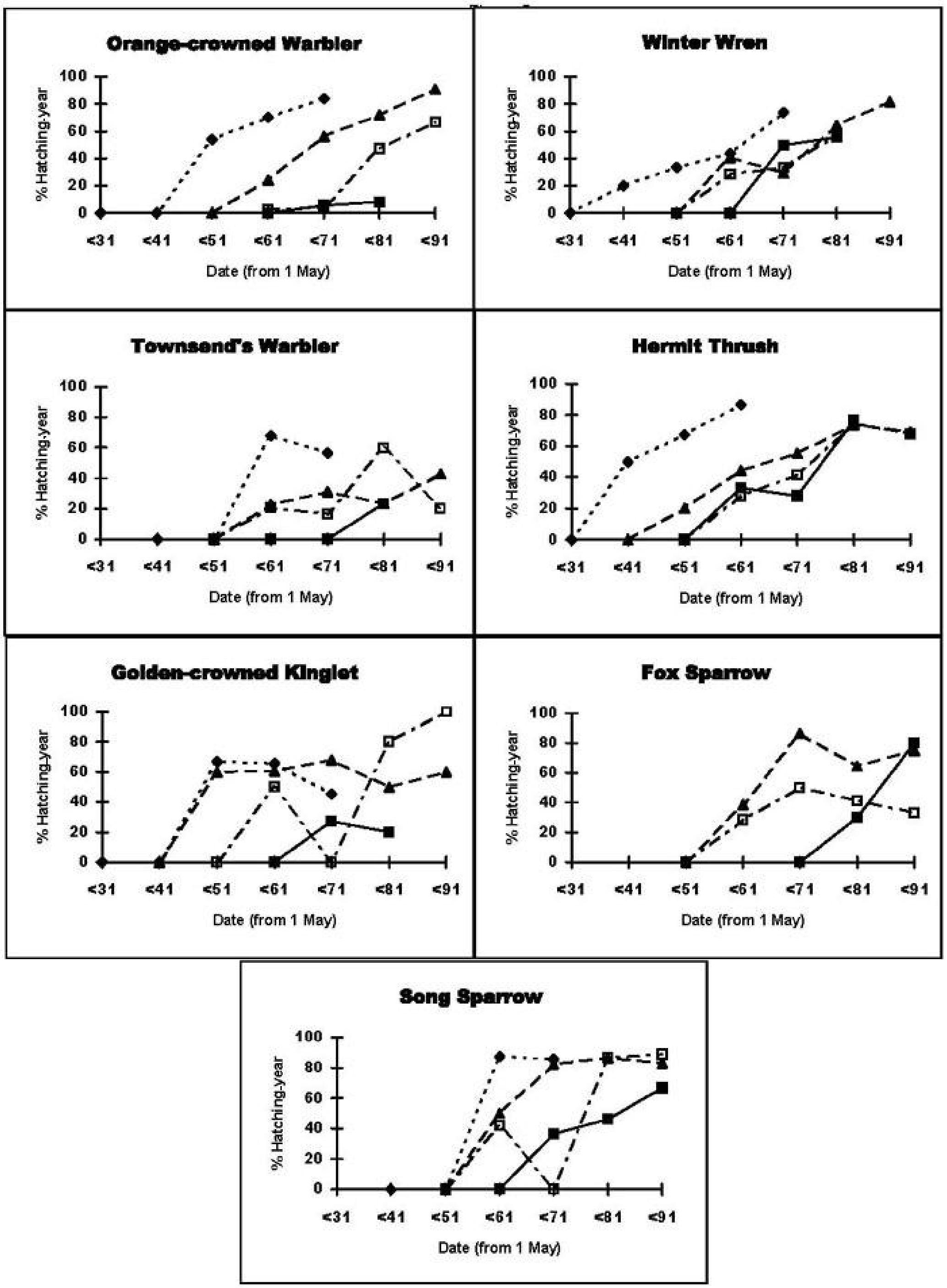
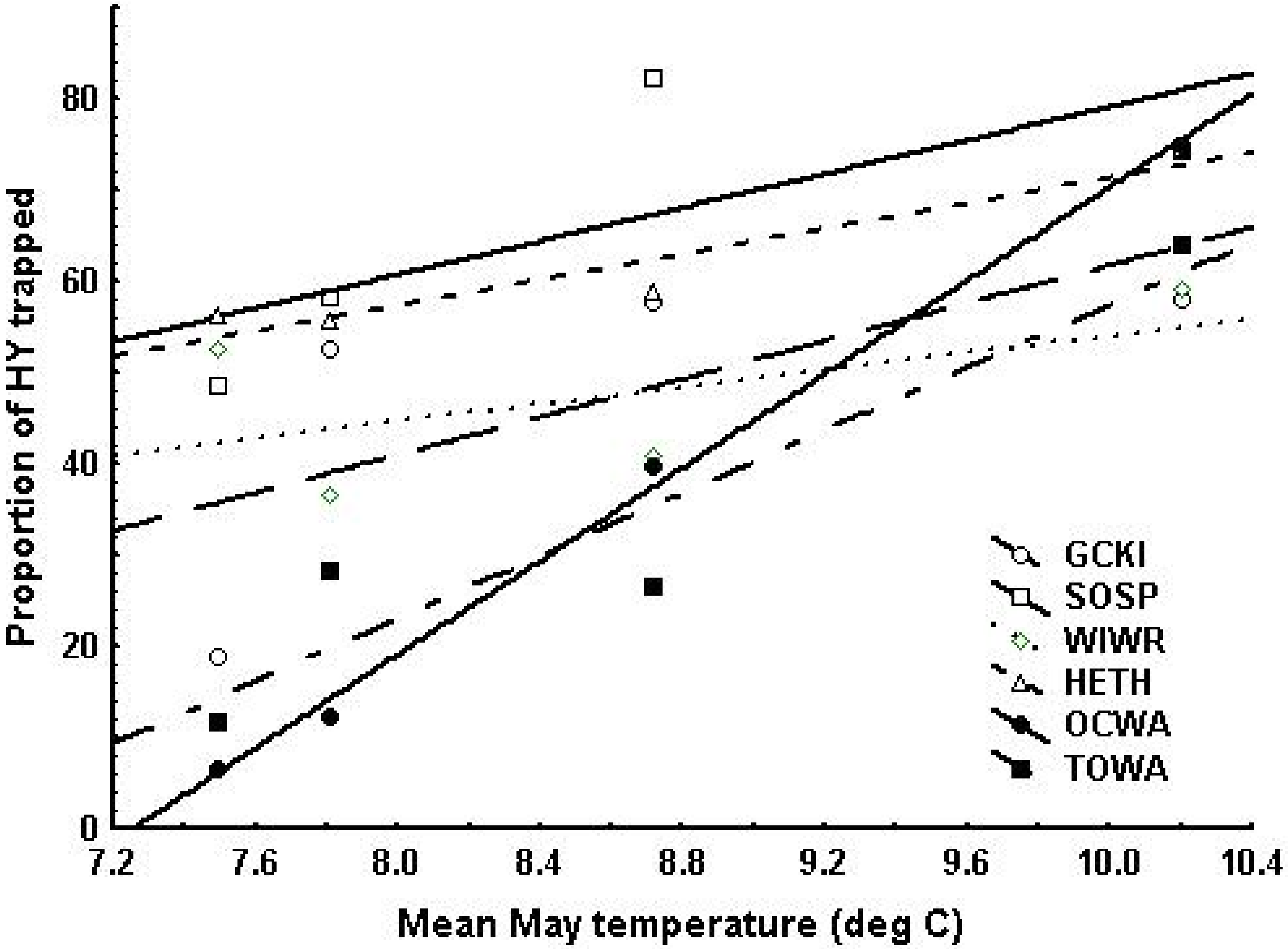


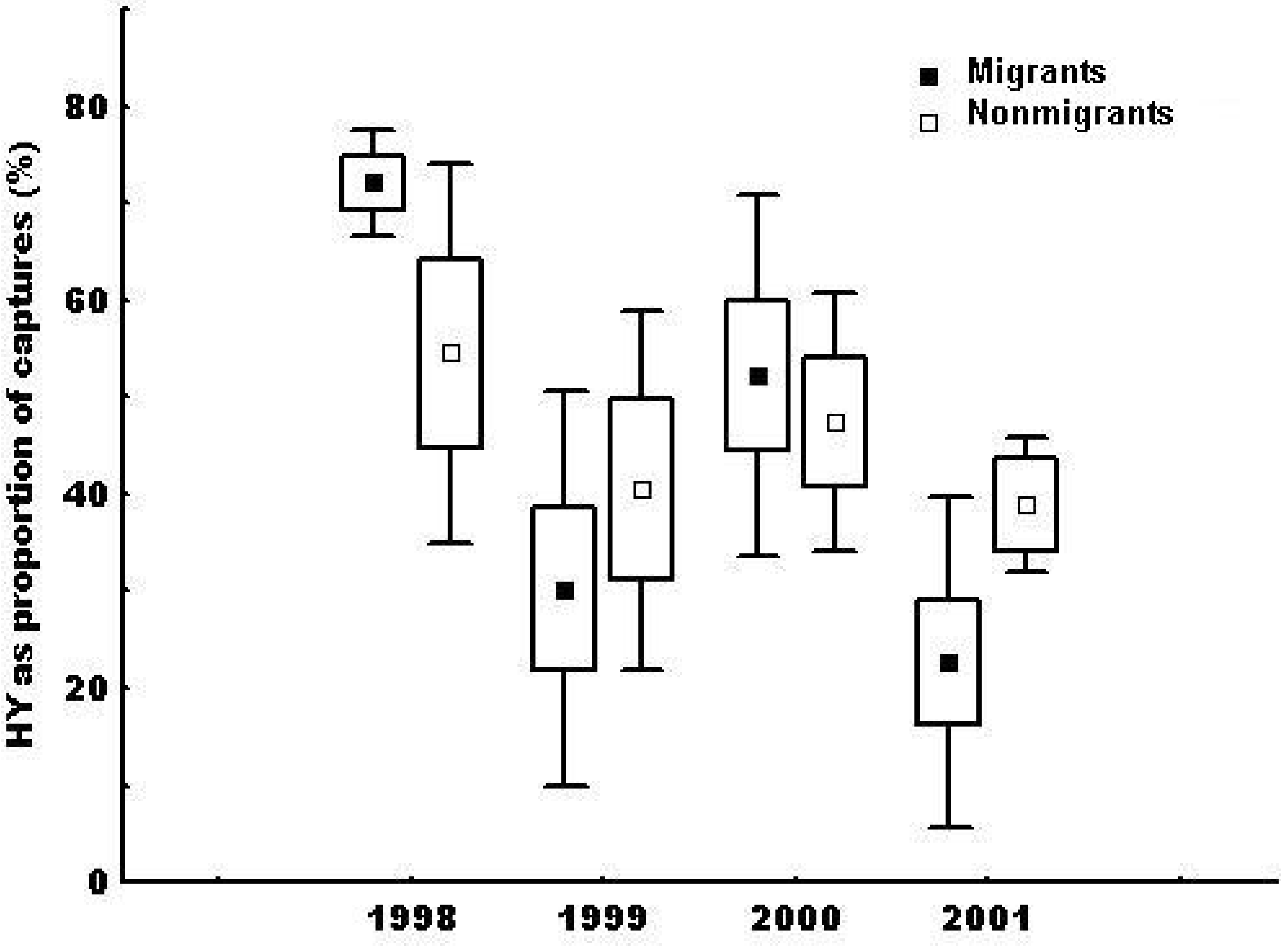
Fig. 5. Relationship between proportion of hatching-year (HY) birds captured during the core mist-netting period and mean May temperature at Sandspit for six species with adequate samples in all four seasons. GCKI = Golden-crowned Kinglet (*Regulus satrapa*), SOSP = Song Sparrow (*Melospiza melodia*), WIWR = Winter Wren (*Troglodytes troglodytes*), HETH = Hermit Thrush (*Catharus guttatus*), OCWA = Orange-crowned Warbler (*Vermivora celata*), and TOWA = Townsend's Warbler (*Dendroica townsendi*).



(*Melospiza melodia*), were separated from nonmigrants Brown Creeper (*Certhia americana*), Chestnut-backed Chickadee (*Poecile rufescens*), Golden-crowned Kinglet, Varied Thrush (*Ixoreus naevius*), and Winter Wren (*Troglodytes troglodytes*), both groups showed similar patterns of interyear variation (Fig. 6), but interyear differences were significant only for migrants (migrants: $F_{3,18} = 4.03$, $P = 0.02$; nonmigrants: $F_{3,12} = 0.55$, $P = 0.66$).

In 1998, 2000, and 2001, maximum proportions of HYs captured in a 10-d period exceeded 50% for all species, except for Townsend's Warbler in 2000, when the maximum proportion of HYs was 43%. In 1999, HYs did not exceed 27% for Golden-crowned Kinglets, 8% for Orange-crowned Warblers, or 23% for Townsend's Warblers (Table 4). Hermit Thrush and Fox Sparrow showed no evidence of lower peak levels of HYs in 1999.

Fig. 6. Mean proportion of hatching-years (HY) among all captures during the core period of mist-netting for species qualifying in more than one year. The symbols represent the median, the boxes contain a range of 25–75%, and the whiskers illustrate the extremes.



DISCUSSION

Timing of breeding

Apart from 2000, few hatching-year (HY) birds were trapped during the first week of mist-netting, suggesting that the dates of the first HY captures gave a good index of the timing of breeding in those years. Both the capture of HY birds by mist-netting and direct nest monitoring indicated strong interyear variation in the timing of breeding for several species of songbirds, with a mean delay for eligible species of about 15 d between the appearance of HY birds in 1999 compared to 1998. The start of the netting period in 2000, the only year in which the start of the core period was 2 d prior to the start of netting, appears to have been a little later relative to the timing of breeding than in the other three years, so that the dates of first HYs in 2000 are probably a little later than would otherwise have been observed. However, the proportions of HY Hermit Thrushes (*Catharus guttatus*), Orange-crowned Warblers (*Vermivora celata*), and Townsend's

Table 4. Maximum % of hatching-year birds captured in any 10-d period during core mist-netting. Sample sizes are given in parentheses.

Species	1998	1999	2000	2001
Brown Creeper (*Certhia americana*)	...	...	78.6 (14)	...
Chestnut-backed Chickadee (*Parus rufescens*)	...	...	100.0 (8)	77.7 (9)
Fox Sparrow (*Passerella iliaca*)	50.0 (4)	80.0 (5)	86.2 (29)	47.1 (17)
Golden-crowned Kinglet (*Regulus satrapa*)	65.5 (29)	27.3 (11)	67.9 (28)	100.0 (7)
Hermit Thrush (*Catharus guttatus*)	86.5 (37)	76.9 (39)	73.7 (57)	74.6 (63)
Orange-crowned Warbler (*Vermivora celata*)	83.8 (61)	8.3 (12)	90.7 (43)	58.3 (12)
Pacific Slope Flycatcher (*Empidonax difficilis*)	...	...	60.0 (10)	0 (21)
Song Sparrow (*Melospiza melodia*)	85.7 (21)	66.7 (9)	87.0 (46)	87.5 (16)
Townsend's Warbler (*Dendroica townsendi*)	68.0 (50)	23.5 (17)	42.9 (14)	60.0 (15)
Winter Wren (*Troglodytes troglodytes*)	73.9 (23)	55.6 (9)	81.5 (27)	60.0 (15)

Warblers (*Dendroica towndsendi*) in June were much higher in 1998 than in 2000 (Fig. 6), suggesting that breeding for these three species was earlier in 1998. HY ratios did not suggest that any species bred earlier in 2000 than in 1998.

HY ratios in Fig. 6 suggest that the difference in mean hatching dates between 1998 and 1999 may have been greater than that indicated by the dates of first capture of HYs, because HY proportions rose faster in 1998 than in 1999. The effect was relatively uniform across species, despite the fact that they included canopy gleaners such as warblers and kinglets as well as shrub and ground foragers such as thrushes, sparrows, and wrens. However, all species are insectivores during the breeding season (Ehrlich et al. 1988, Campbell et al. 1997). The only species for which the appearance of HYs in 1999 was not at least 10 d later than in 1998 was the Brown Creeper (*Certhia americana*), which, because it feeds on pupae in bark crevices, may be less dependent than other species on active insects.

Reproductive success

The lower proportions of HYs captured during the core trapping period in the two years of late breeding, 1999 and 2001, may have been partly a result of a greater spread of fledging dates in those years. However, the low maximum levels attained by some species in 1999 suggest that overall production of fledglings was also affected. It seems probable that the number of young produced by

Golden-crowned Kinglets (*Regulus satrapa*), Orange-crowned Warblers, and Townsend's Warblers, all canopy-feeding insect gleaners, was significantly lower in 1999 than in other years. The fact that some species, e.g., Hermit Thrushes, Fox Sparrows (*Passerella iliaca*), did not show such an effect indicates that the results were unlikely to have been caused by variation in the timing of the trapping period relative to the timing of breeding.

Reproduction in relation to weather

Air temperatures at Sandspit during 1980–2001 were strongly correlated with regional sea surface temperatures (SST), but rainfall was not. During our study, the pattern of variation in the timing of breeding and in the proportion of HYs during the core trapping period followed year-to-year changes in temperature, with later reproduction in the two cooler, wetter years, 1999 and 2001, as well as less successful reproduction in 1999 than in the warmer, drier years, 1998 and 2000. However, with a maximum of 3 d when rainfall exceeded 5 mm during the 15 d prior to mean date of the first HY observations, plus a maximum total accumulation during the same period of only 30.7 mm, it seems unlikely that reproduction would have been affected by heavy and prolonged rain in any year. Overall, the timing and synchrony of breeding seemed to follow May air temperatures better than rainfall. The warm temperatures in 1998 coincided with lower-than-normal rainfall, and this also may have contributed to early breeding in that year. Likewise, above-average rainfall might have contributed to the delayed breeding in 1999 and 2001.

Effects of the El Niño-Southern Oscillation

Our study coincided with a relatively strong El Niño event that began in 1997 and continued through the spring of 1998 (Chavez et al. 1999). This event was responsible for the high SSTs recorded in northern British Columbia waters in the first half of 1998 (Freeland 1998). This was followed by a very strong La Niña, a cold-water event that usually follows an El Niño, which caused SSTs in the Central Pacific to drop very quickly in the second half of 1998, leading, in 1999, to the lowest May SSTs and air temperatures in Haida Gwaii for two decades.

There is a substantial lag between the changes in SSTs associated with the El Niño-Southern Oscillation (ENSO) cycle at the equator and those affecting marine areas off northern British Columbia. In this case, SSTs at the equator began to fall sharply after May 1998 (Chavez et al. 1999), but this signal did not reach waters off northern British Columbia until February 1999. This complicates the analysis of weather patterns in Haida Gwaii in relation to the ENSO cycle. However, Gaston and Smith (2001) showed that SSTs at the same four light stations we used are correlated with the Southern Oscillation Index, a measure of pressure difference strongly connected to ENSO events. Hence, the coincidence between low SSTs and low air temperatures in Haida Gwaii in May 1999 was undoubtedly the result of the sharp onset of the 1998 La Niña. This cold spring seems to have caused the substantial delay in breeding observed in that year as well as lower-than-average productivity among canopy insectivores.

Among the four years examined, both 1999 and 2001 can be considered somewhat exceptional for May temperature, being colder than any other years since 1980. However, the 1980s and 1990s were an exceptionally warm period for the waters of the northern Pacific, as well as across North America (Francis et al. 1998, Freeland and Whitney 2000). Over a longer period, these temperatures were not exceptional. Although it was the warmest of the four years of our study, 1998 was cooler than 1983, 1990, 1993, and 1997, all of which were affected by El Niño conditions. Hence, our observations probably reflect typical interyear variation, rather than being driven by a single, exceptional event. The partial reproductive failure of certain species, especially the two warblers, inferred from HY ratios in 1999, probably forms a normal part of their population dynamics and may help to explain fluctuations in HY ratios observed periodically elsewhere, e.g., at migration stations (Stewart et al. 1974).

These results, taken in conjunction with other studies in western North America (De Sante and Geupel 1987, De Sante 1990, Nott et al. 2002), suggest that avian demographic signals from large-scale ocean-atmosphere circulation indices are frequent on the Pacific coast of North America. Effects of the ENSO cycle on the reproduction of migratory songbirds also have been demonstrated for Black-throated Blue Warblers (*Dendroica caerulescens*) in New Hampshire (Sillett et al. 2000) and for Yellow Warblers (*Dendroica petechia*) at Delta March, Manitoba (Mazzerole et al. 2005).

Such effects may be widespread among terrestrial birds.

Previous observations of variations in breeding by terrestrial birds in relation to the ENSO cycle have mainly involved the effects of changes in rainfall in arid or semi-arid areas (Gibbs et al. 1984, Gibbs and Grant 1987, Grant et al. 2000). However, moisture is unlikely to be an important limiting factor in Haida Gwaii and other temperate rain-forest areas, which are characterized by abundant year-round precipitation. Instead, it appears that May temperatures, possibly through their effects on the availability of arboreal insects, were sufficient to alter the timing of breeding and, in 1999, to reduce fledgling production for several species. This result accords with the findings of Wilson and Arcese (2003) for Song Sparrows in southern British Columbia.

For Darwin’s finches on the Galapagos Islands, Grant et al. (2000) emphasized the importance of demographic context in determining the effects of a particular El Niño event. Likewise, Sillett et al. (2004) found that the effect of increased population density on the reproduction in the Black-throated Blue Warbler (*Dendroica carulescens*) was greatest in El Niño years. In the case of our study, it is worth noting that the cold summer of 1999 came at the end of a particularly prolonged period of above-average SSTs, which had continued since 1992 (Fig. 2). Part of the strong effect of the 1999 La Niña event on the reproduction of songbirds in Laskeek Bay could have been caused by very high population levels for some species, as a result of several consecutive years of higher-than-average reproduction. However, we have no independent evidence for this.

CONCLUSIONS

Our results suggest that both the timing and success of reproduction in a suite of forest birds were affected by local weather conditions, and that these were driven by the El Niño-Southern Oscillation (ENSO) cycle, as measured by the Southern Oscillation Index. The similarity between effects on migrants and nonmigrants suggests that responses were caused by local conditions, rather than by conditions experienced during migration. The temperature, but not the rainfall, was correlated with ENSO phases, being warm during an El Niño year and cool during the subsequent La Niña conditions. Understanding this connection allows us to make predictions concerning the likely timing and success of reproduction for forest songbirds without detailed knowledge of local conditions.

Our results may have implications for the future demographics of coastal songbird communities. Climate predictions suggest that ENSO events will intensify with climate warming (Collins 2000*a,b*, Tsonis et al. 2003). For some species, especially the canopy-feeding insectivores, this suggests that reproduction is likely to become more episodic, possibly more erratic. Future conservation planning needs to take account of this possibility.

In Haida Gwaii, local populations of some songbirds, including Orange-crowned Warblers (*Vermivora celata*), Song Sparrows (*Melospiza melodia*), and Fox Sparrows (*Passerella iliaca*), have been severely depleted by the impacts of introduced black-tailed deer (*Odocoileus hemionus*) on their habitat (Allombert et al. 2005). Further stress from episodic reproduction could have adverse population consequences, especially for the Orange-crowned Warbler, the species most strongly affected by ENSO in our study. Recent studies suggest that Orange-crowned Warblers in Haida Gwaii and adjacent coastal areas represent a genetically distinct population derived from the occupants of a putative Pleistocene refugium (Bull 2005). Our results suggest that careful monitoring of this species in coastal British Columbia is warranted.

Responses to this article can be read online at:
http://www.ace-eco.org/vol1/iss1/art4/responses/

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