Sexual Differences in Spring Migration of Orange-crowned Warblers

Christopher D. Otahal
Coyote Creek Riparian Station
P.O. Box 1027
Alviso, California 95002

ABSTRACT

Mist-netting was conducted in riparian habitat near the southern end of San Francisco Bay, California, during the spring migratory period of Orange-crowned Warblers (*Vermivora celata*) for the years 1988 through 1993. Based upon our banding records, spring migration started in mid-March and ran through late May, with a slight peak in mid-April. Males migrated significantly earlier in each of the six springs examined in this paper.

INTRODUCTION

Male wood warblers tend to migrate earlier than females along the east coast of the United States during spring migration (Francis and Cooke 1986) and thus, exhibit differential migration — the situation in which distinguishable classes of individuals (e.g., sex or age groups) differ with respect to timing or distance of migration (Terrill and Berthold 1989). However, as pointed out by Ramos (1986), the differential migratory patterns seen in wood warblers are highly variable depending on sexual, racial, age, and seasonal factors. In this paper, I investigate the capture data obtained during constant-effort mist-netting operations carried out at Coyote Creek Riparian Station (CCRS) to determine the timing of spring migration at our site and to determine if a differential timing pattern occurs within our west coast populations of Orange-crowned Warblers.

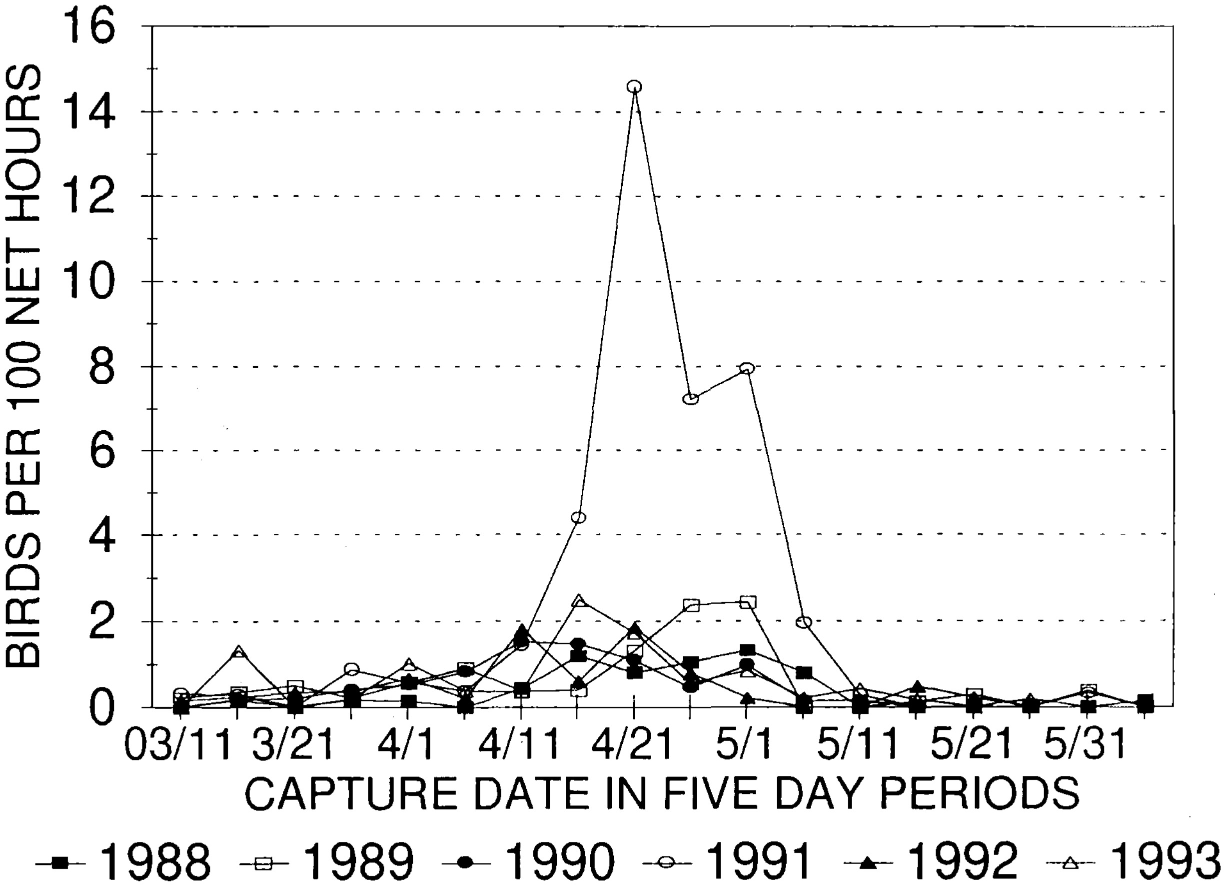
The Orange-crowned Warbler is a fairly common and widespread Neotropical migrant. The race which occurs at CCRS (referred to as the "Lutescent Orange-crowned Warbler" *Vermivora celata lutescens*) breeds from southern Alaska to southern California and winters from Baja California, western Mexico, to Guatemala (Sogge et al. 1994). A few individuals will also overwinter along coastal southern California and in the Central Valley north to Marysville, Yuba County (Grinnell and Miller 1944).

Based on our banding records and census data, most if not all individuals of this species only pass through our study site in migration during spring and normally do not breed in the immediate vicinity of our banding station. Several breeding bird censuses conducted on our study site from 1987 through 1993 (Bruce Katano, pers. comm.) and a six year breeding bird atlas effort on the site (Bill Bousman, pers. comm.) have failed to find any nesting Orange-crowned Warblers at CCRS. A few Orange-crowned Warblers do appear on site during the breeding season and in breeding condition (i.e., with developed brood patches or cloacal protuberances) but these are rare exceptions (4 females with brood patches and 11 males with cloacal protuberances during the five years of this study) and in all cases the brood patches or cloacal protuberances have been only slightly developed.

METHODS

These data were collected during constant effort mist-netting operations carried out at Coyote Creek Riparian Station, Alviso, California. The research site is located along the lower reach of Coyote Creek, approximately 9.2 km south of where the creek enters the southern end of San Francisco Bay. These data include bandings obtained during the spring migratory periods from 1988 through 1993. We used standard 30 mm or 36 mm nets. Nets were opened approximately 1/2 hour before sunrise and closed at approximately 11:00 am. A total of 63.5 nets (one net being 2 meters tall and 12 meters long) were established at permanent locations.

Figure 1. Rates of new captures of Orange-crowned Warblers.



The nets were operated in a staggered rotational fashion with 20 to 45 nets open on any given day with each of the 63.5 nets opened at least twice during any seven day period. Netting was conducted daily unless weather or other emergencies required closures.

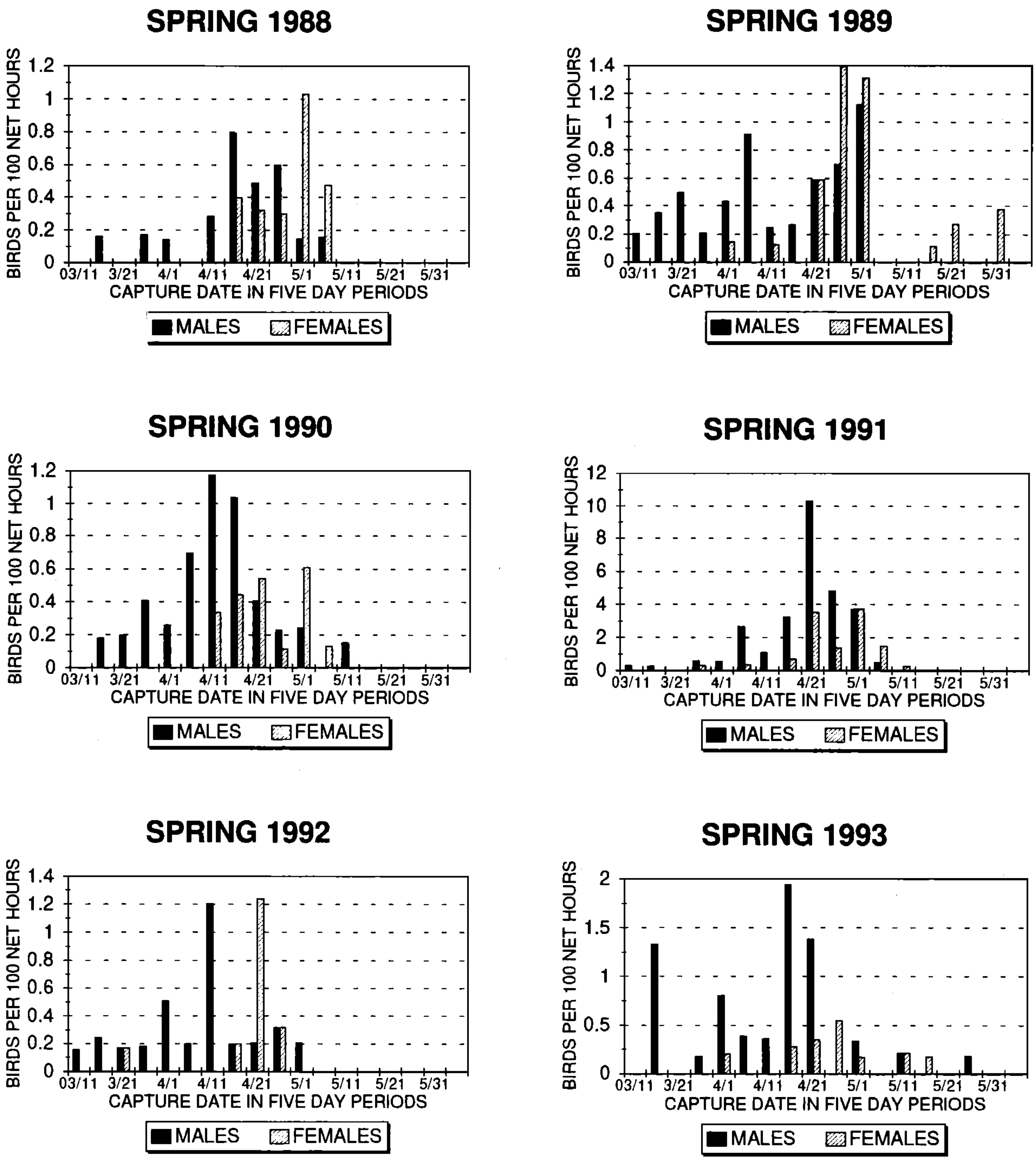
An attempt was made to sex the birds according to criteria based on Pyle et al. (1987). In summary, adult birds with concealed crowns greater than or equal to 14 mm were considered males, adult birds with concealed crowns less than or equal to 5 mm were considered females, and adult birds with concealed crowns of 6-13 mm were not sexed.

To establish the timing of migration for the species, the original capture records of Orange-crowned Warblers were pooled across five-day periods for each of the five years of the study and examined graphically (Fig. 1). All birds banded were included, whether sexed or not. Second, for each of the five years, the data were analyzed graphically by sex and to determine if any differential peaks in migration occurred (Fig. 2). In this second analysis, the data were also pooled into five-day capture periods to test for differences in the timing of migration between males and females. The data were then subjected to Mann-Whitney U tests (Table 1). For the Mann-Whitney tests the raw data, rather than the pooled data, were used.

Table 1. P values derived from Mann-Whitney U tests looking at differences between male and female peak migration.

YEAR	P VALUE
1988	0.001
1989	0.002
1990	0.001
1991	0.000
1992	0.016
1993	0.005

Figure 2. Capture rates of male and female Orange-crowned Warblers during spring migration (new captures only).



RESULTS

Summary of Banding Effort and Captures - A summary of net hours, days of banding and captures is presented in Table 2. For the purposes of this study, March 11 through May 31 was considered the migratory period (see timing pattern subsection) which gives a maximum total of 82 days of banding. Total number of days of operation each year ranged from 74 to 82 days (90%-100%).

Table 2. Summary of banding effort and captures. March 11 - May 31 (Total days possible if banding every day = 82)

YEAR	DAYS BANDING	PERCENT COVERAG	NET HOURS	BIRDS BANDED	BIRDS PER 100 NH	MALES BANDED	FEMALES BANDED	UNIDENT. BANDEDD	PERCENT MALES
1988	74	90.2	14653.4	39	0.27	18	16	5	52.9
1989	75	91.5	14601.9	67	0.46	33	29	5	53.2
1990	75	91.5	14702.7	55	0.37	33	16	6	67.3
1991	76	92.7	7502.7	161	2.15	103	46	12	69.1
1992	82	100.0	12425.3	45	0.36	21	10	14	67.7
1993	75	91.5	9878.0	45	0.46	31	10	4	75.6

Yearly net hours (one net hour representing one 12 meter net run for one hour) ranged from a low of 7502.5 hours to a high of 14653.4 hours. Capture rates ranged from a low of .27 birds per 100 net hours to a high of 2.15 birds per net hour. The percentage of captures which were males ranged from a low of 52.9% to 75.6%.

Table 3 presents a summary of trapping effort by five day periods for each of the years of study. Sampling times for each period ranged from a low of 122.8 net hours to a high of 1011.0 net hours.

Timing Pattern - Spring migration begins in mid-March, with a few individuals moving through as late as the end of May (Fig. 1). The spring of 1991 had an unusually high capture rate (Fig 1, Table 2). There is a general peak in captures at the end of April (Fig. 1).

Differences Between Males and Females in Timing - Male Orange-crowned Warblers were captured earlier than females during spring migration (Fig. 2). This early arrival varied from 2-6 banding periods (10-30 days). The peak capture rates of males were significantly ($P<.05$) earlier than females in all six years (Table 1).

DISCUSSION

Male Orange-crowned Warblers initiate migration earlier and peak captures occur earlier relative to females during spring migration. These findings are consistent with findings reported by Ramos (1988) and Francis and Cooke (1986) with their work on other wood warbler species.

Both the findings of Ramos (1988) and Francis and Cooke (1986) indicate that in order to gain reliable demographic data from migration studies, one must take care to sample the population consistently throughout the entire migratory period. Both of these works have shown that migratory patterns seen in wood warblers are highly variable depending on sexual, racial, age, and seasonal factors. Thus, it is important to have standardized effort throughout the entire season. For example, if effort (increased net hours) was concentrated during the earlier part of the migration period in which males precede females, there is the possibility that sampling would be biased in favor of males over females. This does not seem to be the case in the data presented here. Though there is considerable variation in sampling effort between years (Table 2), the sampling effort within years is fairly consistent with a few notable exceptions (Table 3). Since all analyses were conducted on a yearly basis, the effects of differential sampling effort was kept to a minimum. Also, in each of the years, the sampling period was more or less consistent in terms of the number of days sampled (Table 2) varying from 74 to 82 days. Even in the worst year, 1988, no more than eight days had no banding and in no case was there more than two consecutive days in which no banding occurred.

Table 3.	Summary of trapping effort by five-day periods in net hours.					
	1988	1989	1990	1991	1992	1993
MAR 11-15	274.0	494.5	436.5	326.0	639.3	371.0
MAR 16-20	614.5	284.3	550.0	358.0	416.0	225.0
MAR 21-25	372.0	405.1	507.1	122.8	599.0	221.0
MAR 26-31	587.5	487.5	491.0	343.5	553.8	571.5
APR 1-5	708.0	694.8	770.8	348.8	591.0	496.0
APR 6-10	701.5	547.3	719.3	261.6	501.3	516.0
APR 11-15	694.0	807.5	596.0	276.8	663.6	558.0
APR 16-20	504.5	750.0	675.5	431.5	504.0	361.0
APR 21-25	617.3	681.0	736.3	397.8	484.5	578.0
APR 26-30	669.0	717.0	866.2	291.0	627.3	549.3
MAY 1-5	680.0	533.0	822.0	429.3	477.8	593.0
MAY 6-10	632.8	1011.0	766.9	408.3	632.5	490.8
MAY 11-15	783.5	708.3	647.3	364.8	566.8	474.5
MAY 16-20	730.5	868.8	847.9	219.8	625.1	584.5
MAY 21-25	780.8	734.6	522.0	414.0	497.5	453.0
MAY 26-30	746.5	727.8	322.5	423.2	547.3	557.0
MAY 31-JN 4	784.5	788.8	728.6	307.3	632.5	534.8
JUN 5-9	673.0	644.5	713.8	413.0	458.8	551.0
JUN 10-14	739.5	812.3	773.9	384.5	590.0	335.5
JUN 15-19	792.0	604.8	645.0	426.7	593.8	363.6
JUN 20-24	799.0	757.0	851.8	205.0	604.8	321.5
JUN 25-29	769.0	542.0	712.3	349.0	618.6	172.0
MAXIMUM	799.0	1011	866.2	431.5	663.6	593.0
MINIMUM	274.0	284.3	322.5	122.8	416.0	172.0
AVERAGE	666.1	663.7	668.3	341.0	564.8	449.0

Somewhat different selective pressures may act on males than on females during spring migration. It may be advantageous for males to arrive on the breeding grounds as soon as food resources and climatic conditions are adequate for survival, whereas, it may be more advantageous for females to arrive later when conditions are optimal for nesting (e. g., see Francis and Cooke 1986). Birds arriving on the breeding grounds early may be exposed to enhanced risks such as reduced food availability (Nolan 1978), cooler weather and late storms (e. g., see Whitmore et al. 1977). However, males that arrive on the breeding grounds early may have a better chance of acquiring higher quality territories or mates than males that arrive later (Francis and Cooke 1986) . Thus, the selective advantage of early arrival (within limits) may outweigh the costs for males (Francis and Cooke 1986) and may be a driving factor in selecting for early migration of males.

On the other hand, the benefits of early arrival on the breeding grounds may be less beneficial for females since they do not have to establish territories and the negative factors such as risk of poor weather conditions and lack of prey items may become more important (Francis and Cooke 1986). If females have less to gain by early arrival, natural selection would favor females which migrate later when conditions on the breeding grounds are more favorable for their survival and there are sufficient reserves of food available for nesting and egg production.

It may be that some sexual differences in migratory behavior are sexually-linked, heritable traits (Terrill and Berthold 1989). A strongly heritable basis for migratory behavior has been demonstrated in several species of passerines, primarily migrant Old World warblers of the genus *Sylvia* (Berthold 1988, Berthold and Terrill 1991). One of these species, the Blackcap (*Sylvia atricapilla*), has been experimentally demonstrated to show differential, endogenous, migratory behavior between the sexes (Terrill and Berthold 1989). In the autumn, hand-reared females show significantly more nocturnal migratory activity for a significantly longer period than males. In spring, males initiate migratory activity significantly earlier than females. Ramos (1988) is of the opinion that data such as presented here where migration patterns appear to be repeated very precisely in time serves as evidence that some aspects of migration are affected by endogenous control mechanisms.

The spring of 1991 was a very unusual season in terms of capture rate. There was a substantially increased capture rate for Orange-crowned Warblers in 1991 (Fig. 1, Table 2). This greatly increased spring capture rate was also seen in the Swainson's Thrush (*Catharus ustulatus*) and Wilson's Warblers (*Wilsonia pusilla*) using our area (CCRS, unpublished data). At the same time Yellow Warblers (*Dendroica petechia*) and Pacific Slope Flycatchers (*Empidonax difficilis*) suffered substantial decreases in capture numbers (CCRS, unpublished data) during this year. I have no explanation to account for this unusual year.

Another interesting trend has been an increasing number of males as a percentage of total captures (Table 2). In 1988, 52.9% of the captures were males and this has steadily increased to a high of 75.6% males in 1993. Again, I have no explanation for this trend.

As illustrated by this paper, migration banding can provide important insight into migratory behavior. Data such as these are only obtainable by systematic, long term banding programs such as we have at Coyote Creek Riparian Station and other bird observatories in North America and Europe. When the same patterns are apparent year after year, it is a strong indication that this is a regular and possibly predictable event rather than a random occurrence.

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LITERATURE CITED

Berthold, P. 1988. The control of migration in European warblers. Proceeding XIX Inter. Ornith. Cong. Ottawa. (Pp. 215-249.)

Berthold, P. and S. Terrill. 1991. Recent advances in the study of bird migration. *Ann. Rev. Ecol. Syst.* 22:357-378.

Francis, C. M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (parulinae). *Auk* 103:548-556.

Grinnell, J. and A. H. Miller. 1944. The distribution of the birds of California. Pacific Coast Auifauna No. 27. (Pp. 392-394.)

Nolan, V., Jr. 1978. Ecology and behavior of the Prairie Warbler, Dendroica discolor. *Ornithol. Monogr.* No. 26.

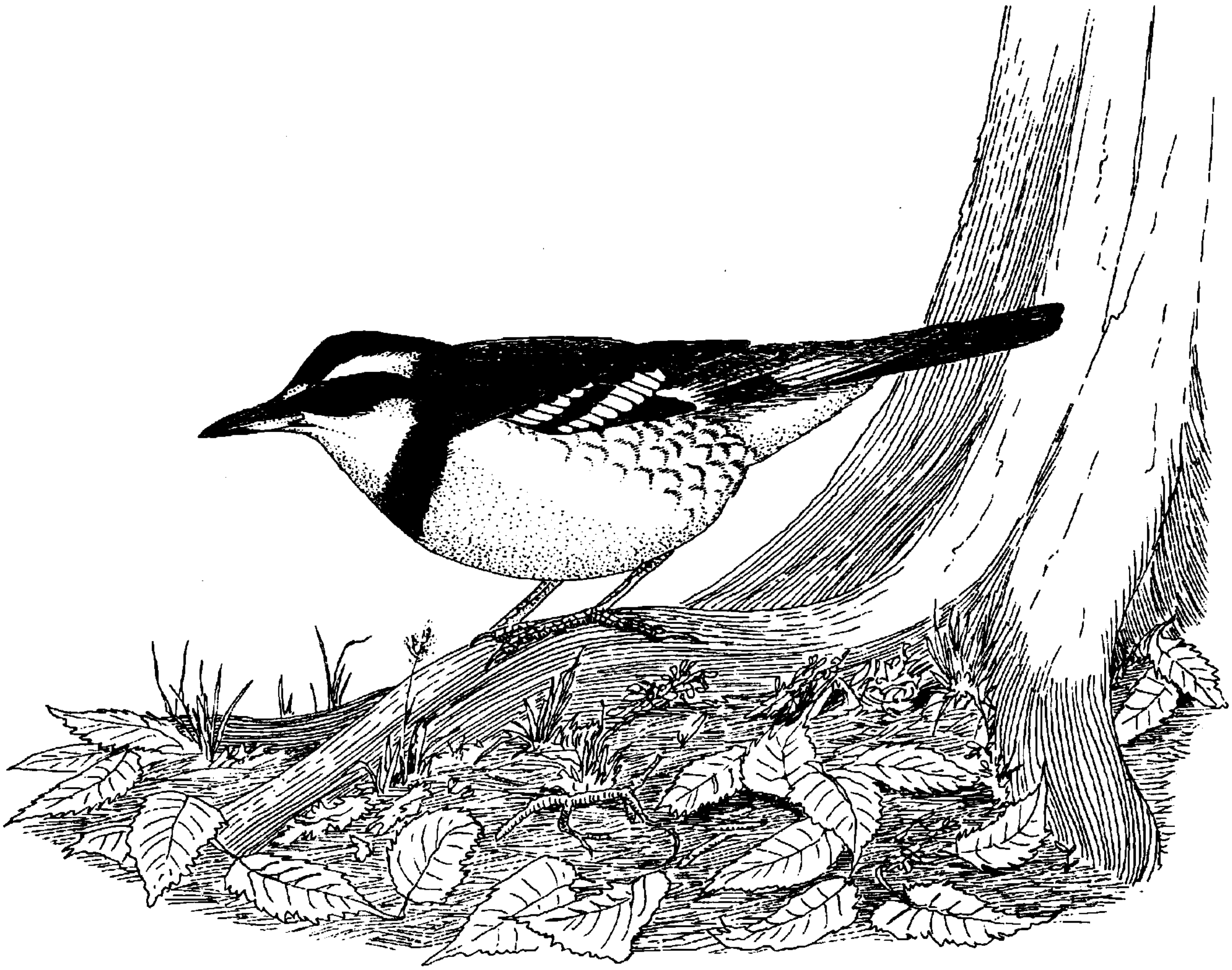
Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA. (Pp. 130.)

Ramos, M. A. 1988. Eco-evolutionary aspects of bird movements in the northern Neotropical region. Proc. XIX Intern. Ornith. Cong. Ottawa. 1:251-293.

Sogge, M. K., W. M. Gilbert and C. V. Riper III. 1994. Orange-crowned Warbler (*Vermivora celata*). *In* The Birds of North America, No. 101 (A. Poole and F. Gill, Eds.). Acad. Nat. Sci., Philadelphia.

Terrill, S. B. and P. Berthold. 1989. Experimental evidence for endogenously programmed differential migration in the Blackcap *(Sylvia atricapilla). Experientia* 45:207-209.

Whitmore, R. C., J. A. Mosher, and H. H. Frost. 1977. Spring migrant mortality during unseasonable weather. *Auk* 94:778-781.



The above computer graphic of a Varied Thrush by George C. West is an example of his excellent work. Many of his graphics have been published in the North American Bird Bander. If you are interested in high quality bird species graphics on computer disks, they are available from Birchside Studio, P.O. Box 841, Homer, AK 99603. Send $1.00 for a catalog containing almost 300 images of 169 species of North American birds. Custom drawings can also be created. Files are available in most formats for DOS and Windows applications.