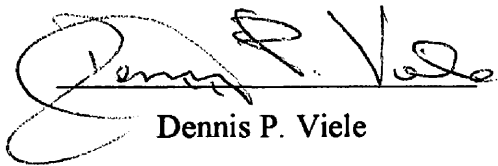# Nutrient utilization

# of winter retained and spring ripened fruit

# by cedar waxwings (*Bombycilla cedrorum*)

Cheryl L. Purdue

Thesis submitted to the Faculty of the

University of Michigan – Flint

in partial fulfillment of the requirements for the degree

of

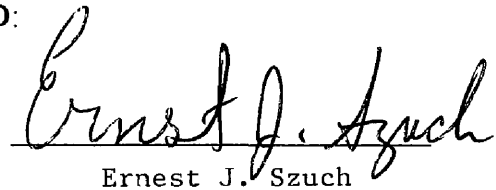Master of Science

in

Biology

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# Nutrient Utilization
## of
## Winter Retained and Spring Ripened Fruits
## by Cedar Waxwings (*Bombycilla cedrorum*)

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## Abstract

Frugivores that winter-over in temperate climates must use strategies that exploit any remaining fruit sources in order to obtain nutrients until spring fruit develops. This study compares nutrients available in persistent, winter retained fruits to nutrients available in late spring ripened fruits and utilization of those fruits by cedar waxwings (*Bombycilla cedrorum*). Uneaten fruit samples from Washington hawthorn (*Crataegus phaeropyrum*), crabapple (*Malus* sp.), serviceberry (*Amelanchier canadensis*), and Japanese scholar tree (*Sophora japonica*) sources along with corresponding resultant fecal waste samples were analyzed for dry mass content of $Na^+$, $K^+$, $Mg^{2+}$, $Ca^{2+}$ and N. Waxwing intakes of

each nutrient were also compared with known requirements for growing eastern bluebirds. Findings suggest that waxwings are in positive balance for $K^+$, $Mg^{2+}$, and $Ca^{2+}$ for the tested winter and spring fruits and that three of the four tested fruits may be adequate in maintaining a nitrogen budget. Winter retained hawthorn fruit may not be an adequate source of $Na^+$. All other nutrients tested in both winter retained fruit diets showed positive balance for wild waxwings. Nutrient levels in over-wintered hawthorn fruit were found to change over time to provide a more optimal nutrient source. Some tested nutrient levels consumed by waxwings fell below levels required by growing bluebirds.

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# Figures and Tables

* includes eastern bluebird growth requirements

# Introduction

Cedar waxwings are migratory frugivores that may winter-over in the temperate climates of North America. Large flocks are known to travel nomadically in search of exploitable fruit sources (Witmer et al., 1997). Toward winter's end, waxwings rely on plants still bearing fruit until spring ripening fruits appear. Typically, and for unknown reasons, fruits left uneaten until winter's end are of the same species each year (Witmer, 1996a; Herrera, 1982; personal obs.).

Questions have long been raised over the degree to which the diet of a frugivore supplies necessary nutrients to the individual (Witmer and Van Soest, 1998; Bairlein, 1996; Johnson et al., 1985; Williams et al., 1999; Witmer, 1998b). Nutrients derived from each fruit eaten are limited by in-digestible seeds (Levey and Grajal, 1991; Witmer, 1998a). Additionally, many fruits are high in sugars, but low in proteins and often fats (Bairlein, 1996; Herrera, 1987; Williams et al., 1999). Lipid rich food is a substantial component in the diets of many North American frugivores, but the waxwing diet is dominated by sugary, seeded fruit (Witmer, 1996a, 1998a). Waxwings are thus presented with the challenge of employing foraging, as well as digestive strategies to overcome the nutritional limitations of their diet. Much of avian frugivore research addresses digestive function and sugar utilization in captive subjects and rarely is fruit choice or the non-sugar nutrients of the free-flying frugivore's diet examined (Sorensen, 1984; Johnson, et al, 1985; but see Witmer and Van Soest, 1998; Studier, et al, 1988; Berthold, 1976).

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There is considerable evidence that there are varying qualities among fruits. Differing lipid and carbohydrate content are major characteristics often used to classify fruits. Herrera (1982) found spring/summer fruits in Spain to be more succulent and less nutritious in lipids and proteins than later ripening fruits. Stiles (1980) explained that the high degree of attractiveness of spring/summer fruits to frugivores is due to the fruits' high sugar contents. Other tests of food preference seem to indicate existence of an ability to discern nutrient qualities in fruits that avian frugivores choose. Using three species of captive frugivorous birds as subjects, Johnson, et al (1985) found a correlation between chosen fruit consumption and protein content. For cedar waxwings wintering in Oklahoma, no correlation was found between percent water content and preference in fruit (McPherson, 1987).

Seasonal changes in caloric demands, may explain why "high quality" fall fruits (with high lipid content) are chosen by birds before "low quality" fall fruits (with low levels of lipids) as Stiles (1980) suggests. Such "low quality" fruits are often retained on the plant long into winter (Stiles, 1980; McPherson, 1987; pers. obs.). Witmer (1996a), however, found fruits chosen by wild waxwings to be consistently high in sugar and low in lipids to the extent that some high lipid fruits are never eaten.

Clearly, frugivores are discerning in fruit choice and differences do exist in protein, lipid and carbohydrate content of various fruits, but the extent to which these major fruit constituents affect fruit choice is not clear. Less is known about other nutrients and their utilization by avian frugivores, particularly wild subjects.

Nutritional budgets in free flying cedar waxwings feeding on Washington hawthorn pomes in late winter were studied by Studier, et al (1988). The findings from a one day feeding bout showed waxwings to exhibit positive nitrogen balance and negative $K^+$, $Na^+$, $Ca^{2+}$, $Mg^{2+}$ and water balances. That previous study left many unanswered questions, including: Why are hawthorn fruits ignored and left to persist so long through the winter? Would the same pattern of consumption and nutrient utilization exist in other over-wintered fruit? Is utilization different between over-wintered and spring ripened fruit?

Hawthorn pomes are one of the fruit types considered "low quality" by Stiles (1980) and as he predicts, are typically left uneaten until winter's end (pers. observ.). The few hawthorn species studied have been shown to have 1% to 8.6% crude fat (Stiles, 1980; Witmer, 1996a) and 8% to 31% sugar (Studier et al., 1988; Witmer, 1996a). These ranges of fat and sugar seem to fall well within the ranges of low lipids and high sugars that Witmer (1996a) finds to be preferred by cedar waxwings but not optimum as stated earlier. Why then is hawthorn overlooked for so long in the year as a food source? Studier et al. (1988) proposed that the timing of feeding on winter retained fruit is such that the fruit is in an advanced state of ripeness and that this might benefit the bird by reducing assimilation time, thus conserving energy. But "ripening" speaks only of the "freeing" of sugar, or the hydrolysis of starch into various saccharides. Might retained fruit, over time, undergo changes in other nutrients – changes that might result in more nutritional benefit for the frugivore?

In this study I compare the non-lipid, non-carbohydrate nutrients of nitrogen, calcium, magnesium, sodium, and potassium present in two pome forming persistent fruits, over-wintered (fall ripened) fruit from Washington hawthorn and over-wintered crabapple. Further comparisons are then made between these two fall ripened fruits and the concentrations of the same nutrients in spring ripened fruit of the serviceberry tree and Japanese scholar tree. I then quantitatively evaluate and compare utilization of the fruits by non-captive cedar waxwings. Suspecting that foraging of winter-retained fruit may be coincidental to some significant change in their nutrient components, I tested for concentration changes of these nutrients in Washington hawthorn fruit for several weeks prior to and during their consumption by wild cedar waxwings (a 42 day span). Ability to collect large samples of over-wintered hawthorn fruit for testing led to its choice. Longitudinal studies of nutrient concentrations in fruits other than hawthorn were not done due to inadequate supply of sampling size after initial foraging day.

## Methods and materials

In order to assess any changes in mineral and nitrogen concentration in winter retained fruit, several samplings of fruit needed to be taken over a reasonable length of time prior to bird foraging. A survey of the local residents revealed that large flocks of cedar waxwings feed on a large group of Washington hawthorn trees at county and municipal offices in Flint, Michigan (Genesee County) during March of each year. From mid-February through mid-March, 2001, individual pomes were snipped weekly from 6-8 trees in this area. No birds were observed foraging on pomes at any time during this period. Fruit samples were double wrapped in plastic bags and frozen at 0° C until analysis.

On 13 March, a large flock of 100+ Cedar Waxwings began their yearly foraging routine on this stand of hawthorns. Over the following two weeks, birds frequented the trees daily at dawn and fed for approximately 2-3 hours. Three times each week, mixed wastes were collected upon plastic sheets that had been spread under the trees prior to the birds' arrival. Elimination time after ingestion for these birds is approximately 20 minutes (Studier et al., 1988), therefore droppings that rapidly accumulated were assuredly resultant from this fruit. Fruit samples were also collected from the same trees immediately prior to birds' arrival or following their departure. Samples of fruits and droppings collected at these times were frozen as described previously.

To locate other fruit sources that routinely draw large flocks of waxwings, I solicited information via internet bulletin boards devoted to bird watching in Michigan.

In mid-April, 2001 waxwings began foraging on over-wintered crab apples from three trees at the University of Michigan – Flint campus (Genesee County). Samples of mixed wastes and individual fruits from these trees were collected as previously described and stored, frozen, for later mineral and nitrogen concentration analysis.

The same collecting and storing procedures were used for spring ripened fruits and resultant mixed wastes from birds feeding on Japanese scholar tree fruits in mid-May of 2002 and serviceberry tree fruits in mid-June, 2002 (both in Washtenaw Co., MI).

All frozen samples, once massed, were dried to constant mass in a 60 ° C oven. Seeds were dried separate from pulp in some samples of hawthorn, crabapple, and scholar fruits. Samples of dried whole fruit, dried pulp, dried seeds, and dried wastes were wet oxidized using 1 ml of boiling concentrated $H_2SO_4$ in 100 ml volumetric flasks containing several non-selenized Hengar granules, followed by addition of 3 ml of 30% $H_2O_2$ : concentrated $H_2SO_4$ (2:1 v/v). Samples were then cooled and diluted to 100 ml. One-half ml aliquots of each sample were analyzed by Nesslerization for nitrogen content and reported as percent dry mass (Treybig and Haney, 1983). Additional aliquots of all samples were diluted, prepared appropriately, and then analyzed for $Na^+$, $K^+$, $Ca^{2+}$, and $Mg^{2+}$ concentrations, using an AA-20 atomic absorption spectrophotometer (Analytical methods for flame spectroscopy, Varian Techtron Ptg. Ltd., Springvale, Australia). Results from these tests were reported as parts per thousand (ppt) dry mass. Statistical analyses were completed using SPSS 10 for Windows (release 10.1, copyright SPSS inc., 1989-2000).

## Results

### Hawthorne fruit changes over time

Multiple regression analysis was performed to evaluate weekly changes in nitrogen, magnesium, calcium, potassium or sodium in winter retained hawthorn fruit for 42 days (J. days 46 – 87)). This period included 19 days prior to and 23 days after waxwings began foraging the fruit.

Nitrogen levels in hawthorn whole fruit rose steadily through preforaging (Julian Days 46-73) and continued to rise while birds foraged from Julian Days 74 – 87 ( [N] %dry mass = 0.00101 (J. day) $^2$ - 0.0899 (J. day) + 2.97; $r^2$=0.334; df = 2,116; F= 29.1; p<0.001) (Figure 1). Hawthorn pulp nitrogen levels also rose steadily during this time ([N] % dry mass = 0.0019 (J. day)$^2$-0.178 (J. day) + 4.36; $r^2$ = 0.706; df = 2,116; F= 85.0; p<0.001). Seed nitrogen changes over this time were not significant.

Calcium concentration increased linearly in winter retained hawthorn pulp over the time of this study ( [Ca] ppt= 0.147 (J. day) – 2.41; $r^2$ = 0.261; df = 1,72; F = 27.0; p<0.001) (Figure 2). There were no significant calcium changes during this time in whole fruit or in seeds of hawthorn.

Pulp of the hawthorn fruit showed a drop in magnesium levels until just prior to bird foraging at which time the regression shows a positive relationship ([Mg] ppt = 0.00352 (J. day) $^2$ - 0.442 (J. day) + 15.7; $r^2$ = 0.5792; df = 2,71; F = 48.9; p<0.001) (Figure 3). The regression for whole fruit magnesium showed the same pattern ([Mg] ppt = 0.0008 (J. day) $^2$ - 0.104 (J. day) + 4.77; $r^2$ = 0.1236;

**Nitrogen Levels in Hawthorne Seeds, Pulp, Whole Fruit and Mixed Wastes**

Figure 1. Nitrogen nutrient level changes in Washington hawthorn seed, pulp, whole fruit and mixed wastes over time. Preforaging fruit samples were taken on Julian Days 46-64. Cedar waxwings began foraging on Julian Day 73. Fruit and mixed wastes were sampled on Julian Days 73-87. (Mixed wastes shown as ◇. Fruit and components data points not shown for clarity. Only utilization of pulp was studied therefore only regression line equations for pulp are shown.)

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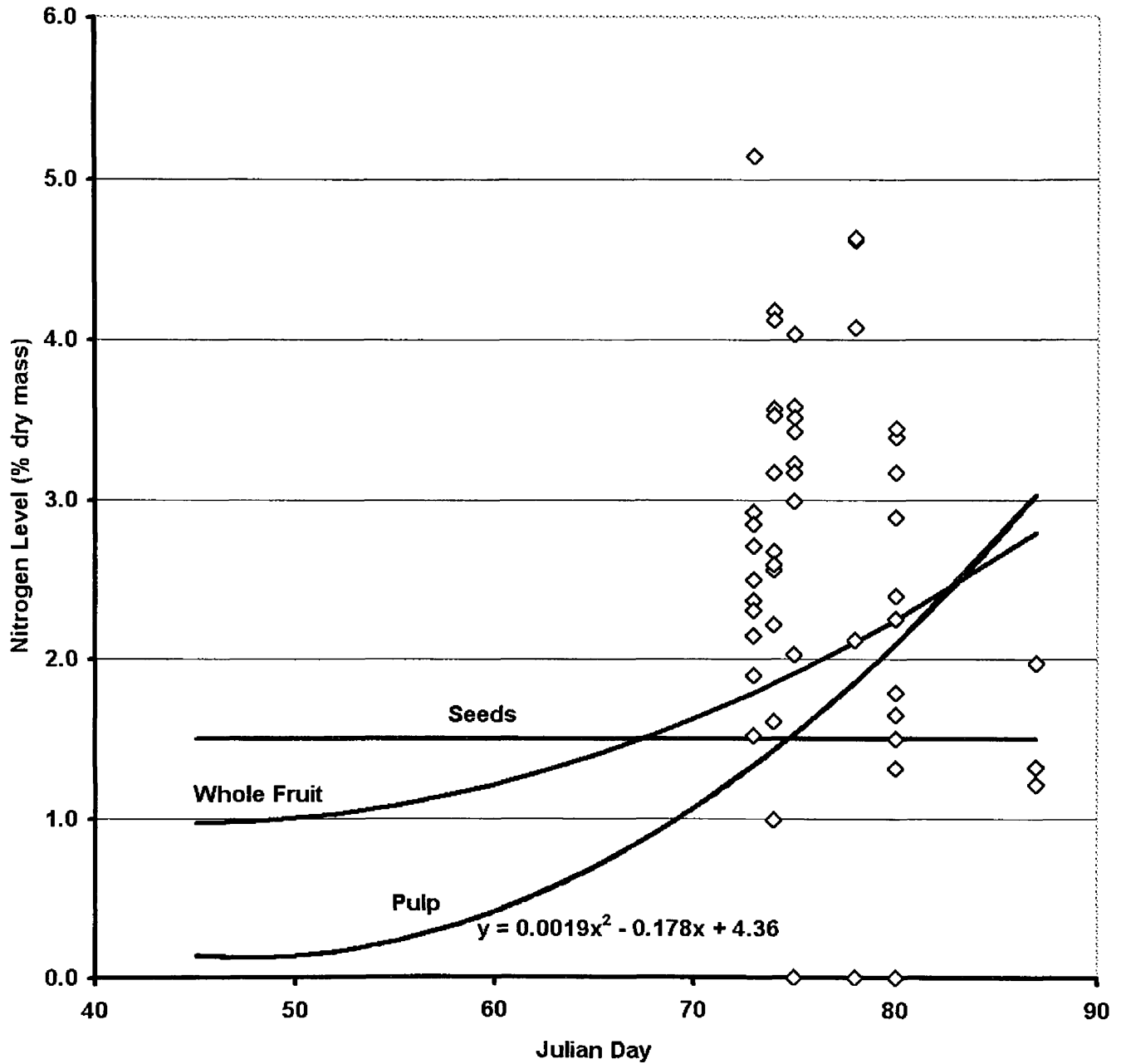**Calcium Levels in Hawthorne Seed, Pulp, Whole Fruit and Mixed Wastes**



Figure 2. Calcium nutrient level changes in Washington hawthorn seed, pulp, whole fruit and mixed wastes over time. Preforaging fruit samples were taken on Julian Days 46-64. Cedar waxwings began foraging on Julian Day 73. Fruit and mixed wastes were sampled on Julian Days 73-87. (Mixed wastes shown as ◇. Fruit and components data points not shown for clarity. Only utilization of pulp was studied therefore only regression line equations for pulp are shown.)

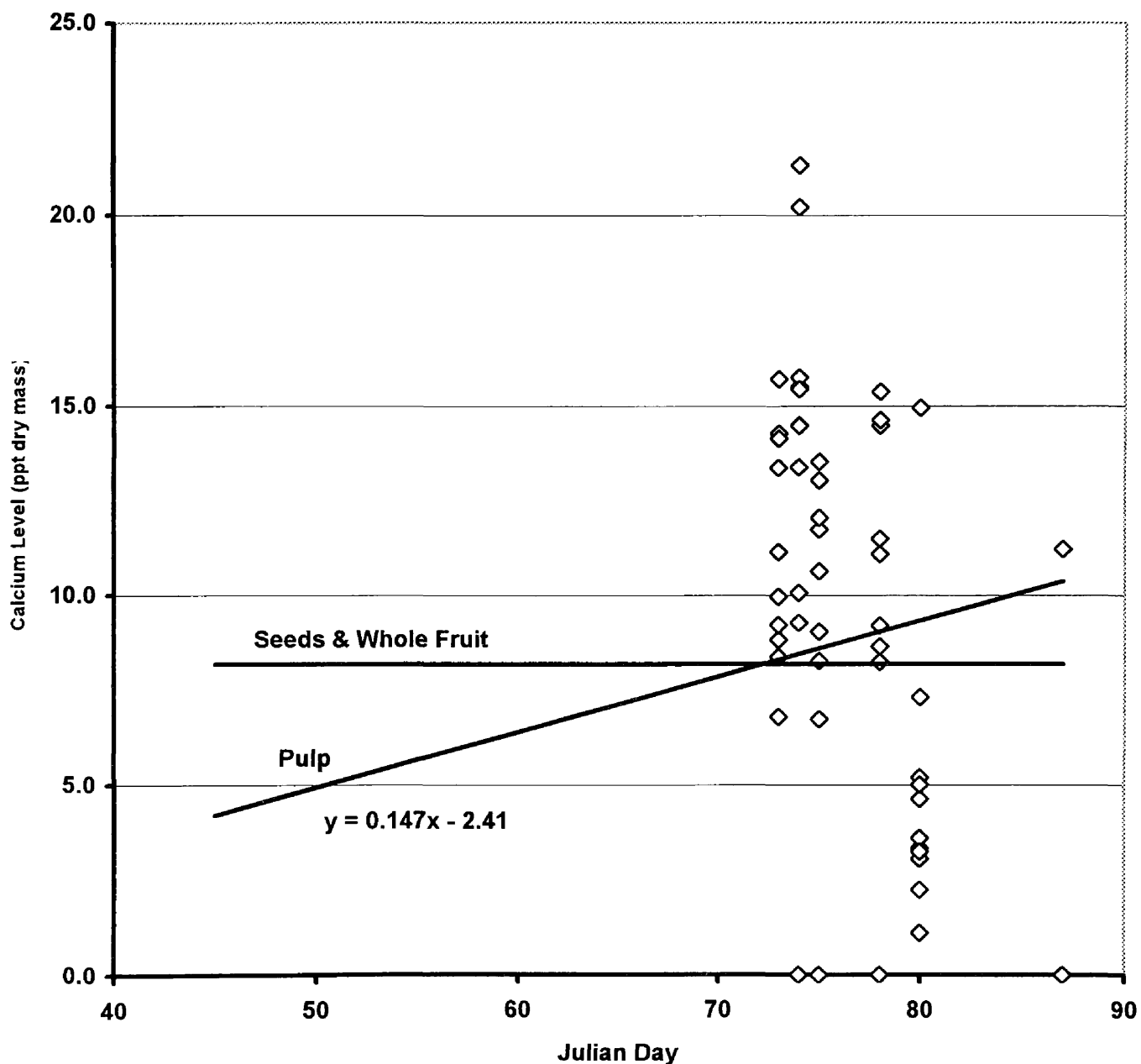# Magnesium Levels in Hawthorne Seed, Pulp, Whole Fruit and Mixed Wastes



Figure 3. Magnesium nutrient level changes in Washington hawthorn seed, pulp, whole fruit and mixed wastes over time. Preforaging fruit samples were taken on Julian Days 46-64. Cedar waxwings began foraging on Julian Day 73. Fruit and mixed wastes were sampled on Julian Days 73-87. (Mixed wastes shown as ◇. Fruit and components data points not shown for clarity. Only utilization of pulp was studied therefore only regression line equations for pulp are shown.)

df $= 2,116$; F $= 8.2$; p<0.001). There was no significant relationship between seed

magnesium concentration and Julian day (p $= 0.117$).

From Julian Day 47 through the end of the study (Julian Day 87), hawthorn

sodium levels increased linearly in pulp ([Na] ppt $= 0.028$ (J. day) $- 0.675$; $r^2 =$

$0.1986$; df $= 1,72$; F $= 17.8$; p<0.001) (Figure 4) . Hawthorn whole fruit sodium

levels also increased linearly during this time ([Na] ppt $= 0.0145$ (J. day) $- 0.256$;

$r^2 = 0.2202$; df $= 1,117$;    F $= 33.0$; p<0.001). The relationship between hawthorn

seed sodium concentration and Julian day was not significant (p $= 0.692$).

Hawthorn pulp potassium concentration showed a slight rise and then a drop just

prior to and continuing throughout waxwing foraging ([K] ppt $= -0.0201$ (J. day) $^2$

$+ 2.51$ (J. day) $- 59.4$; $r^2 = 0.6195$; df $= 2,71$; F $= 57.8$; p<0.001) (Figure 5).

Similar but less pronounced curves represent change in the potassium of hawthorn

whole fruit   ([K] ppt $= - 0.0104$ (J. day) $^2 + 1.35$ (J. day) $- 32.2$; $r^2 = 0.2348$; df $=$

$2,116$; F $= 17.8$; p<0.001), and in seeds ([K] ppt $= - 0.0051$ (J. day) $^2 + 0.595$ (J.

day) $- 12.0$; $r^2 = 0.5256$; df $= 2,68$; F $= 37.7$; p<0.001).


Comparison of (Fall Ripened) Winter Retained and Spring Ripened Fruit

To test for significant differences in mean concentration of each element ($Ca^{2+}$,

$Mg^{2+}$, $N^+$, $K^+$, and N) among the two fall and two spring fruits tested, a one-way

ANOVA and a Tukey's HSD Post Hoc correction was used. Comparing elemental

concentration between seed and pulp and between whole fruit and wastes within

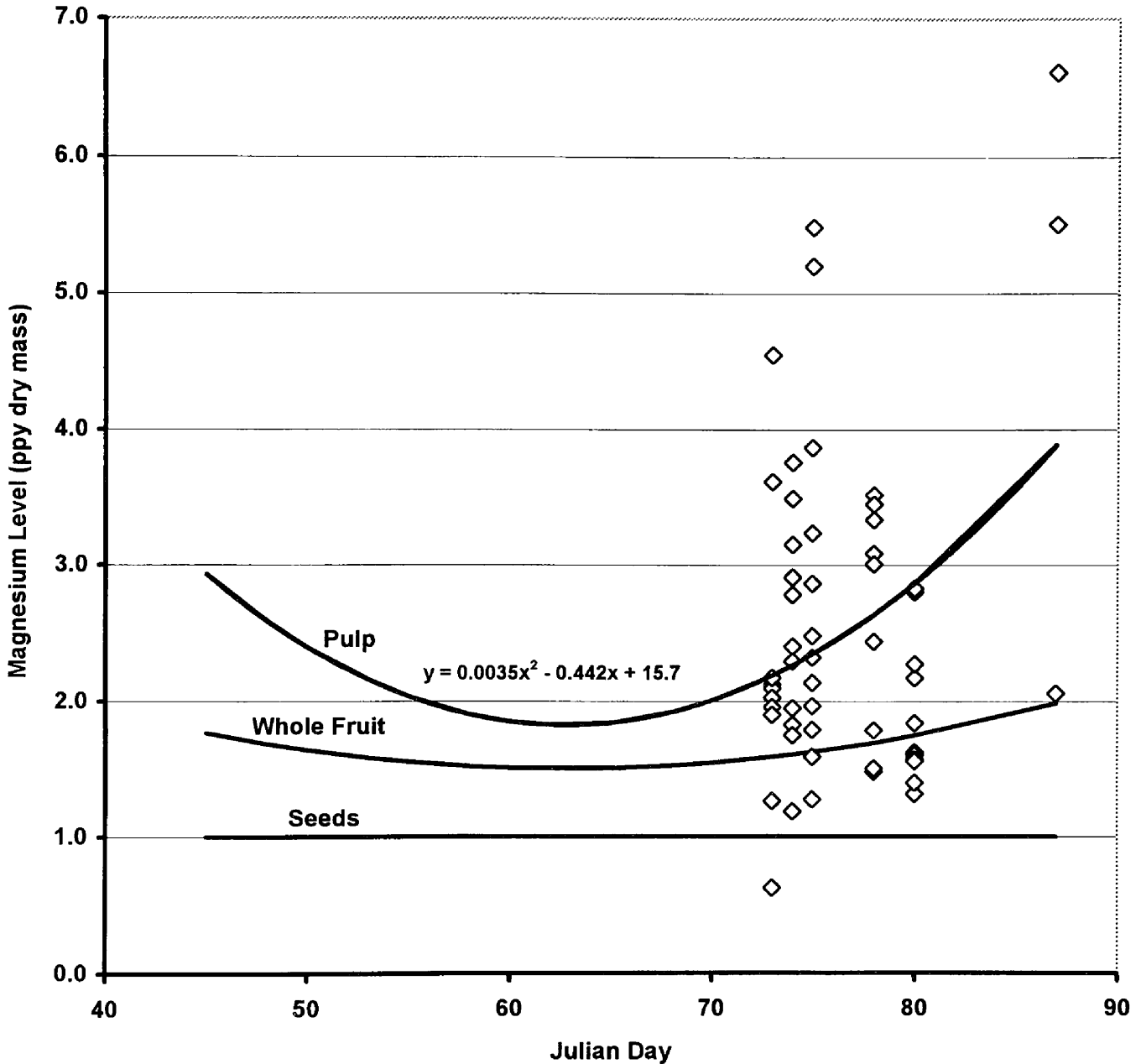Sodium Level in Hawthorne Seeds, Pulp, Whole Fruit and Mixed Wastes

Figure 4. Sodium nutrient level changes in Washington hawthorn seed, pulp, whole fruit and mixed wastes over time. Preforaging fruit samples were taken on Julian Days 46-64. Cedar waxwings began foraging on Julian Day 73. Fruit and mixed wastes were sampled on Julian Days 73-87. (Mixed wastes shown as ◇. Fruit and components data points not shown for clarity. Only utilization of pulp was studied therefore only regression line equations for pulp are shown.)
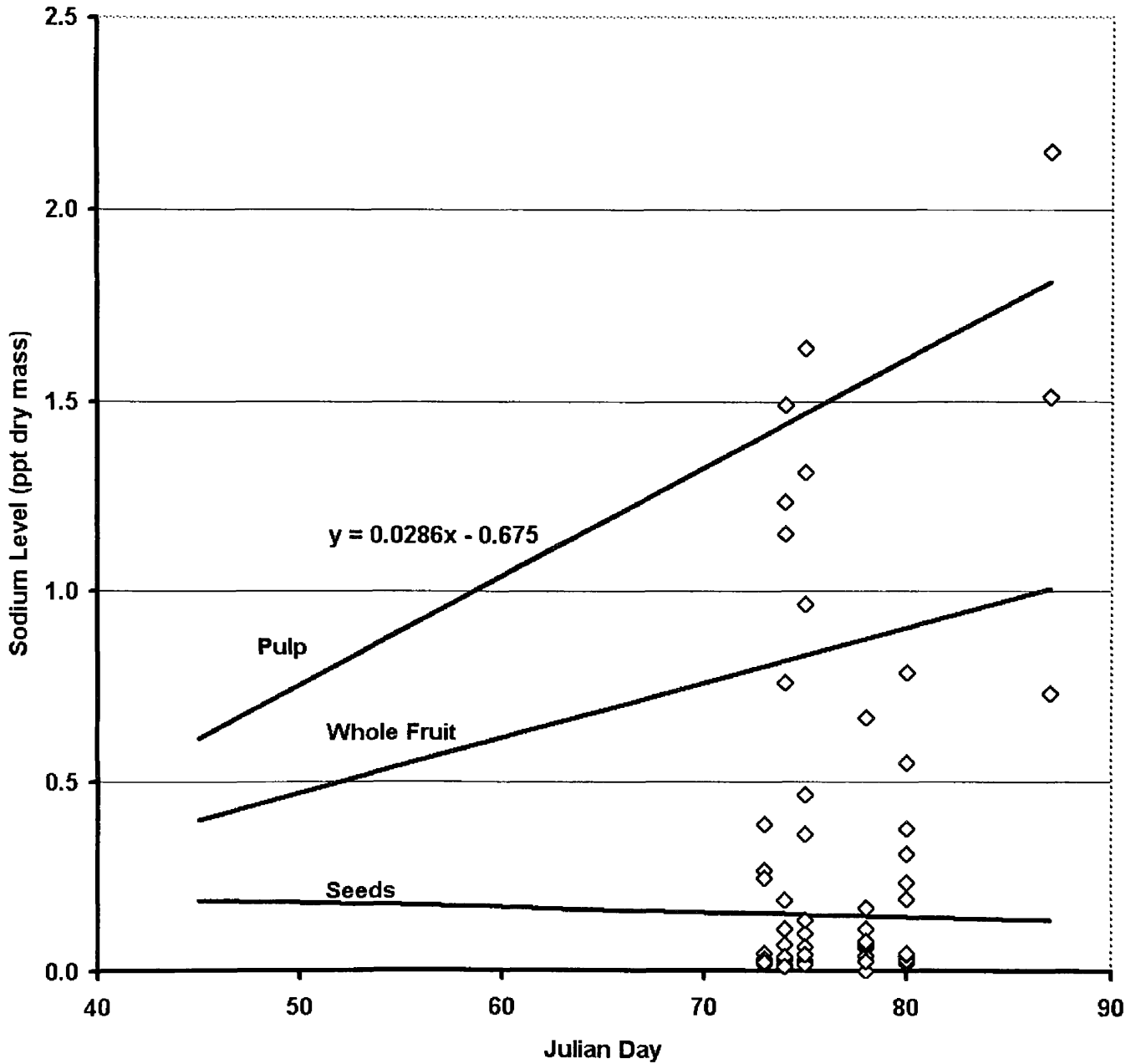
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Figure 5. Potassium nutrient level changes in Washington hawthorn seed, pulp, whole fruit and mixed wastes over time. Preforaging fruit samples were taken on Julian Days 46-64. Cedar waxwings began foraging on Julian Day 73. Fruit and mixed wastes were sampled on Julian Days 73-87. (Mixed wastes shown as ◇. Fruit and components data points not shown for clarity. Only utilization of pulp was studied therefore only regression line equations for pulp are shown.)

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each fruit type required two-sample t-tests. Serviceberry seeds and pulp were not

separated; therefore those components were not analyzed separately in this study.

Levels of nitrogen in whole fruit did not vary much between the four fruits

tested with concentrations ranging between 2.1 and 3.8 mean percent dry mass

(Table 1). There was no significant difference in nitrogen concentration between

the two spring fruits or between the two fall fruits, but both the spring ripened

service berry and scholar fruit have significantly more nitrogen than do the fall

ripened, over-wintered fruits of hawthorn and crabapple (df = 3,121; F = 32.3;

p<0.001) (Table 2).

The only fruit showing a significant difference in pulp and seed nitrogen

concentration was from the scholar tree (Table 3). Seed contained had significantly

more nitrogen than did pulp (t = 12.544; df = 22; p<0.001). There were no

significant differences in nitrogen concentration between whole fruit and waste

concentrations in either crabapple or serviceberry (crabapple: t = 1.622, df = 20;

p = 0.06; serviceberry: t = 0.433, df = 43; p = 0.333). Significantly more nitrogen

was concentrated in wastes excreted after hawthorn foraging than in the fruit (t =

4.499; df = 124; p<0.001) (Table 3). Scholar tree whole fruit was significantly

higher in nitrogen concentration than in the resultant, excreted mixed wastes (t =

7.076; df = 19; p<0.001).

Magnesium levels in the four whole fruits ranged from 0.943 ppt dry mass in

crabapple to 2.929 ppt in serviceberry (Table 1). All tested fruits showed

significant differences in whole fruit magnesium concentrations (F = 79.6; df =

3,124; p<0.001) (Table 2). Serviceberry had the highest levels of magnesium in

| Fruit | Element | Whole Fruit mean ppt ± SE (n) | Pulp mean ppt ± SE (n) | Seeds mean ppt ± SE (n) | Mixed Waste mean ppt ± SE (n) |
|---|---|---|---|---|---|
| Hawthorne | K+ | 11.424 ± 0.800 (63) | 15.635 ± 0.748 (49) | 4.033 ± 0.576 (49) | 20.958 ± 2.889 (52) |
| | Na+ | 0.898 ± 0.362 (63) | 1.587 ± 1.136 (49) | 0.443 ± 1.988 (49) | 0.287 ± 0.781 (53) |
| | Ca++ | 10.816 ± 1.517 (61) | 8.969 ± 1.294 (48) | 9.011 ± 1.056 (47) | 11.486 ± 1.623 (52) |
| | Mg++ | 1.723 ± 0.256 (63) | 2.457 ± 0.296 (49) | 1.032 ± 0.415 (49) | 2.429 ± 0.644 (53) |
| | N | *2.174 ± 0.487 (63) | *1.641 ± 0.422 (49) | *1.512 ± 0.904 (49) | *3.354 ± 1.008 (50) |
| Crabapple | K+ | 13.969 ± 2.814 (13) | 12.907 ± 0.662 (6) | 6.193 ± 0.616 (6) | 19.153 ± 1.480 (12) |
| | Na+ | 0.186 ± 0.035 (13) | 0.123 ± 0.051 (6) | 0.018 ± 0.001 (6) | 0.734 ± 0.258 (12) |
| | Ca++ | 2.681 ± 0.371 (13) | 2.645 ± 0.560 (6) | 4.145 ± 1.867 (6) | 10.887 ± 1.004 (12) |
| | Mg++ | 0.943 ± 0.052 (13) | 0.780 ± 0.071 (6) | 1.448 ± 0.264 (6) | 1.656 ± 0.158 (12) |
| | N | *2.460 ± 0.282 (13) | *1.128 ± 0.256 (6) | *4.164 ± 1.138 (6) | *2.053 ± 0.543 (12) |
| Scholar fruit | K+ | 11.654 ± 0.158 (12) | 13.006 ± 0.272 (12) | 10.262 ± 0.362 (12) | 14.675 ± 0.805 (12) |
| | Na+ | 0.041 ± 0.012 (12) | 0.014 ± 0.002 (12) | 0.013 ± 0.001 (12) | 0.074 ± 0.019 (12) |
| | Ca++ | 2.348 ± 0.118 (12) | 1.870 ± 0.077 (12) | 3.472 ± 0.111 (12) | 7.219 ± 0.514 (12) |
| | Mg++ | 1.475 ± 0.037 (12) | 0.426 ± 0.008 (12) | 2.436 ± 0.087 (12) | 1.633 ± 0.110 (12) |
| | N | *3.815 ± 0.131 (11) | *1.267 ± 0.111 (12) | *7.061 ± 0.448 (12) | *3.044 ± 0.521 (12) |
| Service Berry | K+ | 9.492 ± 0.724 (23) | | | 13.629 ± 0.998 (23) |
| | Na+ | 0.017 ± 0.065 (23) | | | 0.086 ± 0.291 (23) |
| | Ca++ | 10.743 ± 1.381 (23) | | | 12.383 ± 2.040 (23) |
| | Mg++ | 2.929 ± 0.421 (23) | | | 3.520 ± 0.312 (23) |
| | N | *3.289 ± 0.509 (23) | | | *3.284 ± 0.754 (23) |

Table 1. Mean element concentrations in two spring-ripened and two fall-ripened, over-wintered fruits foraged by cedar waxwings. (* Nitrogen reported as % dry mass, all others reported as parts per thousand dry mass.) Serviceberry pulp and seeds were not analyzed separately.

| Element | Sample | Differences | df | F | P |
|---------|--------|-------------|-----|-----|-----|
| Na | Whole fruit | Haw>Crab=Schol.=Sberry | 3,124 | 88.1 | < 0.001 |
| Na | Mixed waste | Crab=Haw=Schol.<br>Haw=Schol.=SBerry | 3,88 | 5.08 | 0.003 |
| K | Whole fruit | SBerry=Haw=Schol.<br>Haw=Schol.=Crab | 3,123 | 3.37 | 0.021 |
| K | Mixed waste | | 3,92 | 2.28 | NS |
| Ca | Whole fruit | Schol.=Crab<Haw=Sberry | 3,111 | 32.4 | <0.001 |
| Ca | Mixed waste | | 3,87 | 2.47 | NS |
| Mg | Whole fruit | Sberry>Haw=Schol.>Crab | 3,124 | 79.6 | <0.001 |
| Mg | Mixed waste | Sberry>Haw>Crab=Schol. | 3,99 | 15 | <0.001 |
| N | Whole fruit | Sberry=Schol.>Crab=Haw | 3,121 | 32.3 | <0.001 |
| N | Mixed waste | Crab=Schol.=Haw<br>Schol=Haw=Sberry | 3,85 | 5.07 | 0.003 |

Table 2. Mean elemental concentration differences between two fall ripened (hawthorn and crabapple) and 2 spring ripened (serviceberry and scholar tree) fruits and wastes produced by foraging cedar waxwings. (Haw: Washington hawthorn; Crab: Crabapple; Schol: Japanese scholar fruit; Sberry: serviceberry).

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Table 3. Mean elemental concentration comparisons of pulp vs. seed and fruit vs. waste in cedar waxwing foraged spring fruits (Jap. Scholar tree and serviceberry) and fall fruits (hawthorn and crab apple).

| Element | Pulp v Seeds | t | df | P | Fruit v Wastes | t | df | P |
|---------|--------------|-----|-----|-----|----------------|-----|-----|-----|
| | | | | Washington Hawthorne | | | | |
| Na | Pulp>Seeds | 13.299 | 116 | <0.001 | Fruit>Wastes | 7.323 | 134 | <0.001 |
| K | Pulp>Seeds | 15.976 | 116 | <0.001 | Fruit<Wastes | 5.849 | 126 | <0.001 |
| Ca | Pulp=Seeds | 0.789 | 107 | NS | Fruit=Wastes | 1.750 | 118 | NS |
| Mg | Pulp>Seeds | 15.758 | 143 | <0.001 | Fruit<Wastes | 5.846 | 134 | <0.001 |
| N | Pulp=Seeds | 1.041 | 106 | NS | Fruit<Wastes | 4.499 | 124 | <0.001 |
| | | | | Crab Apple | | | | |
| Na | Pulp=Seeds | 2.075 | 10 | NS | Fruit=Wastes | 2.186 | 23 | NS |
| K | Pulp>Seeds | 7.426 | 10 | <0.001 | Fruit=Wastes | 1.591 | 23 | NS |
| Ca | Pulp=Seeds | 0.770 | 10 | NS | Fruit<Wastes | 7.909 | 23 | <0.001 |
| Mg | Pulp=Seeds | 2.444 | 10 | NS | Fruit<Wastes | 4.424 | 23 | <0.001 |
| N | Pulp=Seeds | 1.154 | 6 | NS | Fruit=Wastes | 1.622 | 20 | NS |
| | | | | Japanese Scholar Tree | | | | |
| Na | Pulp=Seeds | 0.930 | 22 | NS | Fruit=Wastes | 1.410 | 22 | NS |
| K | Pulp>Seeds | 6.056 | 22 | <0.001 | Fruit<Wastes | 3.684 | 22 | <0.001 |
| Ca | Pulp<Seeds | 11.837 | 22 | <0.001 | Fruit<Wastes | 9.233 | 22 | <0.001 |
| Mg | Pulp<Seeds | 23.086 | 22 | <0.001 | Fruit=Wastes | 1.361 | 22 | NS |
| N | Pulp<Seeds | 12.544 | 22 | <0.001 | Fruit>Wastes | 7.076 | 19 | <0.001 |
| | | | | Serviceberry | | | | |
| Na | not done | | | | Fruit<Wastes | 3.843 | 44 | <0.001 |
| K | not done | | | | Fruit<Wastes | 4.608 | 44 | <0.001 |
| Ca | not done | | | | Fruit=Wastes | 0.135 | 35 | NS |
| Mg | not done | | | | Fruit<Wastes | 3.049 | 44 | <0.001 |
| N | not done | | | | Fruit=Wastes | 0.433 | 43 | NS |

mixed wastes while crabapple and scholar fruit were not significantly different and had the lowest levels of magnesium in mixed wastes ($F = 15$; $df = 3,99$; $p<0.001$).

Three of the four tested fruits contained significantly less magnesium than did their corresponding eliminated wastes. Whole fruit from hawthorn trees had significantly less magnesium than did the wastes from waxwings ingesting hawthorn fruit ($t = 5.846$; $df = 134$; $p<0.001$). Whole fruit crabapple had significantly less magnesium than did resultant wastes after foraging ($t = 4.424$; $df = 23$; $p<0.001$). Magnesium was significantly less concentrated in serviceberry whole fruit than in foraging wastes ($t = 3.049$; $df = 44$; $p<0.001$) (Table 3). Magnesium concentrations in whole scholar fruit and resultant mixed wastes were not significantly different ($t = 1.361$; $df = 22$; $p = 0.094$).

The pulp of hawthorn fruit contained significantly higher magnesium concentrations than did hawthorn seeds ($t = 15.785$; $df = 134$; $p<0.001$). Scholar fruit pulp contained significantly less magnesium than did the seeds ($t = 23.086$; $df = 22$; $p<0.001$). There was no significant difference between pulp and seed concentrations of magnesium in crabapples ($t = 2.444$; $df = 10$; $p = 0.017$).

The only fruit that showed a significant difference between seed and pulp calcium concentration was that of the Scholar Tree ( $t = 11.837$; $df = 22$; $p<0.0001$) (Table 3). Calcium levels in the four whole fruits studied ranged between 2.348 and 10.816 ppt dry mass (Table 1). Calcium levels in the four fruit wastes ranged from 7.219 to 12.383 ppt dry mass (Table 1). In crabapple, whole fruit calcium levels were significantly less than levels of calcium in mixed wastes ($t = 7.909$; $df = 23$; $p<0.001$). Scholar fruit also showed significantly less whole

fruit calcium levels than was in corresponding eliminated mixed wastes (t = 9.233; df = 22; p<0.001) (Table 3). In hawthorn, as well as in service berry there were no significant differences in calcium concentration between fruit and waste (Table 3).

The whole fruit of hawthorn and serviceberry contained levels of calcium equal to each other but higher levels than scholar fruit or crabapple (df = 3,111; F = 32; p<0.001) (Table 1). There was no significant difference in calcium concentrations in mixed wastes between the four fruits (df = 3, 87; F = 2.47; p = 0.067) (Table1).

Whole fruit concentrations of sodium ranged from 0.017 to 0.898 ppt dry mass in the four tested fruits. The range of sodium in mixed wastes of the fruits was 0.074 to 0.734 ppt dry mass (Table 1).

Hawthorn whole fruit contained significantly more sodium than the other three whole fruit types which were not significantly different from each other (F = 88.1; df = 3,124; p<0.001) (Table 2). Mixed waste sodium concentration differed significantly between serviceberry and crabapple (F = 5.08; df = 3,88; p = 0.003).

Sodium was found in higher concentrations in hawthorn fruit than in wastes (t = 7.323; df = 134; p<0.001) but in lower concentrations in serviceberry fruit than in resultant corresponding wastes (t = 3.843; df = 44; p< 0.001) (Table 3). The other two fruits showed no significant differences between whole fruit and waste sodium concentrations.

Sodium levels did not differ significantly between pulp and seed of crabapple or between pulp and seed of scholar tree fruit. Hawthorn pulp, however, contained significantly more sodium than did hawthorn seeds (t = 13.299; df = 116; p<0.001) (Table 3).   .

Mean whole fruit potassium concentrations ranged from 9.492 to 13.969 ppt (Table 1). Whole fruit serviceberry potassium levels were significantly lower than whole fruit crabapple potassium levels (df = 3,123; F = 3.37; p = 0.021) (Table 2).

There was no significant difference in potassium levels in mixed wastes of all four fruits. However, concentrations ranged from 13.629 ppt to 20.9580 ppt (Table 1).

Potassium was significantly less concentrated in hawthorn fruit (t = 5.849; df = 126; p<0.001), scholar fruit (t = 3.684; df = 22; p<0.001), and serviceberry fruit (t = 4.608; df = 44; p<0.001) than in their corresponding wastes (Table 3). The fruit and waste potassium concentration of crabapple were not significantly different (t = 1.591; df = 23).

Pulp potassium concentrations exceeded seed potassium concentrations in hawthorn (t = 15.976; df = 116; p<0.001), crabapple (t = 7.426; df = 10; p<0.001), and scholar fruit (t = 6.056; df = 22; p<0.001) (Table 3). Serviceberry was not tested.

## Discussion

Complete dietary nutrient requirements are unknown for most birds, including

cedar waxwings. Many poultry requirements have been documented (National

Research Council, 1984) but size differences limit comparisons of poultry to cedar

waxwings. Comparison to eastern bluebird (*Sialia sialis*) nutrient requirements for

growth (Hungerford, et al., 1993) is more applicable since both bird species have

more similarities, physical as well as behavioral. Nutritional requirements for

growth in immature free-living bluebirds would be assumed to be lower than

requirements needed for maintenance in mature cedar waxwings. A comparison to

the bluebird growth requirements shows that the fall and spring fruits I tested are

probably adequate sources of $K^+$, $Ca^{2+}$ and $Mg^{2+}$ in a maintenance diet for cedar

waxwings (Figures 6, 7, and 8). Waxwing intake of these nutrients in all fruits

tested was shown to exceed levels required by growing eastern bluebirds.

Reinforcing this is that resultant waste (excreta) concentrations of $K^+$, $Ca^{2+}$ and

$Mg^{2+}$ for all four fruits tested, are equal to or greater than the mineral concentration

consumed by eating the fruits. This suggests that those minerals are being

assimilated at equal or slower rates than they are being ingested and therefore are

probably not limiting nutrients.

Since nitrogen intake by waxwings falls very short of that needed by growing

eastern bluebirds, it appears that none of the fruits would be adequate to maintain a

nitrogen budget in waxwings (Figure 9). When comparing intake to output levels

however, [N] in wastes from ingestion of three of four tested fruits were equal or

higher than [N] in the whole fruit eaten. Scholar tree fruit shows input

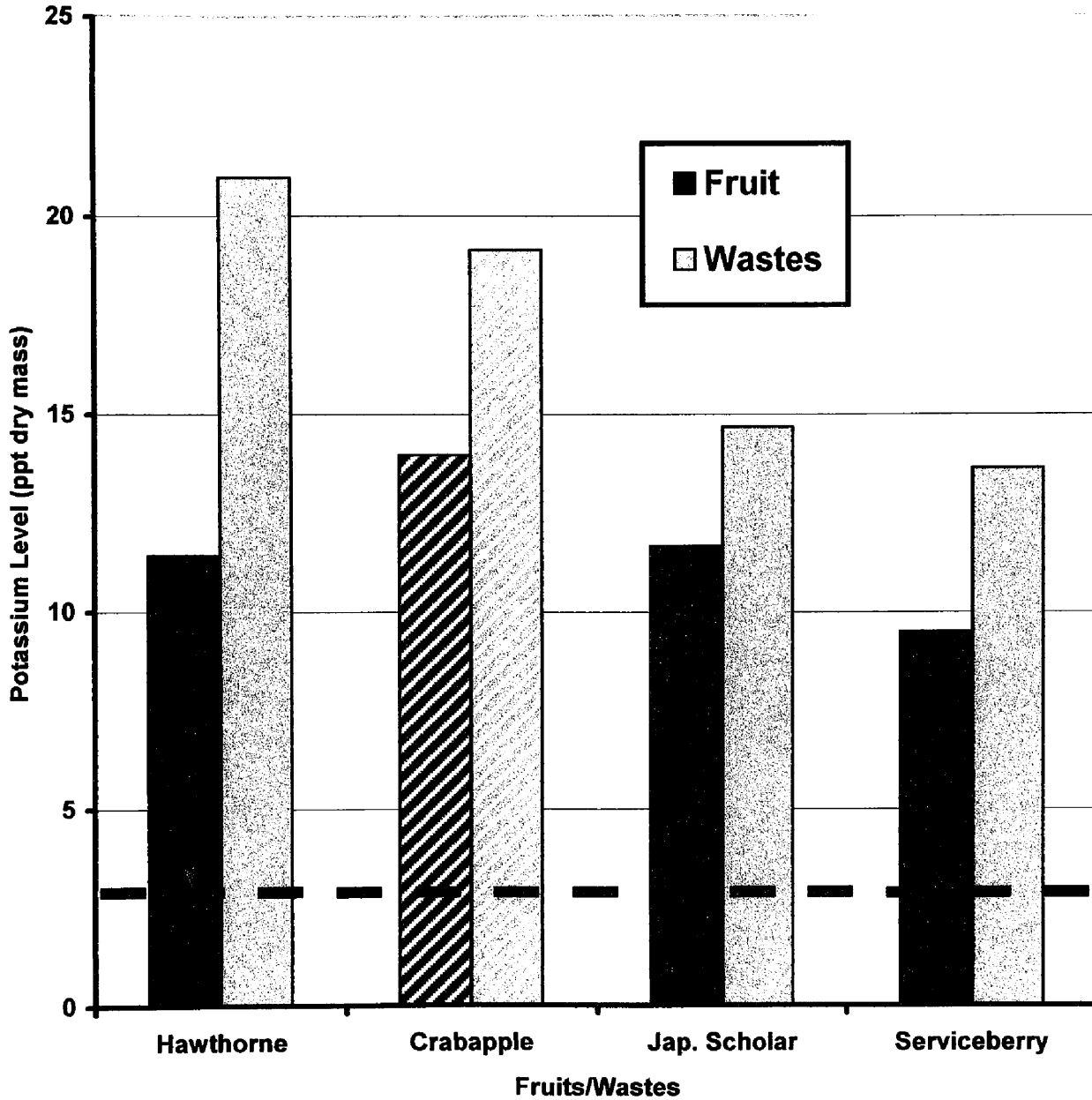**Potassium In Foods and Wastes of Cedar Waxwings**

Figure 6. Food/Waste (In/Out) comparisons of potassium nutrient from two fall ripened, winter retained fruits (hawthorn and crabapple) and two spring ripened fruits (scholar tree fruit and serviceberry) in the diet of the cedar waxwing. Stripes indicate no statistically significant difference between concentrations of nutrients in fruit intake and wastes output. Dashed line (-----) indicates (as comparison) eastern bluebird growth requirements at approximately 80% assimilation efficiency (Hungerford, et al., 1993).
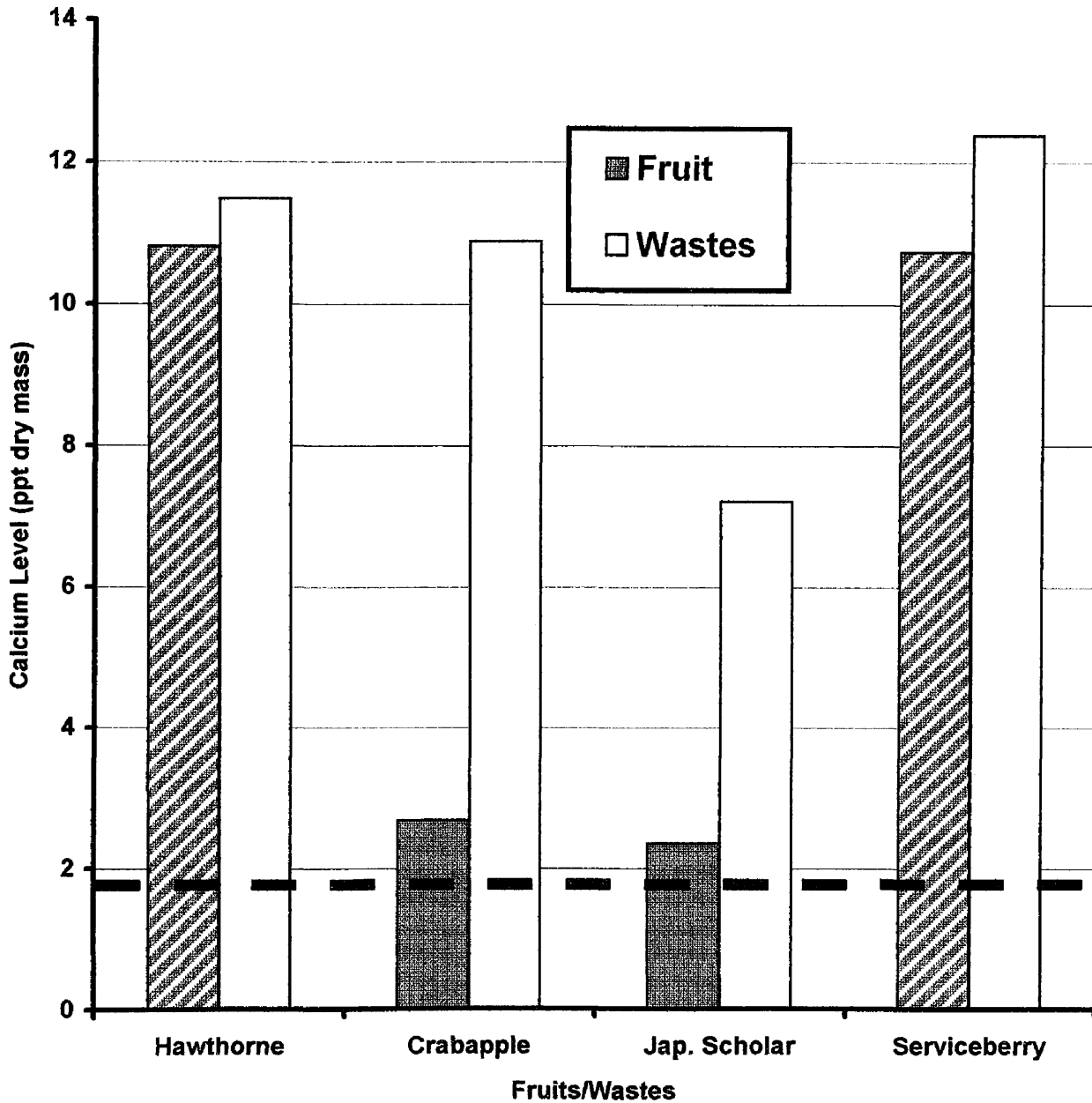
# Calcium in Foods and Wastes of Cedar Waxwings



Figure 7. Food/Waste (In/Out) comparisons of calcium nutrient from two fall ripened, winter retained fruits (hawthorn and crabapple) and two spring ripened fruits (scholar tree fruit and serviceberry) in the diet of the cedar waxwing. Stripes indicate no statistically significant difference between concentrations of nutrients in fruit intake and wastes output. Dashed line (-----) indicates (as comparison) eastern bluebird growth requirements at approximately 80% assimilation efficiency (Hungerford, et al., 1993).
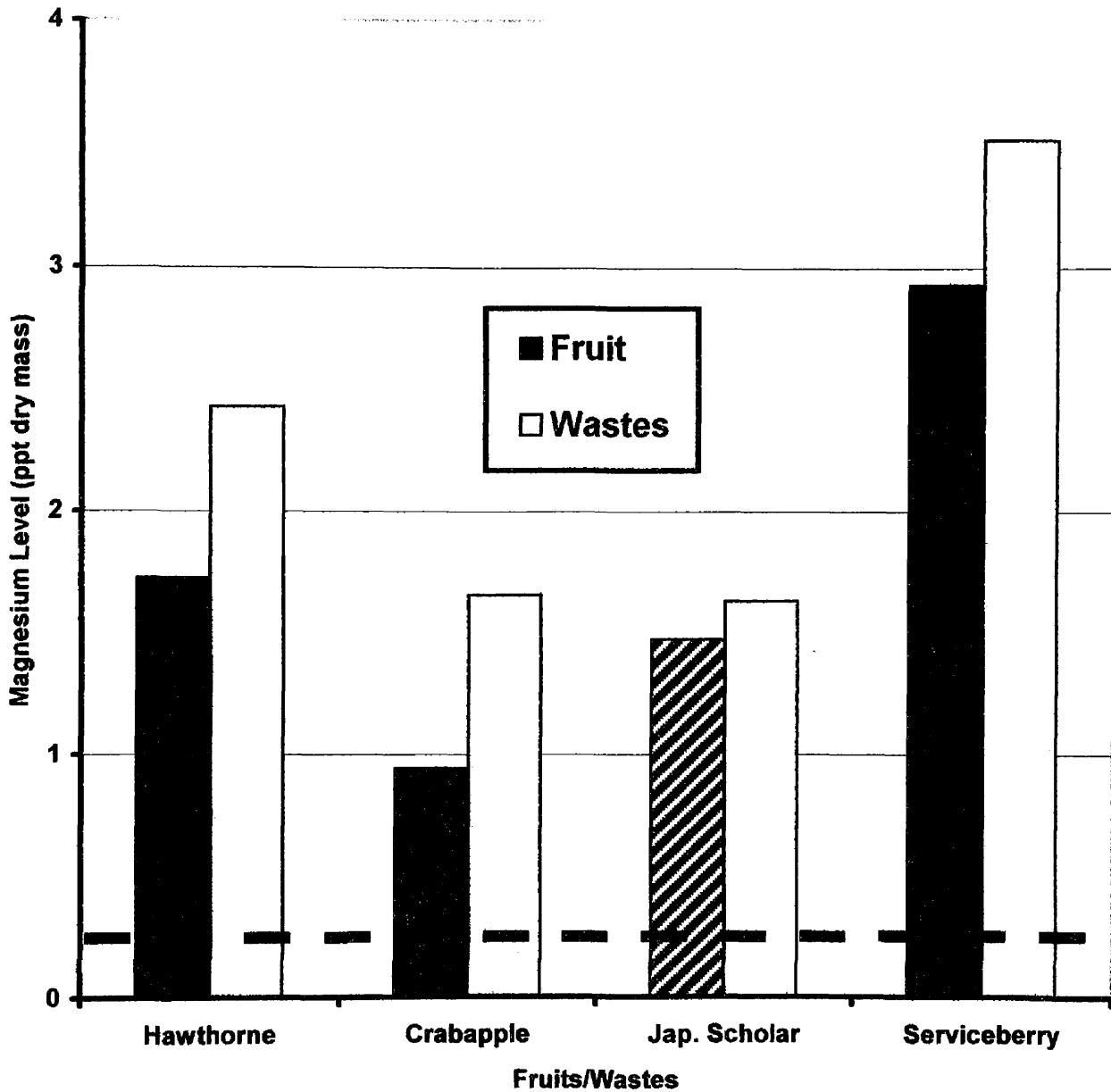
# Magnesium In Foods and Wastes of Cedar Waxwings



Figure 8. Food/Waste (In/Out) comparisons of magnesium nutrient from two fall ripened, winter retained fruits (hawthorn and crabapple) and two spring ripened fruits (scholar tree fruit and serviceberry) in the diet of the cedar waxwing. Stripes indicate no statistically significant difference between concentrations of nutrients in fruit intake and wastes output. Dashed line (-----) indicates (as comparison) eastern bluebird growth requirements at approximately 80% assimilation efficiency (Hungerford, et al., 1993).
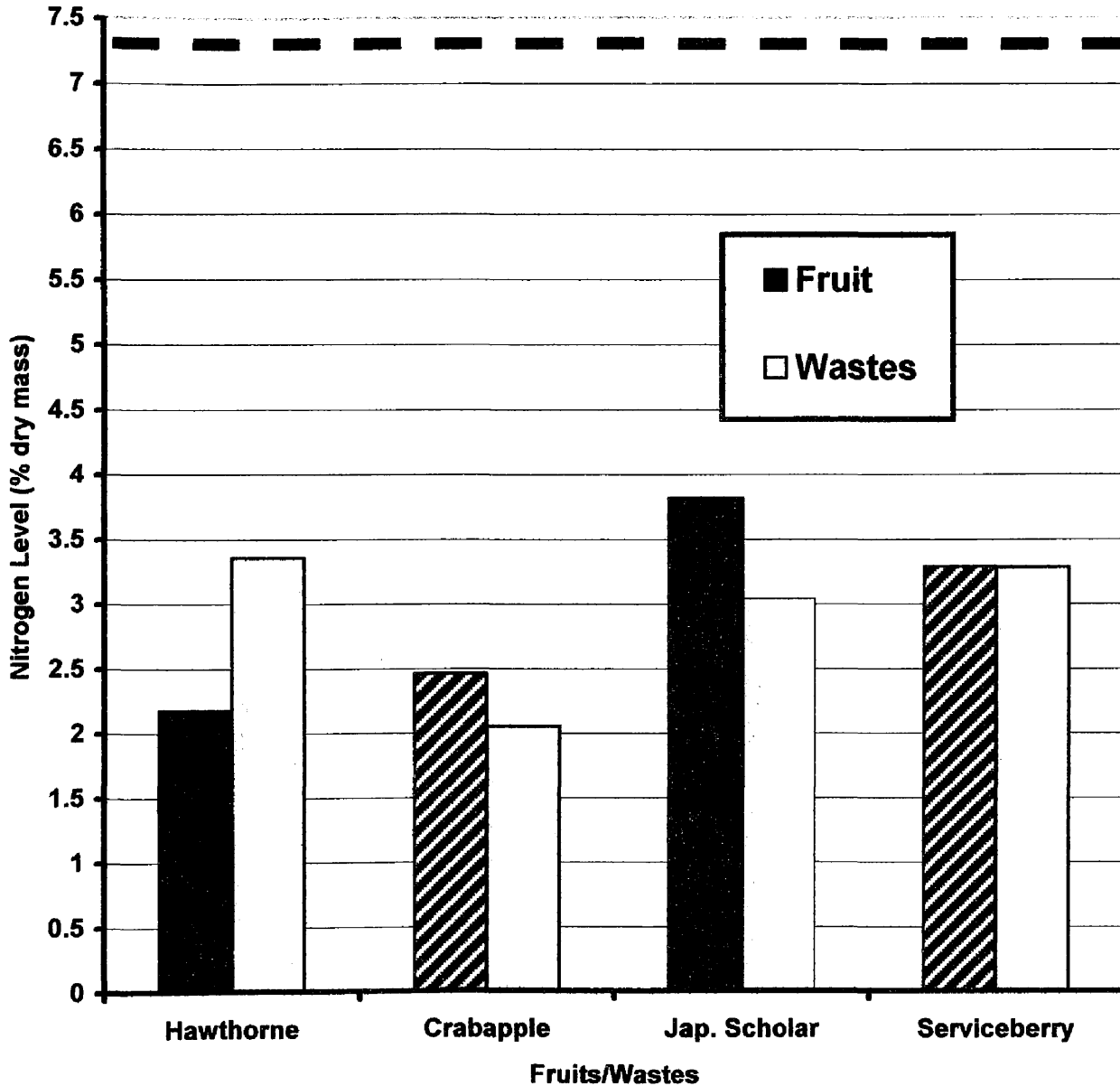
Figure 9. Food/Waste (In/Out) comparisons of nitrogen nutrient from two fall ripened, winter retained fruits (hawthorn and crabapple) and two spring ripened fruits (scholar tree fruit and serviceberry) in the diet of the cedar waxwing. Stripes indicate no statistically significant difference between concentrations of nutrients in fruit intake and wastes output. Dashed line (-----) indicates (as comparison) eastern bluebird growth requirements at approximately 80% assimilation efficiency (Hungerford, et al., 1993).

concentration of N to exceed output, indicating that N is not being ingested fast enough to match assimilation rates. Therefore, waxwings on a diet of scholar fruit would be nitrogen limited.

Research has suggested that highly frugivorous species may have low nitrogen requirements (Karasov and Levy, 1990). Berthold (1976) also found that fruit diets are generally protein limiting for eastern bluebirds, an omnivorous frugivore, but not for highly frugivorous Bohemian waxwings (*Bombycilla garrulous*). Witmer (1998b), however, found that captive cedar waxwings could thrive on the same low nitrogen, sugary fruit diets that were found deficient for thrushes. Laboratory held waxwings were able to maintain positive N balance in two of three fruit diets that held several species of thrush in negative N balance (Witmer and Van Soest, 1998). Several studies (McPherson, 1987, Johnson et al., 1985; Sorenson, 1981) have also found no correlation between protein content of fruits and selection by avian frugivores. This suggests that many low protein fruits may be satisfactory for the waxwing diet. Cedar waxwings may be able to meet their protein requirements if those requirements are low and if they have atypically high intake rates of sugary, albeit low-protein fruits (Witmer and Van Soest, 1998).

Cedar waxwings may also have low sodium requirements. In this study, sodium intake levels fell far below the bluebird growth requirement levels and still showed balanced sodium budgets for waxwings eating crab-apple, scholar-tree, and serviceberry fruit diets (Figure 10). Sodium intake: output ratios (i.e. fruit: wastes) showed that waxwings did not take in enough sodium when eating a hawthorn diet and that sodium is a limited nutrient in this case.
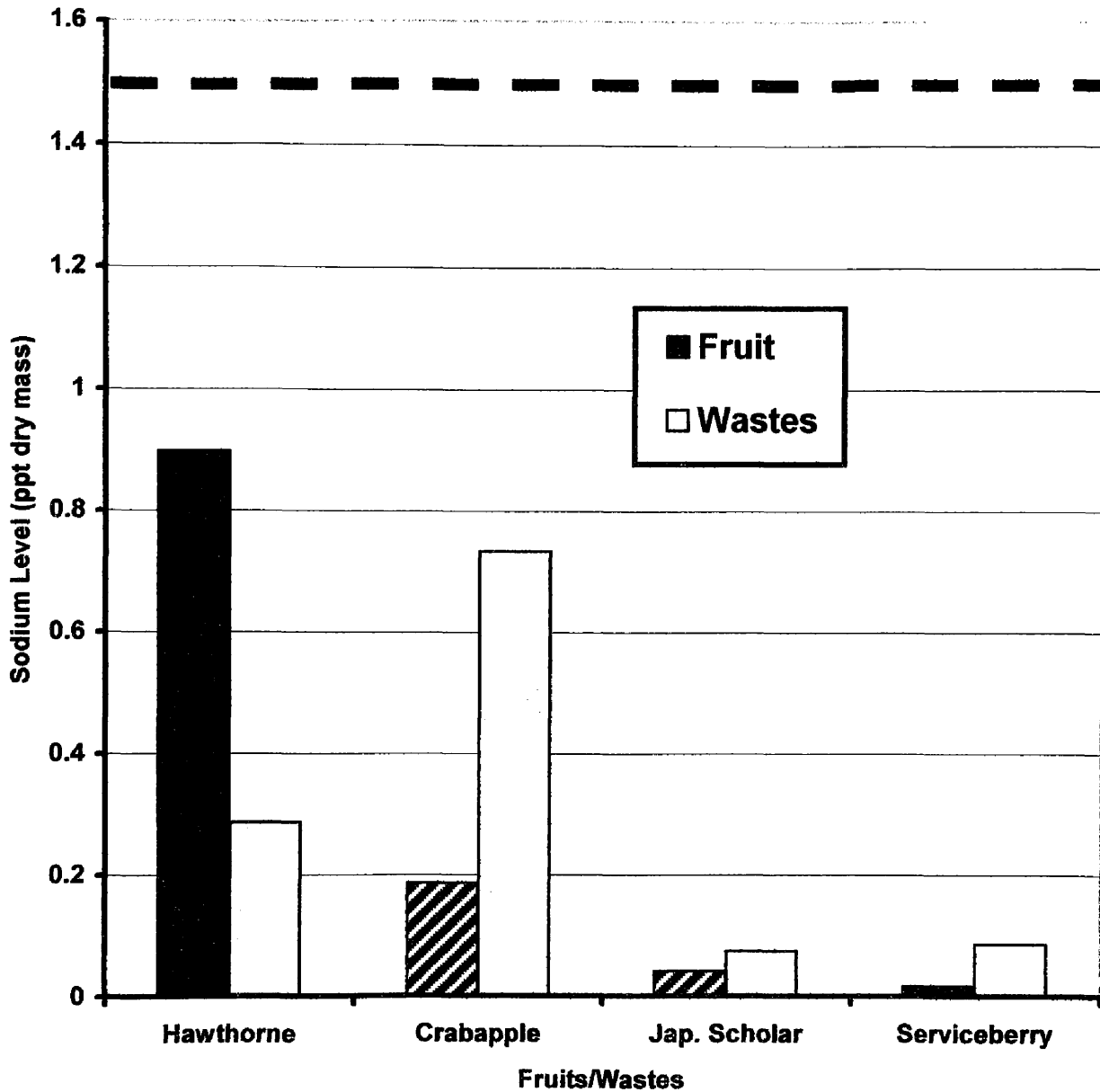
## Sodium In Foods and Wastes of Cedar Waxwings



Figure 10. Food/Waste (In/Out) comparisons of sodium nutrient from two fall ripened, winter retained fruits (hawthorn and crabapple) and two spring ripened fruits (scholar tree fruit and serviceberry) in the diet of the cedar waxwing. Stripes indicate no statistically significant difference between concentrations of nutrients in fruit intake and wastes output. Dashed line (-----) indicates (as comparison) eastern bluebird growth requirements at approximately 80% assimilation efficiency (Hungerford, et al., 1993).

One common theory holds that a fruit will persist through the winter if it is low in nutrient content (Stiles, 1980; Jones and Wheelwright, 1987; Witmer, 2001), yet the two persistent fruit diets I tested show waxwings to be in balance for all nutrients I tested except one. A hawthorn diet did not appear to supply enough sodium for dietary needs of the cedar waxwing. All spring fruits supplied enough of the nutrients to maintain dietary balance in waxwings except for scholar fruit which lacked adequate nitrogen. Paradoxically, while nitrogen balance occurred during the hawthorn fruit diet in February and March, two months later when ingesting two different spring ripened fruits with higher nitrogen concentration, waxwings were limited for nitrogen. Also puzzling was that sodium levels were highest in hawthorn fruit, but that was the only fruit diet tested that showed to be sodium limiting. Hawthorn fruit is "chosen" at the end of winter in many temperate climates, after many months of persistence. Since winter presents heightened challenges for foraging, one may presume uncertain success for a frugivore seeking to meet nutritional requirements by depending upon persistent fruit.

Foraging success might be more certain if nutrient requirements for the frugivore are not consistent over the entire year. Nutritional needs of birds may change seasonally (Berthold, 1976; Stiles, 1980; Witmer,1996a; Herrera, 1982; Williams et al., 1999) and choice in fruit selection during these times may reflect these changing needs (Berthold, 1976; Herrera, 1982; McPherson, 1987; Bairlein, 1996; Witmer, 1996a). Witmer (1996a) compiled and documented yearly waxwing dietary habits in eastern United States. He reported that in May, the birds' diet

typically changes to less than 20% fruit in composition, instead switching to flowers and insects as their main dietary components. One might suspect that this change is a behavioral response to loss of fruit variety characterized until more species of fruit set, a month later. The diet switch may also be in response to increased protein demands dictated by an impending breeding/nesting season (Witmer, 1996a). In a study showing another adaptive behavior to physiological need, Witmer (2001) observed cedar waxwings in New York during April and May, supplementing a protein poor diet of highbush cranberries (*Viburnum opulus*) with protein rich catkins of eastern cottonwoods (*Populus deltoids*).

Adaptive physiological responses induced by nutrient availability have also been documented. Bairlein (1996) showed two species of captive facultative frugivores actually regained lost body mass after adapting to an enforced all fruit, low protein diet. Another study showed that captive Bohemian waxwings that were fed rotten, nutrient-poor fruits for up to 18 days did not greatly loose body mass, but in fact maintained or gained body mass in some cases (Berthold, 1976). Physiology of the wild cedar waxwing may adapt by winter's end, to "enforced" decreased nitrogen and other nutrient requirements so that persisting fruits adequately supply their needs.

A fruit might not be consistent in its composition either. Seasonal trends were seen in pulp analysis of 22 fleshy, commonly foraged fruits native to Illinois revealing increases later in the year in absolute quantities of protein and potassium (Johnson, et al., 1985). I showed that at least one winter retained fruit (hawthorn) undergoes significant nutrient changes over time. While all fruit

components were analyzed, I limit my discussion to pulp since that is the only part of the fruit digested by cedar waxwings. I detected changes in hawthorn pulp nutrients for 41 days from mid-February until late March at which time birds had nearly stripped trees clean of fruit, (Figure 1). Myr findings show that the longer birds wait to eat hawthorn fruit, the more N, $Ca^{2+}$, $Na^+$ and $Mg^{2+}$ is available to them per unit of fruit eaten. Calcium, magnesium and nitrogen were shown to be non-limiting in previous intake/output studies, therefore increases of these in pulp only ensures continued dietary balance. This time study of hawthorn changes, shows pulp $K^+$ to be the only nutrient in decline when birds begin foraging (Figure 5). Since the waxwings' diet was likely in balance for $K^+$ as they began foraging on hawthorn fruit, this would probably not compromise them. In fact, the decline in $K^+$ levels is to their advantage. Studies of mammals (Studier, 1983; Weeks and Kirkpatrick, 1978) have shown that lowering dietary $[K^+]$ lowers $Na^+$ requirements of the individual. This study may be illustrating the same potassium-sodium connection in frugivorous birds as mammals. The longer cedar waxwings wait to eat hawthorn fruit, the less $K^+$ they ingest, thereby possibly reducing their sodium requirements. This mechanism could correct the apparent $Na^+$ imbalance I found for birds on a diet of hawthorn fruit and might also explain why the intake level of $Na^+$ fell so far below levels required for growth in bluebirds. Bairlein (1996) found birds were able to detect and remedy nutrient deficiencies by selecting diets of specific nutrients and adjusting intake. If deficiencies in fruit can be detected by birds, perhaps so too can nutrient or other chemical abundance.

Since seasonal time passage causes heightened nutritional benefits from a hawthorn fruit diet, one might wonder why the birds do not let the fruit age even longer before foraging. I believe this is simply due to accumulation of secondary components and fermentation products in the fruit.

Fermenting fruits are usually avoided by wild vertebrates due to the production of toxic products (Janzen, 1977). While most reports are anecdotal, some documented ones have shown that cedar waxwings can suffer alcohol intoxication and death after eating fermented fruit (Witmer, et al.,1997; Miller, 1932; Janzen, 1977). Alcohol can also act as stimulant or deterrent to the frugivore appetite (Dudley, 2000; Janzen, 1977; Levey and Martinez del Rio, 2001). Dudley (2000) believes that since frugivores undoubtedly have more dietary exposure to alcohol, they may have a higher tolerance for it than non-frugivores do. Frugivores may actually have a tendency to choose alcohol in fruits, having learned that alcohol signals a nutritional presence by association. Dudley also suggests that fruits with alcohol are easily located due to volatile and odiferous plumes they give off.

Studies in Finland, however, (Eriksson and Ehrlen, 1991) showed low ethanol concentrations in hawthorn and other persistent fruits during cold autumn and winter months. If high alcohol content is more unlikely in extremely cold months, once seasonal warming occurs in temperate climates, alcohol levels might also raise. My study may have found that waxwings begin a hawthorn fruit diet at an optimum foraging time. That is, when nutrients in the over-wintered fruit are at peak levels but alcohol is not yet at toxic levels.

Waxwings ignoring persistent fruit to allow nutrient levels to rise would be contrary to Witmer's (2001) findings in which waxwings chose early season over December picked hawthorn fruit. Any unpalatable fermentation products or secondary compounds present in the late winter fruit Witmer offered, however, could explain the birds' choice.

Many persistent fruits are thought to contain secondary compounds that act as anti-microbials for the long time they remain on the plant (Herrera, 1982; Cipollini and Stiles, 1993; Cipollini and Levey, 1997; Levey and Cipollini, 1998). The physiological effects of known secondary compounds are not fully known for birds, but since many birds exhibit ability to taste and distinguish between different nutrients ( Martinez del Rio, et al., 1989), it is possible that frugivores may have the ability to detect by taste or other methods, physiology altering compounds in their food sources (see Witmer, 2001). If so, another factor in the complexities of explaining fruit choice in the avian frugivore's diet is introduced.


This study shows that both winter retained and spring ripened fruits probably supply necessary maintenance requirements of the nutrients $K^+$, $Ca^{2+}$ and $Mg^{2+}$ for the cedar waxwing diet. If waxwings have low or seasonally fluctuating (or otherwise) $Na^+$ and nitrogen requirements, these fruits will probably be adequate sources of these nutrients also.

Nutrient level changes occurred over time, seasonally in at least one of our tested fruits. I suspect that these changes were perceived and acted on by foraging waxwings. Foraging response to fluctuating nutrients and differences in patterns of

utilization of the $Na^+$ and nitrogen available in different amounts in the winter and spring foraged fruits leads us to speculate that waxwings may vary their dietary objectives. Whether these are behavioral adaptations to meet changing physiologic needs or physiological adaptations to meet a changing environment is not clear from our research. The literature suggests cedar waxwings may be capable of both (McPherson, 1987; Witmer, 1996a; Witmer, 1998b; Witmer, 2001; and Berthold, 1976; Dudley, 2000). There are probably more than a few mechanisms governing the nutrition of the avian frugivore. Instead, there is undoubtedly a dynamic and networked interplay between physiology and ecology.

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