

AVIAN PREDATION ON THE MONARCH BUTTERFLY,
DANAUS PLEXIPPUS (NYMPHALIDAE: DANAINAE), AT A
CALIFORNIA OVERWINTERING SITE

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ABSTRACT. Avian predation on monarch butterflies (*Danaus plexippus* L.) was observed at a California monarch overwintering site. A pair of rufous-sided towhees (*Pipilo erythrophthalmus* Linnaeus) exerted a 6.51–7.43% annual mortality on the overwintering colony, consuming an average of 22.7 butterflies/day. A characteristic predatory signature was observed on the uneaten remains left by the towhees. Tagging studies indicate that tagged butterflies were at greater risk of predation than were untagged butterflies.

Additional key words: rufous-sided towhee, sex ratios, cardenolides, tagging.

There are several reported examples of predation of monarch butterflies at overwintering sites. In Mexico, avian predators include black-headed grosbeaks (*Pheucticus melanocephalus* Swainson), Scott's oriole (*Icterus parisorum* Bonaparte), and black-backed oriole (*Icterus abeillei* Lesson) (Calvert et al. 1979, Brower & Calvert 1985). In California, avian predators include chestnut-backed chickadees (*Parus rufescens* Townsend) (Tuskes & Brower 1978, Brower & Fink 1985, Bell & Dayton 1986), starlings (*Sturnus vulgaris* L.) (Dayton & Bell, pers. comm.), and scrub jays (*Aphelocoma coerulescens* Bosc) (Peterson, pers. comm.). Mammalian predators found at Mexican overwintering sites include *Peromyscus spicilegus* J. A. Allen, *Microtus mexicanus salvus* Hall, and *Peromyscus melanotis* (= *P. maniculatus labecula* Elliott) (Brower et al. 1985, Glendinning et al. 1988). Leong et al. (1990) reported monarch predation in California by yellowjackets (*Vespula vulgaris*). In the 1989–90 season, I discovered a pair of rufous-sided towhees (*Pipilo erythrophthalmus* Linnaeus, Emberizidae) preying upon monarchs in a moderate-sized overwintering colony in the Santa Monica Mountains, Los Angeles County, California. During the course of tagging monarch butterflies at this site, I measured predation rates.

METHODS

From 13 September 1989 to 28 March 1990, I made weekly visits to a monarch overwintering site along the coast in Los Angeles County, California, 18 km west of Malibu, to tag monarch butterflies. Tags of the type developed by Urquhart (1960, 1976, 1987) were used to de-

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TABLE 1. Observations of a single pair of rufous-sided towhees feeding activities on 31 January 1990.

Time	Activities observed
06:53 h	Sunrise (Anon 1989).
07:00 h	Unsuccessful sally.
07:03 h	Unsuccessful sally. Monarch flies, bird sally-strikes unsuccessfully.
07:08 h	Successful sally.
07:13 h	Successful sally.
07:45 h	Sunlight hitting site. No bird activity.
08:03 h	Picks up monarch fallen on ground.
08:07 h	Picks up monarch fallen on ground.
08:13 h	Successful sally.
08:15 h	Picks up monarch fallen on ground.
08:27 h	Picks up monarch fallen on ground.
08:30 h	Successful sally, does not eat it.
08:31 h	Successful sally.
08:51 h	Successful sally.
09:01 h	Successful sally.
No bird activity after this.	

termine predation rate and selectivity. All butterfly remains were collected from the litter under the clustering areas during my weekly visits. On 12 and 13 January 1990, the site was visited, and butterfly remains were collected to measure daily predation rate.

Field observations of bird predation were made by binoculars. Continuous early morning observations from before sunrise until no further predation activity was observed were made on three occasions. Because rufous-sided towhees are not sexually dimorphic, I was unable to distinguish between the sexes. Terms used to describe monarch predation by towhees follow Remsen and Robinson (1990).

RESULTS

Towhee activity recorded on 31 January 1990 is presented in Table 1. The pair of towhees "perched" on small shrubs. Looking about, the towhee would "sally" up some 10–15 m into the tree, "pounce" upon a butterfly, and bring it to the ground near or under a shrub. On other occasions, the attacked butterfly fell to the ground, where the bird would pick it up. The towhee also attacked monarchs that previously had fallen to the ground. It appears that the towhee "snips" the butterfly between the head and thorax based on examination of intact dead butterflies. All four wings were removed by the bird by "snipping" between the body and wing and "shaking" the prey until the wings fell off before the body was consumed. Characteristic piles of the four wings were often found under or near shrubbery.

TABLE 2. Tagging and recapture summary KSP site in 1989-90.

Date	♂ tagged	♀ tagged	Total tagged	% ♂	Recaptures	Recap % ♂	Total captured
4 Oct 89	3	1	4	75.0	0	0	4
11 Oct 89	22	1	23	95.7	1	100	24
18 Oct 89	63	41	104	60.6	4	100	108
25 Oct 89	180	124	304	59.2	32	71.9	336
1 Nov 89	157	124	281	55.9	11	45.5	292
13 Nov 89	242	219	461	52.5	15	60.0	476
15 Nov 89	173	204	377	45.9	57	61.4	434
22 Nov 89	249	225	474	52.5	36	61.1	510
29 Nov 89	135	115	250	54.0	30	70.0	280
6 Dec 89	58	50	108	53.7	17	64.7	125
13 Dec 89	275	265	540	50.9	67	65.7	607
20 Dec 89	384	385	769	49.9	93	66.7	862
27 Dec 89	362	330	692	52.3	90	61.1	782
3 Jan 90	142	113	255	55.7	80	58.8	335
10 Jan 90	168	138	306	54.9	92	56.5	398
17 Jan 90	271	169	440	61.6	183	57.9	623
24 Jan 90	104	16	120	86.7	42	85.7	162
31 Jan 90	267	14	281	95.0	67	95.5	348
3 Feb 90	89	14	103	86.4	72	94.4	175
10 Feb 90	84	2	86	97.7	45	95.6	131
14 Feb 90	47	4	51	92.2	30	96.7	81
21 Feb 90	11	0	11	100	3	66.7	14
28 Feb 90	2	0	2	100	0	0	2
Totals	3488	2554	6042	57.7	1067	69.3	7109

♂ = ♂ tagged/(♂ tagged + ♀ tagged); Recap % ♂ = % of ♂ recaptures; Total captured = total tagged + recaptures.

Fresh intact but damaged butterflies also were found. Two were found walking around in the litter almost decapitated, damage only in the area between the head and thorax, where the towhee immobilized the prey by biting the butterfly. The heads, occasionally found in the litter, were then lost as the towhee removed the wings.

Predation by towhees occurred in the early morning hours from an hour before until two hours after sunrise (see Table 1). The towhees were observed sallying ("sally-strike") for flying monarchs on two occasions but were unsuccessful. On one occasion, a butterfly was dislodged from the tree and "flutter-chased" unsuccessfully. The sallying behavior occurred when the butterflies were beginning to fly and were quite slow. Predation was never observed during the rest of the daylight hours or during sunset, even though monarchs were seen roosting and flying about.

Table 2 shows the tagging record for 6042 monarchs during the 1989-90 season at this site. The sex ratio is skewed favoring males (57.7%, Chi-square = 72.625, df = 1, $P < 0.001$).

Predation was noticed first on 3 January 1990, rose dramatically thereafter, and remained high until late February when the colony size

TABLE 3. Summary of predated butterflies collected at weekly intervals from the litter at KSP site for 1989–90.

Date	♂	♀	% ♂	?	Total	\bar{x} /day
3 Jan 90	3	3	50.0	0	6	0.9
10 Jan 90	29	27	51.8	2	58	8.3
17 Jan 90	105	69	60.3	4	178	25.4
24 Jan 90	81	58	58.3	7	146	20.9
31 Jan 90	73	27	73.0	2	102	14.6
3 Feb 90	74	56	56.9	0	130	43.6
10 Feb 90	98	46	68.1	2	146	20.9
14 Feb 90	133	47	73.9	1	181	45.2
21 Feb 90	163	66	71.2	2	231	33.0
28 Feb 90	47	14	77.0	1	62	8.9
7 Mar 90	22	9	71.0	1	32	4.6
14 Mar 90	10	6	62.5	0	16	2.3
21 Mar 90	13	1	92.5	0	14	2.0
Totals	851	429	66.5	22	1302	

? = sex undetermined; Total = $\delta + \varphi + ?$; % $\delta = \delta / (\delta + \varphi)$; \bar{x} /day = average number of butterflies eaten per day each week.

declined to a few hundred individuals. Predation ceased by 21 March 1990 when the butterflies left. Table 3 shows the total number and sex ratio of butterflies remains collected at each sampling period. The rate of predation varied from 14.6 to 43.3 butterflies per day for samples from 17 January to 21 February 1990. Earlier samples were omitted as the towhees were learning to exploit the resource, and later samples were omitted as the resource diminished. The average for this period was 22.7 butterflies per day. Since this was the work of a single pair of rufous-sided towhees, each bird was eating an average of 11.4 butterflies/day.

Thirty-eight butterflies were found on 12 January, two days after the previous census, and 38 butterflies were found on 13 January. An average of 19 butterflies was eaten on 10–12 January and 38 butterflies were eaten on 12–13 January.

The total number of dead butterflies collected in the litter was 1302. Taking this colony with a peak population visually estimated at 20,000, this was a 6.51% mortality. A mortality estimate of 7.43% can be derived based on the number of butterflies tagged and the number of butterflies preyed upon by the towhees. These estimates were, however, misleading as the population size was steadily declining (visually estimated at 5000 on 17 January) when predation plateaued. By late February, the towhees were taking most of the remaining butterflies; thus, the 6.51–7.43% annual mortality estimate is extremely conservative.

A Chi-square was calculated comparing the actual sex ratio of the butterflies when the birds were feeding based on Table 2 with the sex ratio of eaten butterflies in Table 3. The Chi-square value of 0.185 (df

TABLE 4. Summary of preyed upon tagged and untagged butterflies collected at weekly intervals from the litter at KSP site for 1989-90.

Date	Untagged				Tagged				?	T
	δ	φ	% δ	X_u	δ	φ	% δ	X_t		
3 Jan 90	3	3	50.0	6	0	0	0	0	0	6
10 Jan 90	14	21	40.0	35	15	6	71.4	21	2	58
17 Jan 90	76	58	56.7	134	29	11	72.5	40	4	178
24 Jan 90	37	39	48.7	76	44	19	69.8	63	7	146
31 Jan 90	42	23	64.6	65	31	4	88.6	35	2	102
3 Feb 90	39	46	45.9	85	35	10	77.8	45	0	130
10 Feb 90	37	28	56.9	65	61	18	77.2	79	2	146
14 Feb 90	56	39	58.9	95	77	8	90.6	85	1	181
21 Feb 90	74	40	64.9	114	89	26	77.4	115	2	231
28 Feb 90	29	11	72.5	40	18	3	85.7	21	1	62
7 Mar 90	17	5	77.3	22	5	4	55.6	9	1	32
14 Mar 90	7	6	53.8	13	3	0	100	3	0	16
21 Mar 90	12	0	100	12	1	1	50.0	2	0	14
Totals	443	319	58.1	762	408	110	78.8	518	22	1302

% δ = $\delta/(\delta + \varphi)$; X = $\delta + \varphi$ (u = untagged and t = tagged); ? = sex undetermined; T = $X_u + X_t + ?$.

= 1, $P < 0.68$) indicates that the birds were not selective based on the butterfly's sex.

The proportion (17.7%) of previously tagged butterflies (recaptured butterflies in Table 2) in the sample of butterflies being tagged (total captured in Table 2) was compared with the proportion (31.3%) of tagged butterflies found in the preyed upon butterflies collected (Table 4). The data strongly suggest that the birds were selecting tagged butterflies (Chi-square = 130.70, df = 1, $P < 0.001$). The data also were separated on a weekly basis and a paired Student's t -test was calculated. The data indicate that there was a very high probability that the tags increased the chances of avian mortality at this site ($t = -3.86$, $n = 9$, $P = 0.0048$).

DISCUSSION

I first noted predation at the colony late in the season in 1988-89. This and the fact that I looked for it regularly beginning on 13 September 1989 and did not notice it until 3 January 1990 suggests that a learning process was involved. Rufous-sided towhees were seen on several occasions earlier in the season, although it is uncertain whether it was the same pair seen throughout the study. But if it was, they were not eating the monarchs. Once they learned to eat monarchs, the resource was exploited as shown in Tables 3 and 4.

Field observations indicate that monarchs are difficult to spot when roosting in trees. But as sunrise approaches, they begin to open their wings and shiver, or after sunrise, they open their wings to bask to warm up to flight temperature. It was at this time that the towhees

began to find and attack the butterflies in the trees. But once the monarchs became warm enough to fly, towhee predation quickly ceased. Rufous-sided towhees belong to a ground feeding and seed eating sub-family of birds (Emberizinae); thus, the lack of success in sallying is expected once the butterflies are capable of flying (Bent 1968).

In Mexico, Brower and Calvert (1985) found that birds preyed selectively upon males either because they had a lower fat content, higher wet weight, and/or a lower cardenolide content. This was not the case in this study, as the birds ate males in the proportion that they were found in the colony. Certainly the fact that the towhees are cueing in on the tagged monarchs affects the data. Since there is a difference between California and Mexican sites relative to the proportion of monarchs that are emetic as well as in their emetic toxicity (Brower & Moffitt 1974, Fink & Brower 1981, Brower & Fink 1985), the same mechanisms working in Mexico may not apply in California. Fink et al. (1983) have data suggesting that rufous-sided towhees in Mexico are not as sensitive to cardenolides, so the lack of prey selectivity by sex is consistent.

Brower and Calvert (1985) estimated a 9.04% annual morality of butterflies killed by birds in one overwintering Mexican colony. Bell and Dayton (1986) reported annual mortality due to chestnut-backed chickadees to range from 0.345–2.21% in California. This study conservatively estimated a 6.51–7.43% annual mortality.

Bell and Dayton (1986) and Brower and Calvert (1985) found that predation intensity was higher on colder days in California and Mexico, respectively. The lowest predation rate during this study was 14.6 butterflies per day during 24–31 January. During this week, an onsite hygrothermograph showed that there were two 36 hour periods when the temperature never fell below 19°C, well above monarch flight temperature of 13°C. There were essentially five days of warm Santa Ana conditions in southern California. The high temperature kept the butterflies constantly agitated making it difficult for the towhees to catch them. On one such morning, butterflies were able to fly at 0400 h when disturbed.

Based on observations of Bell and Dayton (1986) and Calvert et al. (1979), predators leave a characteristic signature on monarch remains. Perches regularly used by the towhees often had the remains (i.e. wings) of five or six butterflies in the litter under them. Brower et al. (1985) found such caches to be associated with small mammal predators in Mexico.

Orioles, grosbeaks, and chickadees feed in the canopy where the clusters are, so body parts and wings simply rain down onto the ground. Calvert et al. (1979) and Fink and Brower (1981) described the different

methods used by orioles and grosbeaks that feed on monarchs. Bell and Dayton (1986) found the chickadees' mode of feeding is similar to that of orioles. As a comparison, yellowjacket predation involves biting off and carrying away the head and abdomen leaving the thorax with the four wings still attached (Leong et al. 1990, Sakai pers. obs.)

The characteristic signature of rufous-sided towhees is a cluster of four wings found in the litter lacking a body. The heads occasionally are found but are difficult to find in the litter. I suspect that the towhee eats the entire body (head, thorax, and abdomen). Occasional heads in the litter are an artifact of the way the towhees kill the butterflies.

Forty dead, intact butterflies were found in the litter during the course of the study. Towhees were observed attacking and picking up butterflies but later dropping and ignoring them. An untested possibility is that these were highly emetic individual butterflies. Mexican and California monarchs are different in their cardenolide biology, which is expected since they feed on different milkweed species. Brower and Moffitt (1974) report California monarchs were 4.6 to 6.5 times more emetic than their Mexican counterparts, and Brower and Fink (1985) report that 49% of California monarchs contain enough cardenolides to make them emetic to birds while only 10% of the Mexican monarchs were considered emetic. Brower and Calvert (1985) suggest that in Mexico birds feed cyclically because they accumulate cardenolides and must periodically desist to purge their bodies of these toxins. Based on these findings, one would expect less avian predation in California compared to Mexico, since California monarchs are both more emetic and have a greater percentage of emetic butterflies.

Towhees may have learned to distinguish between emetic and non-emetic butterflies. Since the cardenolides are concentrated in the wings and exoskeleton, towhees may avoid eating, or learn not to eat, the most toxic ones as orioles do in Mexico. Assuming attacked but uneaten butterflies are the most toxic, the percent of emetic butterflies in this population is only 3.07% (40/1302). This is quite different from the findings of Fink and Brower (1981) and Brower and Fink (1985) of 49% emetic butterflies in California. There are several possibilities. Towhees are able to distinguish the butterflies without killing the monarchs. Towhees may be like grosbeaks and may be relatively insensitive to high doses of cardenolides. It also may be that the percentages of emetic butterflies and/or the degree of emetic strength found by Brower and his co-workers are not consistent throughout California. These questions certainly deserve investigation.

Brower and Calvert (1985) found that grosbeaks and orioles ate more males than females in the Mexican colonies, as females had $\frac{1}{3}$ more lipid but a higher cardenolide concentration. Brower and Moffitt (1974)

found that in California males are heavier but females had a higher cardenolide concentration, meaning that it would be more advantageous to eat male butterflies. In this study, more males were eaten, but this may have reflected the skewed sex ratio in the colony rather than any selection of one sex over another.

The actual impacts of butterfly tagging have never been addressed. This study indicates that tagged monarchs are at greater risk of predation by rufous-sided towhees in the overwintering colony. It may be that the white tags serve as a flag to attract the birds and the birds learn to cue in on the tags. Tagged monarchs are certainly quite visible in the trees even to the naked eye. On the other hand, tagged wings are also much more visible in the litter. How much these tags serve to attract predators once the butterfly leaves the colony is unknown. Certainly the migratory nature of the monarch would prevent predators from learning to cue in on the tags.

CONCLUSIONS

A single pair of rufous-sided towhees was found to be an important predator on monarch butterflies at this southern California overwintering colony site, eating as many as 11.4 butterflies per bird per day, representing a 6.51–7.43% annual mortality. The predation rate seemed to be correlated with weather conditions with warmer weather resulting in lower predation rates. Towhees did not select prey by sex but were found to select a higher proportion of tagged monarchs. The characteristic pile of four wings may be used as a signature of rufous-sided towhees for determining them as a specific avian predator.

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