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DIURNAL PREDATION ON ROOSTING BUTTERFLIES DURING INCLEMENT WEATHER: A SUBSTANTIAL SOURCE OF MORTALITY IN THE BLACK SWALLOWTAIL, *PAPILIO POLYXENES* (LEPIDOPTERA: PAPILIONIDAE)

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Abstract.—To investigate the effect of inclement weather on mortality in adult butterflies, black swallowtails were tethered to typical night roosts and monitored during favorable and adverse weather periods. Fair weather mortality averaged less than 10%, yet mortality during weather-prolonged roosting was about 35%. This significant difference was primarily due to increased predation during daylight periods. Starvation was restricted to older butterflies since freshly-emerged individuals could survive 7 or more days without feeding. Vertebrates, particularly birds, accounted for 65% of the predation. Predators attacked the sexually dimorphic males and females equally which supports the role of the more similar ventral patterns in effective mimicry. Predators showed no preferences for individuals roosting on living or dead roosts. Predation on roosting individuals is probably a primary source of mortality for many butterfly species, especially when inclement weather forces individuals to extend roosting during daylight periods.

Adverse weather has been implicated as a significant source of mortality in a number of butterfly populations (Ehrlich et al., 1972, 1980; Shapiro, 1979; Calvert et al., 1983; Lederhouse, 1983). Death may result directly from exposure to severe conditions (Calvert et al., 1983), but this increased mortality has more commonly been correlated with reduced larval or adult resources (Ehrlich et al., 1972, 1980; Singer, 1972) or prolonged periods of predatory risk (Lederhouse, 1983). In cold weather, exothermic butterflies have reduced ability to avoid or escape attacks by predators (Brown and Neto, 1976; Bowers et al., 1985). Also, birds may forage more during periods of adverse weather (Brower and Calvert, 1985). Mechanisms by which adverse weather actually produces increased mortality remain largely unclear.

Lederhouse (1983) documented shorter average longevity of male black swallowtail butterflies correlated with periods of unfavorable weather. Mortality of adults is highest while roosting (Rawlins and Lederhouse, 1978). In this paper, we report the results of experiments which clearly determine the relative importance of exposure, starvation and predation as sources of weather-related mortality on roosting black swallowtails.

MATERIALS AND METHODS

Black swallowtail butterflies typically search for a roost about 2 hr before sunset. They bask on the roost until decreasing sunlight and temperature trigger a roosting posture with the wings dorsally appressed. This posture is maintained throughout the night. The butterflies bask again in the morning as soon as direct sunlight reaches them (Rawlins and Lederhouse, 1978). They continue to bask until their thoracic temperatures reach or exceed 24°C; they are then able to fly (Rawlins, 1980). If ambient temperatures remain below 24°C with little or no solar radiation, black swallowtails cannot fly to escape predators that discover them during the extended roosting period.

Chilled, well-fed black swallowtails were placed on typical evening roosts (Rawlins and Lederhouse, 1978) just prior to sunset (Bishop, 1984) at early successional field locations in Great Swamp National Wildlife Refuge, Morris County, New Jersey. A natural population of *P. polyxenes* was observed in this area, and during a pilot trial wild individuals roosted on perches within the study area that were similar to those chosen for the experiments. Males and females were placed on both living and dead roost plants in equal proportions and in a random sequence. Roosts were generally 5 m apart and arranged in a semicircle to aid observation. An inconspicuous blue flag was placed at the base of each roost to facilitate relocation. Goldenrod (*Solidago* spp.) was the roost most frequently utilized for experiments because of its abundance.

All subjects were checked at dawn the following day. Damaged and dead individuals were removed as discovered, and a thorough search was made for remains of any missing butterflies. The butterflies were checked again when the sun had fully risen (e.g., 0700 hr EST in mid-July) and for a final time at the onset of favorable flight conditions (Rawlins, 1980). The setup was then dismantled. Periods of inclement weather, with reduced temperature and solar radiation, extended the roosting period into the afternoon and at times into the next day. In the latter case, the butterflies were checked again at sunset and likewise at sunrise on the following day, and finally when the weather cleared.

All butterflies were secured to their roosts by means of tethers which prevented escape without inhibiting normal wing postures (Brower, 1959). Each consisted of a short black cotton thread "harness" looped around the bases of the wings and tied to a 10 cm leader of monofilament. The leader was fastened to a 3 cm "alligator clip" which in turn was clamped to the roost stem. The tethers offered several advantages. They aided in the retrieval of predatory remains and eliminated losses due to strong winds (R. C. Lederhouse, pers. obs.) or unexpected flight from warmer microhabitats. In such instances, absence from the roost would have been misinterpreted as evidence of predation. Tethered butterflies could not escape attacks through crawling or falling off the roost, although Shapiro (pers. comm.) observed high rates of predatory attack on butterflies removed from night roosts and placed on the ground. Since all trials were terminated when flight temperatures were attainable, all acts of predation were realistic within the context of the experimental design. Because tethers were used in all cases, comparisons between experimental treatments should be valid even if actual rates of predation were altered.

After the experiments, all butterflies were classified into one of five mutually exclusive categories. Alive and undamaged individuals showed no ill effects from the experiment and were frequently used in subsequent trials. Alive but damaged butterflies showed evidence of predator harrassment. Dead but undamaged butterflies were assumed to have resulted from advanced age or exposure to weather. Dead and damaged individuals resulted from predation; body remnants (wings, abdomen, etc.) were found. Missing butterflies were not attached to the harness, and no remains were located.

Table 1. Fates of tethered *P. polyxenes* in relation to weather for 1984 and 1985. All fates are given as percentages of individuals for an entire trial regardless of duration.

	1984		1985	
	Fair weather	Inclement weather	Fair weather	Inclement weather
Trials (N)	12	6	5	4
Individuals (N)	217	96	76	58
Alive/undamaged	99.0	64.6	88.2	67.2
Dead/undamaged	0.5	6.3	4.0	5.2
Total predation	0.5	29.1	7.9	27.6
Alive/damaged	0.5	1.0	2.6	1.7
Dead/damaged	0	20.8	4.0	20.7
Missing	0	7.3	1.3	5.2

The only categories that could possibly be confused were the dead but undamaged and the dead and damaged groups. Predators such as spiders or sucking insects could kill and feed on butterflies without producing easily detectable damage. Occasionally, predators might scavenge already dead individuals. Such possible confusion was limited by the frequency of field checks and careful examination of carcasses. Preliminary tests of tether reliability showed that individuals could not free themselves. Thus, missing butterflies must have been removed by predators.

A portable bird blind was used to facilitate the observation of predation. In the majority of instances, however, the type of predator was inferred from the damage suffered by the butterfly. Examples of typical bird damage were observed during concurrent experiments with caged blue jays, *Cyanocitta cristata* (Codella and Lederhouse, in manuscript). In addition to the beak marks routinely used to verify bird damage (e.g., Carpenter, 1933; Collenette, 1935; Sargent, 1973; Shapiro, 1973; Edmunds, 1974; Bowers and Wiernasz, 1979), avian attacks produced intact wings, often associated with disarticulated legs or antennae, and wing fragments split cleanly along veins. Beak marks were noted on only a fraction of the wings of butterflies eaten by the jays. The severing of an abdomen from the thorax likely resulted from the constricting of a tether when a strong predator (a vertebrate) pulled at a butterfly. An alternate explanation for this is mishandling by a predator, which was also observed among the aviary birds. It is assumed that all missing butterflies resulted from vertebrate predation. No invertebrate could break the tethers, and very meticulous searches reduced the likelihood of overlooked remains.

Invertebrate damage was characterized by wings (whole or fragmented) with chewed edges, carcasses with punctures or holes in the eyes or abdomen, and partially consumed bodies with fragments of cuticle adhering to the remains. Observed invertebrate attacks resulted in similar damage.

To determine the duration that starved *P. polyxenes* could live, newly-emerged adults were placed in individual cages in two controlled temperature chambers at either 15 or 20°C. These temperatures are typical of those during roosting but too low for adult flight and feeding without supplemental radiation (Rawlins, 1980). The butterflies spent the majority of time perched at these temperatures and were checked daily until all had died.

Table 2. Longevity of starved *Papilio polyxenes* at two temperatures. Values are in days ± one standard deviation. The probability of a larger t under the H_0:t = 0 is given.

Sex	N	15°C	*P*	N	20°C
Male	20	7.8 ± 1.9	ns	18	7.2 ± 1.2
		P < 0.05			ns
Female	14	12.1 ± 4.2	0.01	8	7.5 ± 1.3

RESULTS

The mortality of roosting black swallowtail butterflies was considerably higher during periods of unfavorable weather in both 1984 and 1985. In 1984, only 1.0% of the individuals exposed for a typical fair-weather overnight roosting period died or were attacked by predators. However, 35.4% of those exposed for a prolonged period due to inclement weather died or were attacked. In 1985, death and damage during a typical overnight was 11.9%. This compares with 32.8% for extended roosting periods in 1985 (Table 1). In both years the differences were significant (χ^2, 2 × 2 contingency table: 1984, $P < 0.001$; 1985, $P < 0.01$).

Dead but undamaged individuals accounted for only 19.4% of the total mortality in 1984 and 21.4% in 1985. Invariably, these individuals were old and frequently had been used in several trials. Although it is difficult to differentiate between exposure and starvation, 84.6% of these deaths occurred during the first night, which suggests exposure.

In our laboratory test of starvation, freshly emerged *P. polyxenes* survived five or more days without feeding (Table 2). Females survived significantly longer than males at 15°C (*t*-test, $P < 0.05$) but only slightly longer at 20°C. Both sexes survived longer at 15°C than 20°C. This difference was significant for females (*t*-test, $P < 0.01$). Since overnight and inclement day temperatures were often less than 15°C, these results indicate that starvation in itself may only be a factor for very old butterflies.

Predation was the greatest cause of mortality of roosting black swallowtails. In 1984, 0.5% of fair weather roosting black swallowtails were preyed upon, compared with 29.1% of butterflies roosting under adverse conditions. A similar comparison for 1985 shows an increase from 7.9% to 27.6%. In both years the differences were significant (χ^2, 2 × 2 contingency table: 1984, $P < 0.001$; 1985, $P < 0.01$). Part of these differences was due to the longer period at risk during inclement weather. However, the predation rate per hour of exposure was higher during inclement weather in both years (Table 3).

Predation on roosting black swallowtails occurred predominantly during daylight

Table 3. Rates of predation on roosting *P. polyxenes*. Values are predation events per hour at risk.

Year	Fair weather	Inclement weather
1984	0.006	0.162
1985	0.093	0.112

Table 4. Predation on roosting *Papilio polyxenes* by time of day in relation to risk. There were 7 predation events during 218.7 hr at risk in fair weather and 28 during 315.6 hr of inclement weather where the time of day could be accurately determined.

	Fair weather			Inclement weather		
Time	% of predation	% of exposure	Rate per hr	% of predation	% of exposure	Rate per h
Night	42.9	77.0	0.02	10.7	53.2	0.02
Morning	57.1	23.0	0.08	0	13.0	0
Day	—	—	—	89.3	33.8	0.23

(Table 4). This was true for both fair and adverse weather. However, the primary difference was the substantial loss on inclement days during the period when the butterflies would have been flying had conditions been favorable. Since the daylight exposure period was shorter than the dark exposure period, these differences are accentuated when calculated as rates (Table 4). The rates for the night were almost identical whether the daytime was fair or foul.

Predation rates were highly variable. Although predation during unfavorable weather occurred primarily during daylight, the number of black swallowtails attacked did not correlate with the duration of the daylight period that they were exposed. This held whether the daylight periods over two-day trials were considered separately or summed ($r = 0.02$ or -0.36, respectively; neither significant). Predation occurred in all but one trial during inclement weather, with a percent of butterflies attacked ranging from 0 to 100 with a mean of 29.5 ± 29.9.

Predators attacked roosting male and female black swallowtails equally in both 1984 and 1985 (Table 5). Males were somewhat more likely to die from exposure/starvation than females but not significantly so. Predators attacked butterflies on dead roosts slightly more often than those on living roosts in 1984, but this was not significant. This trend was reversed in 1985 but still not significant. Thus, the combined data gave nearly identical attack rates on butterflies on the two roost types (Table 6). Neither vertebrate nor invertebrate predators attacked black swallowtails preferentially by roost type.

Predators were identified by direct observation in five cases. These included 2 attacks by ants (Formicidae) and one each by a damsel bug (Nabidae), a bald-faced

Table 5. Mortality of tethered, roosting *P. polyxenes* in relation to sex.

	1984		1985	
	Male	Female	Male	Female
N	152	151	54	54
Alive/undamaged	133	136	44	44
Dead/undamaged	4	1	3	2
Total predation (%)	9.9	9.3	13.0	14.8
Alive/damaged	1	1	0	3
Dead/damaged	10	10	4	5
Missing	4	3	3	0

Table 6. Mortality of tethered, roosting *P. polyxenes* in relation to roost type.

	1984		1985	
	Dead	Living	Dead	Living
N	153	150	66	68
Alive/undamaged	132	137	54	52
Dead/undamaged	4	1	4	2
Total predation (%)	11.1	8.0	12.1	20.6
Alive/damaged	1	1	0	3
Dead/damaged	15	5	6	7
Missing	1	6	2	4

hornet (*Vespula maculata*) and a yellow jacket (*V. maculifrons*). In the majority of instances, however, the type of predator was inferred from the damage suffered by the butterfly as indicated in Materials and Methods. Our analysis indicates that birds and possibly other vertebrates performed 64.7% of the predation, and invertebrates were responsible for the remaining 35.3%.

DISCUSSION

The results of this experiment demonstrate significantly higher mortality for roosting butterflies during periods of adverse weather. Most of this increase was due to greater predation. Exposure and starvation accounted for only 20% of the increase. Newly-emerged black swallowtails survived a week or more without feeding in our study and Rawlins (1980) demonstrated that young, well-fed individuals can withstand periods of freezing temperatures.

Although a bird blind was used during part of this study to identify individual predators, the only cases observed involved invertebrates. However, by using reasonable assumptions and by comparing remains to those produced by feeding black swallowtails to a variety of known predators, we are fairly confident that vertebrate predators are the major source of predation. The high incidence of beak marks (35.0% of all retrieved remains attributed to vertebrates) and the occurrence of over 80% of all predation during daylight suggest that birds are the major source of vertebrate predation, although one of the overnight losses reported by Rawlins and Lederhouse (1978) was probably due to a skunk (*Mephitis mephitis*).

The actual level of predation in this study may have been influenced by our choice of study areas and individual roosts, the use of tethers, and the density at which the butterflies were placed during the trials. Artificially high densities may have provided the opportunity for traplining by birds. Although these and possibly other factors may have influenced the absolute values, the relative importance of weather, time of day, sex and roost type would be unaffected since each experimental group was treated in the same way.

Although the fair weather rate of predation was very low in 1984, the rate in 1985 was quite similar to the natural loss rate under similar conditions reported by Rawlins and Lederhouse (1978). The 8.0% per night predation loss yields adult longevities typical for fair weather broods (Lederhouse, 1983). Assuming that the average black swallowtail was confronted by one prolonged roosting period during harsh weather broods, again the life expectancies calculated from predation observed in this study agree quite well with those reported for an unusually inclement period by Lederhouse (1983).

The increased predatory losses during extended roosting periods were not simply due to the longer periods of risk. Rates were lower during the night and higher during daylight. Black swallowtails that roosted during fair weather were relatively safe because 75.0% of the roosting period was in the dark. Individuals forced to remain on the roost because of inclement weather faced the double hardship of prolonged durations and greater conspicuousness during daylight. The unpredictable and sporadic nature of predation is further indicated by concurrent tests with roosting wood nymphs, *Cercyonis pegala* (Satyridae). In one test, none of ten individuals were attacked over the 13 hr of the trial, yet 7 of 10 individuals were attacked within 2 hr 21 min between checks in another trial (Lederhouse and Codella, unpubl. data). Given that insectivorous passerine birds frequently show peaks of foraging shortly after dawn and again in late afternoon, high daytime predation rates for roosting butterflies are not surprising. Jeffords et al. (1980) suggest a late afternoon peak for predation on day-flying males of the moth, *Callosamia promethea* (Saturniidae).

Although roosting black swallowtails demonstrated a preference for dead roosts under natural conditions (Rawlins and Lederhouse, 1978), our data do not support an anti-predator explanation for this behavior. Perhaps the greater stability and relative isolation of such dead roosts decreased the likelihood that an individual would be dislodged by wind or rain. This advantage was difficult to investigate in our study due to the use of tethers.

In New Jersey, the black swallowtail produces two to three broods per summer (Shapiro, 1966, 1974; Lederhouse, 1983). Bad weather typically affects adult butterflies at the beginning of the first brood and the end of the last brood. Therefore, increased mortality during the first brood should be primarily due to increased predation, and the late-season increases should reflect both predation and exposure/starvation losses. The tendency for males to suffer greater exposure/starvation mortality under roosting conditions agrees with the shorter lifespan of starved male black swallowtails. Since males have a lower fat content (Lederhouse et al., 1982), they are probably more dependent on a steady diet of nectar for energy.

Male and female black swallowtails are sexually dimorphic in color patterns. Jane Brower (1958) demonstrated that the black swallowtail is an effective mimic of the aposematic pipevine swallowtail *Battus philenor* (Papilionidae). However, she primarily used females, and thus did not investigate sexual differences. A number of authors (e.g., Remington and Remington, 1957; Waldbauer and Sternburg, 1975; Turner, 1978) state that the male is non-mimetic, but this assumption has not been tested. Rawlins and Lederhouse (1978) suggested that mortality on the roost would select for a mimetic ventral pattern since it is exposed during roosting. Male and female black swallowtails are much more similar in pattern ventrally than dorsally (Rawlins and Lederhouse, 1978). The similar rates of predation on both sexes support these contentions. Since it was inferred that birds did most of the predation during daylight, it is unlikely that the similar predation rates for males and females were significantly influenced by low light levels or the inability to detect colors. The effectiveness of dorsal and ventral color patterns of both sexes in mimicking *B.*

philenor has been investigated with caged birds as well as in the field and will be reported in detail at a later time (Codella, 1986; Codella and Lederhouse, in manuscript).

Reports of butterflies being preyed upon while active are scarce (Young, 1971; Davies, 1977). Such acts of predation are probably most successful when the butterfly is distracted by nectaring, puddling, mating or ovipositing (Rawson and Bellinger, 1953; Wright, 1981; Ehrlich and Ehrlich, 1982). Except for a few communal species (Benson and Emmel, 1973; Turner, 1975; Young and Thomason, 1975; Brower et al., 1977), detailed information on the roosting behavior of butterflies is quite limited. The inconspicuousness of roosting individuals and the deliberate nature of their roost search flights suggest that roost choice is under strong selection pressures. Additional studies of *Cercyonis pegala* in New Jersey and of *Battus philenor* and the zebra swallowtail, *Eurytides marcellus* (Papilionidae), in eastern Texas revealed substantial mortality on the roost that was considerably increased during periods of inclement weather (Lederhouse and Codella, unpubl. data). We believe that predation on roosting individuals is a primary source of mortality for many butterfly species. This is particularly so at those latitudes and altitudes where weather causes prolonged roosting during daylight hours. This has implications on the interpretation of proposed cases of aposematism and mimicry, as the warning or mimetic wing surface should be exposed during this high-risk period.

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