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BIRD PREDATION ON LEPIDOPTERA AND THE RELIABILITY OF BEAK-MARKS IN DETERMINING PREDATION PRESSURE

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ABSTRACT. Visually hunting predators such as birds are thought to have influenced the evolution of the wing markings and colorations of Lepidoptera. Although studies have been conducted to quantify and characterize predation by birds on butterfly populations, field observations of bird predation on butterflies have rarely been reported. A request for information on predation yielded 50 previously unpublished accounts of bird predation on butterflies.

The combination of laboratory interactions of *Pieris rapae* and blue jays and field collections of *P. rapae* allowed several variables to be examined which affect the reliability of using frequency of beak-marks on lepidopteran wings as an index of predation pressure. Beak marks occur four times more frequently during attacks on flying *P. rapae* than on ones at rest and blue jays were five times more efficient at capturing resting butterflies than capturing flying butterflies. Variation in wing strength makes the area where the ipsilateral wings overlap and the costal vein area of the forewing more resistant to beak-marks than the marginal areas of the fore- and hindwings and the distal tip of the forewings. These differences in wing strength may confound the use of beak-marks as an index of predation pressure.

Finally, predation efficiency and the frequency of occurrence of beak-marks during attacks, as determined in the laboratory, were used in conjunction with field data to estimate avian predation pressure on *P. rapae* populations.

Although birds have long been thought to be the major predators on adult Lepidoptera (Poulton, 1890, 1913; Fryer, 1913; Swynnerton, 1915; Dover, 1920; Carpenter, 1937), field observations of bird predation on butterflies in temperate North America have rarely been reported. The short time that it takes birds to capture and manipulate butterflies while feeding may account for the rarity of field observations (Bowers & Wiernasz, 1979; Collins & Watson, 1983). There is strong circumstantial evidence in the form of beak-marks and tears on wings of Lepidoptera to indicate that birds act as significant predators on butterflies (e.g., Wheeler, 1935; Carpenter, 1937; Kolyer, 1968).

TABLE 1. Avian–lepidopteran interactions.

Lepidoptera	Bird	Notes	Location	Reference
Family—Danaidae				
Subfamily—Danainae				
Danaus plexippus (Monarch)	*Falco peregrinous* (Peregrine Falcon)	Fledgling seen repeatedly chasing, catching, and often releasing monarchs	Minnesota	Evans, pers. observ., 1983
D. plexippus	*Parus rufescens barbei* (Chestnut-backed Chickadee)	Captured, pecked, and released monarch	Santa Cruz, Mexico	Tuskes and Brower, 1978
D. plexippus	*Athene cunicularia* (Burrowing Owl)	Wings found at burrow entrance with other prey remains	Southern Idaho	Reil, pers. observ., 1981
D. plexippus	*Buteo platypterus* (Broad-winged Hawk)	Captured in flight in talons, eaten in flight	Hawk Mountain, Pennsylvania	Braun, pers. observ., 1974–1975
D. plexippus	*Falco sparvervus* (American Kestrel)	During butterfly migration, four aerial captures while soaring, captured in beak	Salton Sea National Wildlife Refuge, Indigo, California	Abbott, pers. observ., 1973
D. plexippus	*Icterus parisorum* (Scott's Oriole) *I. abeillei* (Lesson) (Black-backed Oriole) *Pheucticus melanocephalus* (Black-headed Grosbeak)	37% of the captured monarchs were handled, damaged, and released by the birds	Mexico	Calvert et al., 1979
D. plexippus	*Toxostoma rufum* (Brown Thrasher)	110 of 112 wingless monarchs consumed from a dish outdoors	Milford, Iowa	Petersen, pers. observ., 1964

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
D. plexippus	*Aphelocoma coerulescens* (Scrub Oak Jay)	27 winged monarchs consumed in winter from a dish outdoors	Colorado Springs, Colorado	Petersen, pers. observ., 1964
Family—Satyridae				
Subfamily—Satyrinae				
Cercyonis pegala (Wood Nymph)	*Falco sparverius* (American Kestrel)	Captured in air	Salt Marsh, Rouley, Massachusetts	Schlinger, pers. observ., 1982
Family—Nymphalidae				
Subfamily—Nymphalinae				
Vanessa atalanta (Red Admiral)	*Tyrannus tyrannus* (Eastern Kingbird)	Attacked while Red Admiral was sunning, missed	Pt. Pele, Canada	Pilkington, pers. observ., 1983
V. atalanta	*Sayornis phoebe* (Phoebe)	Handling observed, Red Admiral escaped, was pursued and recaptured	Baltimore, Maryland	Blackbill, pers. observ., 1951
V. cardui (Painted Lady)	*Empidonax traillii* (Flycatcher)	Captured and perched. Some wings removed and consumed—no unpleasant reaction	Austin, Travis County, Texas	Johnson, pers. observ., 1983
V. cardui	*Melospiza melodia* (Song Sparrow)	Butterflies migrating. Sagebrush Swift (Reptilia) captured and consumed the body. Most evidence of wing damage suggests birds are the major predators	Tooele and Box Elder County, Utah	Knowlton, 1953

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
Euphaydras chalcedona (Checkerspot)	*Toxostoma redivivum* (California Thrasher)	Attacked and ate several tethered butterflies	San Mateo County, California	Bowers et al. (unpubl. ms.)
E. c. kingstonensis	*Tyrannidae* (Flycatcher)	Several observations	Providence Mts., San Bernardino County, California	Shields, pers. observ., 1983
Nymphalis antiopa (Mourning Cloak)	*Myiarchus crinitus* (Great Crested Flycatcher)	Captured from behind in flight. Body in beak hit and killed on branch prior to eating	Pt. Pele, Ontario, Canada	Pilkington, pers. observ., 1980
N. antiopa	*Iridoprocne bicolor* (Tree swallow)	Pursued only. BF dropped to water surface just as swallow closed in. Attacked 4 times	Cedar Creek, Essex County, Ontario	Pilkington, pers. observ., 1982
Subfamily—Argynninae				
Speyeria edwardsii (tent. I.D.)	*Contopus sordidulus* (Western Wood Peewee)	Taken in flight and carried to perch	El Paso Co., Colorado	Johnson, pers. observ., 1963
Family—Lycaenidae				
Subfamily—Plebejinae				
Lycaenopsis argiolus (Spring Azure)	*Passer domesticus* (House Sparrow)	Captured in flight and consumed entirely	New York, New York	Zirlin, pers. observ., 1976
L. argiolus	*Melospiza melodia* (Song Sparrow)	Hawking	Florissant, Missouri	Olson, 1962
Everes comyntas	*Melospiza melodia* (Song Sparrow)	Hawking	Florissant, Missouri	Olson, 1962

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
Strymon spp.	*Melospiza melodia* (Song Sparrow)	Hawking	Florissant, Missouri	Olson, 1962
L. americana	*Melospiza melodia* (Song Sparrow)	Hawking (also took unidentified moths)	Florissant, Missouri	Olson, 1962
Lycaenids	*Melospiza melodia* (Song Sparrow)		Otsego County, Michigan	
Family—Pieridae				
Subfamily—Colladinae				
Colias eurytheme (Orange Sulfur)	*Tyrannus verticalis* (Western Kingbird)	One attack in flight	Sacramento Valley, California	Shapiro, 1974
Colias spp. (Sulfur Butterfly)	*Sayornis phoebe* (Phoebe)	Consumed all	Baltimore, Maryland	Blackbill, pers. observ., 1944
Subfamily—Pierinae				
Pieris rapae (Cabbage White Butterfly)	*Sturnus vulgaris* (Starling)	Tried to catch by hopping off ground but missed	Baltimore, Maryland	Blackbill, pers. observ., 1950
P. rapae	*Passer domesticus* (House Sparrow)	Male House Sparrow with butterfly in beak, fed to young, no adverse reaction	Fenway Gardens, Boston, Massachusetts	Wourms, pers. observ., 1983
P. rapae	*Passer domesticus* (House Sparrow)	Female House Sparrow pursued butterfly in air, no contact, no capture	Fenway Gardens, Boston, Massachusetts	Wourms, pers. observ., 1983
P. rapae	*Pipilo erythrophthalmus* (Rufous-sided Towhee)			Morris, pers. observ., 1953, to Adler, 1982

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
P. rapae	*Quiscalus quiscula* (Common Grackles)			Morris, pers. observ., 1953 to Adler, 1982
Pieris protodice	*Progne subis* (Purple Martin)	Pursuit, no capture BF dove into grass and stayed there	Austin, Travis County, Texas	Johnson, pers. observ., 1979
Pieris spp.	Fringillidae (Sparrows no I.D.)	Pursued and captured.	Black Donald Lake, Ontario	Holliday, pers. observ., 1983
Pieris or *Colius*	*Myiarchus crinitus* (Great Crested Flycatcher)	Captured in air at perch dropped but captured before hit ground. 1 wing removed and consumed	Baltimore, Maryland	Blackbill, pers. observ., 1938
C. eurytheme *P. rapae* *P. protodice*	*Eupagus cyanocephalus* (Brewer's Blackbird) *Sturnella neglecta* (Western Meadowlark)	21 attacks on resting Pierids in open alfalfa fields	Sacramento Valley, California	Shapiro, 1974
Family—Papilionidae				
Subfamily—Papilioninae				
Papilio glaucus (Tiger Swallowtail)	*Myiarchus crinitus* (Great Crested Flycatcher)	Captured in flight consumed wings and all at perch	South Charleston, Kanawha County, West Virginia	Adler, pers. observ., 1968
P. glaucus	*M. crinitus*	Capture and consumption not observed, held by thorax or abdomen	Reelfoot Lake, National Wildlife Refuge, Obion County, Tennessee	Pitts, pers. observ., 1983

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
P. g. canadensis	*Zonotrichia leucophrys* (White Crowned Sparrow)	Seen pecking at puddling BF and many wings found nearby	Fairbanks, Alaska	Rawson, 1953
Papilio polyxenes (Black Swallowtail)	*Cyanocitta cristata* (Blue Jay)	Female captured while ovipositing	Ithaca, New York	Erickson, 1973
	Dumetella carolinensis (Catbird)	Male taken on wing just after taking flight	Ithaca, New York	Erickson, 1973
Family—Hesperiidae				
Subfamily—Pyrginae				
Erynnis juvenalis (Skipper)	*Pipilo erythrophthalmus* (Rufous-sided Towhee)		Location not provided	Morris, 1953, pers observ. to Adler
	Spizella passerina (Chipping Sparrow)			
	Melospiza melodia (Song Sparrow)			
	Zonotrichia leucophrys (White Crowned Sparrow)			
Butterflies not identified	*Lanius ludovicianus* (Loggerhead Shrike)	29 successful attacks out of 30 attempts	Whittier Narrows, Nature Center, Los Angeles Co., California	Morrison, pers. observ., 1977–1978
Family—Geometridae				
Subfamily—Brephinae				
Brephos infans *Leucobrephos brephoides*	*Melospiza melodia* (Song Sparrow)	4 observed captured while puddling, bird ran and captured them		Donahue and Newman, 1967

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
Lomographa semiclarata	*Pipilo erythrophthalmus* (Rufous-sided Towhee)			Morris, pers. observ., 1953–1982
Adler	*Spizella passerina* (Chipping Sparrow) *Melospiza melodia* (Song Sparrow) *Zonotrichia leucophrys* (White Crowned Sparrow)			
Family—Saturnidae				
Subfamily—Attacinae				
Callosamia promethia (painted yellow-like tiger swallowtail)	*Melanerpes erythrocephalus* (Red-headed Woodpecker)	Moth attempted evasive flight, but captured in flight, bird flew off	Monticello, N.Y.	Jeffords, 1979
	Richmondens cardinalis (Cardinal)	Attempted to capture moth in air, grasped one wing, wing tore, moth got away		Jeffords, 1979
Actias luna (Luna Moth)	*Cyanocitta cristata* (Blue Jay)	Captured in flight, handled on perch—wings removed	Middlesex Co., New Jersey	Zirlin, pers. observ., 1979
A. luna	*Melanerpes erythrocephalus* (Red-headed Woodpecker)	Luna hand released, captured in air seconds later	Southern Wisconsin	Reil, pers. observ., 1972
Hyalophora cecropia (Cecropia Moth)	*Passer domesticus* (House Sparrow)	Killed on ground, 2 observations	Black Donald Lake, Ontario	Holliday, pers. observ., 1983
H. cecropia	*Passer domesticus* (House Sparrow)	Chased but not captured (2 obs.), Cecropias dove at moment of imminent capture	Black Donald Lake, Ontario	Holliday, pers. observ., 1983

TABLE 1. Continued.

Lepidoptera	Bird	Notes	Location	Reference
Virgo Tiger Moths	*Tyrannus tyrannus* (Eastern Kingbird)	Wings neatly clipped off	Black Donald Lake, Ontario	Holliday, pers. observ., 1935–1939
Various small diurnal moths	*Passer domesticus* (House Sparrow)	Fly-catching	Black Donald Lake, Ontario	Holliday, pers. observ., 1975
Dryocampa rubicunda *Nadata gibbosa* *Lapara coniferarum* Geometridae Arctiidae Noctuidae Notodonitidae	*Piranga rubra* (Summer Tanager)	Captured moths at rest on side of building, 2–5 seconds handling time, two occasions	Piedmont National Wildlife Refuge, Jones Co., Georgia	Lee, pers. observ., 1983

Predation by birds on Lepidoptera have been reported in studies that have been concerned with interactions between European Lepidoptera and birds (Carpenter, 1933, 1937, 1941; Collenette, 1935) or tropical Lepidoptera and birds (Fryer, 1913; Young, 1971; Brown & Neto, 1976; Smith, 1979; Collins & Watson, 1983). This study reports on the interactions between North American Lepidoptera and birds and investigates the reliability of butterfly wing-damage frequencies as a predictor of predation pressure in the European cabbage butterfly, *Pieris rapae* L.

METHODS

A request for information from professional and amateur lepidopterists and ornithologists regarding butterfly-bird interactions yielded 50 previously unpublished accounts of predation by birds on butterflies in temperate North America (Table 1). The results of a literature survey of the frequency of beak-marks reported in butterfly populations is summarized in Table 2 and a survey of defensive compounds found in adult Lepidoptera is presented in Table 3.

In order to document avian predation on *P. rapae* in the field *P. rapae* adults were collected for a 30 minute period every seven to 10 days in Boston, Suffolk Co., Massachusetts (Fenway Victory Gardens) and for a one hour period every seven to 10 days at two sites in Lexington, Middlesex Co., Massachusetts (Dunback Meadows and Carroll Field, 71° West, 42° North). The difficulty of moving through the Middlesex Co. sites, due to dense vegetation, *Phragmites* spp. and goldenrods, *Solidago* spp., necessitated the longer collection time per period. Captured butterflies were sexed, and the presence and location of bird-attributable wing damage were recorded for each specimen. Initially, nine possible locations of attack were identified. These were condensed to represent three directions of attack; from the front, side, or from behind (Fig. 1).

One factor that may influence the reliability of beak-marks as an index of predation is the strength of the wings. The strengths of (1) three areas on the forewing, (2) one area on the hindwing, and (3) the area where the ipsilateral fore- and hindwing overlap, were measured on 25 specimens of *P. rapae* (Fig. 2). Strength measurements were obtained by removing the wings from the specimen, and positioning one wing at a time in the testing device (Fig. 3). The device slowly increased the force on the wing until tearing occurred. Data were analyzed with a single factor repeated measures analysis of variance and a Student Newman-Keuls multiple pairwise test (Zar, 1974).

To observe predatory behavior and to quantify the frequency and

TABLE 2. Frequency of bird-attributable damage on the wings of Lepidoptera.

Lepidoptera	Family	Frequency of bird damage	Comments and references
Colias eurytheme	Pieridae	4.8%	Sacramento Valley, California, Shapiro (1974)
Pieris rapae	Pieridae	5.1%	Sacramento Valley, California, Shapiro (1974)
P. rapae	Pieridae	7.9% males 9.9% females	Boston, Massachusetts, Wourms (this study)
Pieris protodice	Pieridae	6.8%	Sacramento Valley, California, Shapiro (1974)
Pieris coenia	Pieridae	6.8%	Sacramento Valley, California, Shapiro (1974)
Ascia monuste	Pieridae	22.8%	Everglades Nat. Park, Florida, Pought and Brower (1977)
Lycaenid spp.	Lycaenids	10%	Malaya, Robbins (1978)
	Hairstreaks	7.9%	Colombia, Robbins (1978)
Lycaenid spp.	Lycaenids	7.9%	Colombia, Robbins (1978)
Lycaenid spp.	Lycaenids	7.0%	Panama, Robbins (1978)
Euphydryas chalcedona	Nymphalidae	5.4% males 8.1% femlaes	San Mateo Co., California, Bowers, Brown and Wheye, submitted, 1983
Danaus plexippus	Nymphalidae	2%	Santa Cruz, Mexico, Tuskes and Brower (1978)
D. plexippus	Nymphalidae	40%	Mexico, Calvert et al. (1979)
D. plexippus	Nymphalidae	30.7%	Mexico, Carpenter and Hope (1941)
Danaus chrysippus	Nymphalidae	7.3%	Tanzania, Smith (1979)
Hypolimnas misippus	Nymphalidae	3.2%	Tanzania, Smith (1979)
Morpho amathonte centralis	Morphidae	0%	Costa Rica, Young (1971)
Morpho granadensis polybaptus	Morphidae	65.3% 83%	Costa Rica, three locations, Young (1971)
Morpho peleides limpida	Morphidae	83%	Costa Rica, three locations, Young (1971)
Cercyonis pegalia	Satyridae	10% 7.1%	Massachusetts, two sites, Bowers and Wiernasz (1979)
Maniola jurtina L.	Satyridae	8% males 13% females	Southern Sweden, Bengston (1981)
Catocala spp.	Noctuidae	4%	Massachusetts, Sargent (1973)

TABLE 3. Secondary compounds sequestered by Lepidoptera.

Lepidoptera	Compound sequestered	Food plant	Reference
Family—Papilionidae (Swallowtails)			
Battus philenor	aristtolochic acids	Dutchmans Pipe, *Aristolochia* spp.	Bowers, 1980
B. polydamas			
Pachlioptera aristolochiae			
Troides aeacus	acetylcholine-like		Rothschild et al., 1970
Family—Nymphalidae			
Danaus plexippus	cardiac glycosides	Milkweeds, *Asclepias* spp.	Reichstein et al., 1968
D. chrysippus			Brower et al., 1968
Subfamily—Ithiomiinae	alkaloids	Solanaceous plants, tomatoes, potatoes	Bowers, 1980
Subfamily—Acraeinae Heliconiinae	cyanogenic glycosides and alkaloids	Passion Flower, Passafloraceae	Hegnauer, 1969
Heliconius erato			
Family—Pieridae (Cabbage Whites)			
Pieris rapae	sinigrin and mustard oils	Cruciferaceae, wild mustard, cabbage	Marsh and Rothschild, 1974 Aplin et al., 1975
P. brassicae			
Family—Zygaenidae			
Zygaena filipendulae	histamine	*Jenecio* spp.	Rocci, 1916
Family—Arctiidae			
Arctia caja	acetylcholine, hydrocyanic acids		Frazer and Rothschild, 1960 Morley and Schachter, 1963 Rothschild et al., 1970

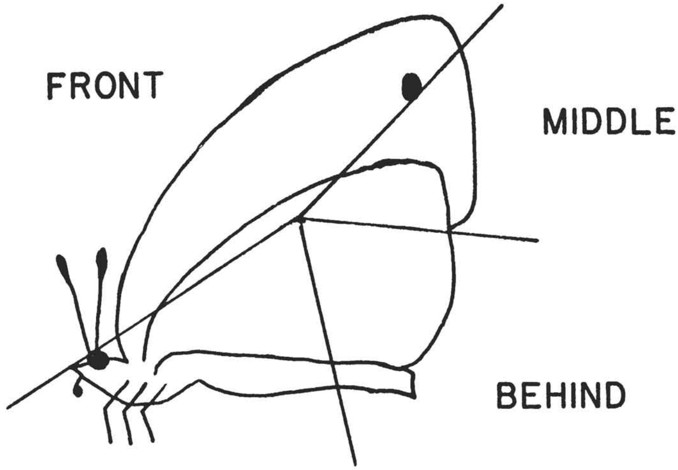

FIG. 1. Front, middle, behind locations of bird damage for field collected *Pieris rapae*.

type of butterfly wing damage that occurs during attacks, *P. rapae* adults were brought into the laboratory in a wire cage (25 cm high × 15 cm in diameter), where they were released into a 1 × 0.5 × 1 m holding cage made of mosquito netting. Sugar water and wild flowers were provided *ad libitum*. Four blue jays, *Cyanocitta cristata*, were captured in mist nets and baited traps. They were housed individually in 1 × 1 × 1 m wire screen cages under a long-day light cycle (18 h light, 6 h dark). All birds were provided water and sunflower seeds *ad libitum*, and were given canned dog food, fresh chopped vegetables, and 5–10 mealworms each morning. Two weeks prior to trials with live *P. rapae*, one bird was placed in a flight cage (3 × 4 × 3 m). The experimental procedure consisted of (1) placing a single live *P. rapae* in a 4 cm box, (2) introducing the box into a flight cage through a slot in the side of the cage, and (3) releasing the butterfly by pulling a string attached to the lid of the box.

The activities of the butterfly and the blue jay were monitored for 15 minutes with a video recorder. If the butterfly was not consumed during the 15 minute trial it was removed and another individual was presented after a 15 minute interval. No more than six trials were conducted per day. Video tapes were analyzed with slow motion and freeze-frame to identify attacks and contact points. A new blue jay was transferred to the flight cage and trained, after the previous bird had had 10 days of live presentations.

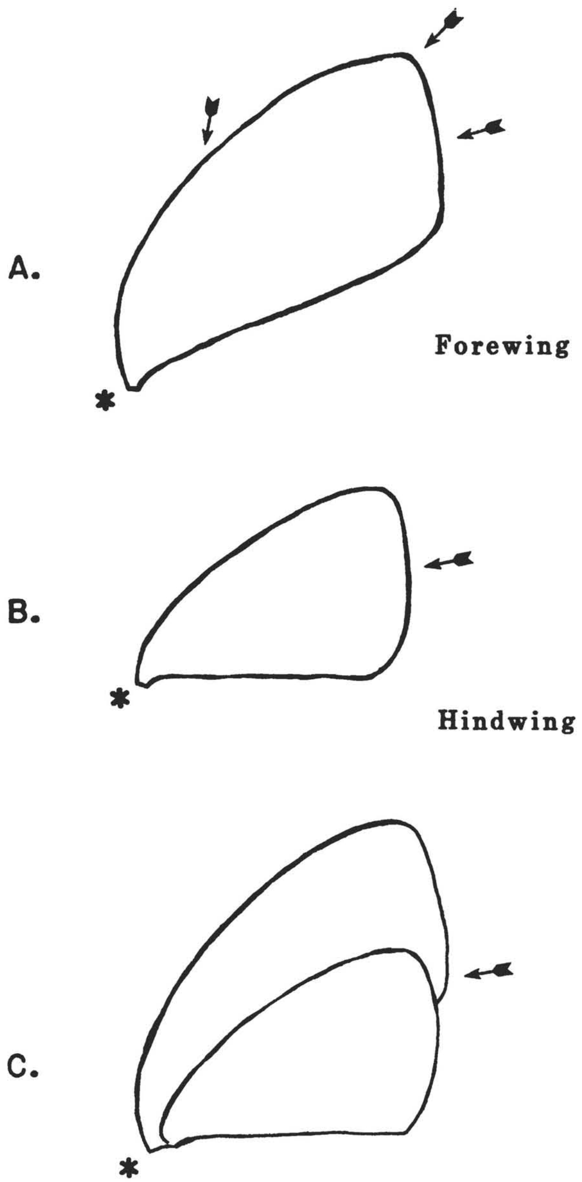

FIG. 2. The areas of *Pieris rapae* wings where resistance to tearing was measured. (* indicates points of anchoring during measurements.) **A.** The arrows indicate points of strength measurements, the forewing costal vein, wing tip, and distal margin. **B.** Distal margin of the hindwing. **C.** Ipsilateral overlap of fore and hindwings.

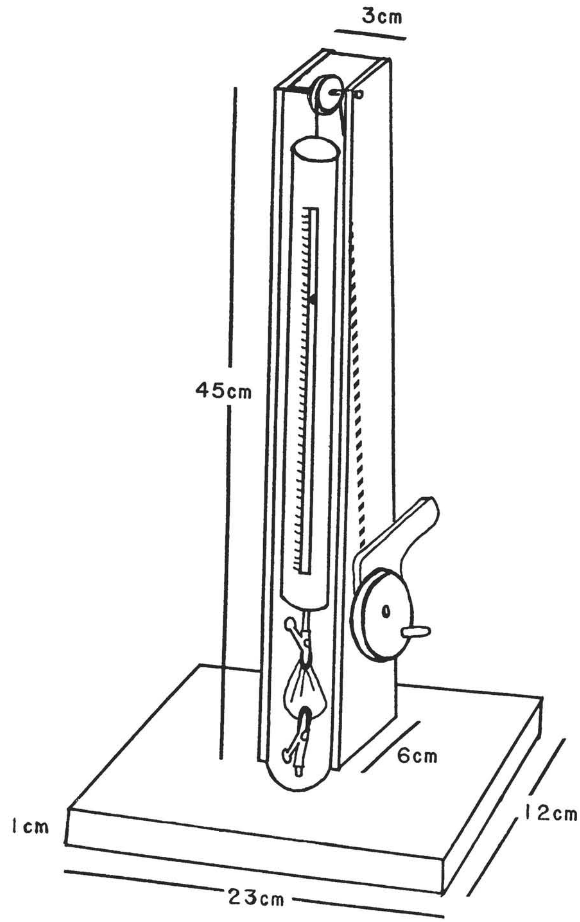

FIG. 3. Wing strength (resistance to tear) measurement device. The wing was anchored by the clip of the Pesola scale, and the area measured by the lower clip. The crank was turned pulling upward. The resistance (g) was shown on the Pesola scale, and was recorded to the nearest 0.5 g the moment the wing tore apart.

RESULTS

Of the 1179 *P. rapae* collected during the three field seasons, an average of 7.2 ± 0.28% (S.D.) of the specimens had beak-marks or beak tears. There were no significant differences in frequency of bird damage among sites or within sites over different seasons (Table 4, 6 × 2 Chi-square contingency table; $\chi^2 = 0.49$, df = 4, $P > 0.05$). Only two of the 91 specimens collected showing bird damage had impressions of a bird's beak on the wings of the butterfly; the other 89 specimens

TABLE 4. Butterfly sampling and beak-mark frequencies.

Year	Site	Collected	Beak-marked	% damaged
1981	Fenway	182	12	6.2
1982	Fenway	351	28	7.4
	Lexington	104	8	7.1
1983	Fenway	241	17	6.6
	Lexington	247	22	8.2
	Carroll	54	4	6.9
Totals		1179	91	7.2 ± 0.28

had beak tears. Henceforth, unless otherwise stated, "beak-marks" implies both marks and tears.

In 1981, sex was not distinguished during the collection of *P. rapae.* In 1982 and 1983, 838 (78.2%) males and 238 (21.8%) females were collected (Table 5). Chi-square analysis reveals that in 1982 and 1983 the frequency of bird damage on *P. rapae* was independent of sex (Table 5).

No specimen showed evidence of more than one attack. Symmetrical damage on both sets of wings suggests that the damage occurred while the butterfly was at rest with wings folded. Butterflies with damage on one wing or on an ipsilateral forewing and hindwing were assumed to have been attacked in flight (Bowers & Wiernasz, 1979; Sargent, 1973). Two specimens from 1982 and one from 1983 were omitted because symmetrical or single wing damage could not be determined.

Of the 76 bird-damaged *P. rapae* collected in 1982 and 1983, 51 (67%) were damaged in flight, and 25 (33%) were damaged at rest (Table 6). Significantly more specimens were damaged in flight than at rest (expected values are calculated as half of the total number of damaged specimens; $\chi^2 = 4.4$, df = 1, P < 0.05). The distributions of attacks from the front, side and from behind are presented in Table 6. There was no significant difference between the distribution of attack positions occurring in flight from the distribution of attack positions occurring at rest (Table 6; 3 × 2 Chi-square contingency table; $\chi^2 = 2.44$, df = 2, P > 0.05). Regardless of whether the butterfly was in flight or at rest, significantly more bird damage occurred from behind than from the side or from the front (expected values are calculated assuming equal numbers from each of the three directions: Table 6; flight, $\chi^2 = 25.52$, df = 2, P < 0.05; rest, $\chi^2 = 18.39$, df = 2, P < 0.05).

Analysis of variance indicated a significant difference in strengths of the five wing areas (F = 68.3, df = 96, P < 0.05). The costal vein area and the ipsilateral overlap were three times stronger than the distal margin of the hindwing and twice as strong as the distal margin

TABLE 5. Comparison of the sex ratios of bird damaged and undamaged specimens for each year.

	Damaged	Undamaged	Total
		1982	
Male	27	345	372
Female	9	110	119
Total	36	455	491
	$\chi^2 = 0.012$, df = 1, P > 0.05		
		1983	
Male	32	434	466
Female	11	108	119
Total	43	542	585
	$\chi^2 = 0.82$, df = 1, P > 0.05		

of the forewing (Table 7). Using Student-Newman-Keuls multiple pairwise test, we found no significant difference between the costal vein area and the ipsilateral overlap area, and no significant difference between the margins of the fore- and hindwings and the tip of the forewing, but there was a significant difference between these two groups of wing areas ($P < 0.01$).

The presentation of 104 *P. rapae* to four blue jays in a flight cage resulted in 182 attacks and 69 butterflies captured (Table 8). Sixty-nine percent (57/83) of the attacks on resting butterflies resulted in captures, while only 12% (12/99) of the attacks on flying *P. rapae* resulted in captures. The blue jays were significantly more efficient in capturing butterflies at rest than in flight. (Table 8; $\chi^2 = 27.73$, df = 1, $P < 0.05$).

Few of the butterflies that were attacked showed wing damage. Of the 83 butterflies attacked at rest, only one of the 21 *P. rapae* which escaped had wing damage. Only four of the 87 *P. rapae* which escaped attacks in flight received wing damage.

DISCUSSION

Despite the presence of mustard oils (Rothschild et al., 1970; Aplin et al., 1975) *P. rapae* were acceptable prey to blue jays in the field and laboratory and to house sparrows, *Passer domesticus*, purple martins, *Progne subis subis*, and various other avian species in the field (Table 1). In this study, an average of 7.2% of the *P. rapae* collected showed evidence of attacks by birds in the form of beak imprints and beak tears, and no specimen showed evidence of being attacked more than once. In California, Shapiro (1974) collected *P. rapae* and found 5.6% of the specimens bird-damaged, and between 0.33% and 0.50% of the

TABLE 6. Frontal and rear attacks on *P. rapae*.

		Attacked in flight from			Attacked at rest from		
Year	Site	Behind	Side	Front	Behind	Side	Front
1983	Fenway	8	3	0	3	0	2
	Lexington	8	1	4	6	1	2
	Carroll	0	1	1	2	0	0
1982	Fenway	14	2	4	5	0	2
	Lexington	4	1	0	2	0	0
Total		34	8	9	18	1	6

damaged specimens had multiple beak-marks. The percentages of bird damage reported by Shapiro (1974) and this study fall within the range of damage found in other lepidopteran species studied (Table 2).

At least four variables can affect the relationship between beak-marks and predation pressure (Benson, 1972; Shapiro, 1974; Robbins, 1980, 1981): 1) Damage may occur more readily during attacks on flying Lepidoptera than during attacks on resting Lepidoptera; 2) different avian predators may be many times more successful during attacks on resting prey than during attacks on flying prey; 3) different avian predators may vary significantly in capture efficiency on Lepidoptera; and 4) the strength of various butterfly wing areas differs, and this may influence the probability of obtaining beak-marks.

The live presentations of cabbage butterflies to blue jays indicates that bird damage may occur up to four times more readily during attacks on flying butterflies than during attacks on resting butterflies. Therefore, if equal numbers of butterflies are attacked in flight and at rest, a field sample would reveal a greater number of specimens showing evidence of being attacked in flight due to the higher frequency at which damage occurs (Table 6). This was also found by Bowers and Wiernasz (1979) in *C. pegala* and is expected if avian predators are less efficient during attacks in flight than at rest. The reliability of a beak-mark predation index is seriously jeopardized by unequal chances of obtaining beak-marks in flight and at rest. If most predation occurs while the butterflies are in the vegetation and few beak-marks result, the index would underestimate the amount of predation occurring. Likewise, if most attacks occur in flight the amount of damage may be overestimated if many prey are damaged and few captured. No previous study had quantified the relative occurrence of beak-marks due to attacks at rest and in flight.

Live trials support the hypothesis that avian predators may be much more efficient at capturing resting butterflies than at capturing butterflies in flight (Table 8). The attack efficiency of blue jays on flying *P.*

TABLE 7. The strengths of *P. rapae* wing areas.

Area	Strength (g ± S.D.)
Forewing tip	9.24 ± 2.4[a]
Forewing margin	8.28 ± 2.6[a]
Hindwing margin	6.95 ± 2.5[a]
Costal vein	19.76 ± 6.0[b]
Overlap of ipsilateral wings	20.16 ± 4.2[b]

The strength of wing areas with identical superscripts were not significantly different from each other. Groups with the 'a' superscript were significantly different from those with 'b' at the $P < 0.01$ level.

rapae was 12%. This was lower than that of an aerial insectivore, the spotted flycatcher, *Muscicapa striata*, which was reported in the field to have captured four flying *P. rapae* in 17 attempts for a success rate of 23.5% (Davies, 1977) and was still lower than the success rate of 100% on flying butterflies reported for a hunting northern shrike, *Lanius borealis* (Morrison, 1980; and pers. comm.). The predation index could be complicated by differences in the composition of avian communities in different habitats. For example, if shrikes were common in one habitat and relatively rare in another, many butterflies could have been consumed in the first area with little damage occurring, while the second area might have shown a high frequency of beak-marks but with little actual predation occurring. In this study, the avian communities of all three field sites were predominated by house sparrows, *Passer domesticus*, song sparrows, *Melospiza melodia*, and European starlings, *Sturnus vulgaris*.

Avian predators not only show variation in their probability of attacking butterflies, but may preferentially attack different areas on the butterfly in response to butterfly wing-markings. Butterflies attacked in stronger wing areas may show fewer beak-marks if they escape. Therefore, due to species differences in strengths of the areas of the wings, the frequencies of beak-marks may not be a reliable index of predation pressure for comparisons among species.

The percentage of bird-damaged specimens actually represents only the number of individuals which successfully survived attacks and escaped with bird damage. No data exist from field observations on the percentage of escaped butterflies showing no bird damage or on the percentages of attacked butterflies actually killed or eaten. If the laboratory efficiencies of blue jays preying on *P. rapae* are extrapolated to the field, avian predation on Lepidoptera becomes a much more significant selective force than previously suspected. Of the 1179 *P. rapae* collected, 76 had wing damage. Fifty-one specimens were attacked in flight, and 25 specimens were attacked at rest. In the laboratory only 4% of butterflies attacked in flight actually showed wing

TABLE 8. Live presentations of *P. rapae* to blue jays.

Bird	Presented		Attacked		Captured		Efficiency (%)	
	Rest	Flight	Rest	Flight	Rest	Flight	Rest	Flight
1	29	11	41	22	28	3	68.3	13.6
2	23	0	22	25	16	4	72.7	16.0
3	11	12	18	41	11	5	61.1	12.2
4	5	6	2	11	2	2	100	0
	68	36	83	99	57	12	68.7	12.1

damage. Therefore, given the 4% probability of obtaining a beak-mark, the 51 specimens collected in the field that were attacked in flight may represent attacks in flight on approximately 1275 individuals.

Blue jays consumed 12% of the *P. rapae* they attacked in flight in the laboratory. If this efficiency is extrapolated to the field, 12% of approximately 1275 *P. rapae* attacked or 153 would have been consumed after capture in flight.

Blue jays damaged only 1% of the butterflies attacked at rest in the laboratory. The 25 field-collected specimens which had damage from attacks while at rest would represent 2500 butterflies attacked at rest in the field. However, 68% of the resting *P. rapae* attacked in the laboratory were consumed. Therefore, according to this extrapolation, approximately 1700 *P. rapae* would have been consumed in the field after capture while at rest.

The disparity in predation pressure in flight and at rest suggests that the major selective force of avian predation is directed at the butterfly wing surface that is exposed while the butterfly is at rest. This is the ventral surface of the wings for most butterflies (Platt et al., 1971) but may be the dorsal surface of the wings of most moths (Sargent & Keiper, 1969; Endler, 1978) and for butterflies which expose the dorsal surfaces of the wings during basking, nectaring, and other activities. Rawlins and Lederhouse (1978) found that in the *Battus philenor* mimicry complex, the resemblance of model and mimic is closest on the ventral wing surface. They suggest that selection may be most intense on the underside of the wings, which are exposed while the butterflies are at rest, rather than on the dorsal surface of the wings which is only exposed in flight. This hypothesis previously had not been evaluated critically, and in fact, is not supported by accounts of avian predation on Lepidoptera (Table 1). Attacks on resting butterflies may be less noticeable than attacks in flight because they occur rapidly and are often obscured by vegetation.

Laboratory data obtained in the present study on predation by blue jays on *P. rapae* are the first to quantify differential predation pressure on the ventral and dorsal surfaces of the wings of *P. rapae* due to variation in success rates of attacks on flying and resting butterflies. Recently, this has been supported by work on *Euphydryas chalcedona* (Bowers et al., unpubl. manuscript). *Euphydryas chalcedona* males which had less red on the dorsal surface of their wings were under greater predation pressure when their wings were spread while resting, basking, and nectaring. Although the ventral surfaces of the wings were essentially identical in both groups, avian predation appears to favor dorsally red males. Realistic estimates of predation pressure on Lepidopteran populations are impossible due to the lack of field data. Yet, the extrapolation of laboratory and field data supports the concept that bird predation on butterflies may be a more significant selective force on Lepidopteran populations than previously assumed.

Many variables can influence the reliability of using the frequency of beak-marks on the wings of butterflies as an index of predation pressure. Thus, the interpretation of beak-mark frequencies is complicated and may not provide a reliable index of the amount of avian predation pressure on Lepidoptera.

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