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ON THE RELATIVE ACCEPTABILITIES OF LOCAL BUTTERFLIES AND MOTHS TO LOCAL BIRDS

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ABSTRACT. A total of 162 species of butterflies and moths are classified into 10 acceptability categories, ranging from very highly acceptable to totally unacceptable, on the basis of presentations of dead specimens in over 300 discrete trials to birds coming to a feeding tray in Leverett, Massachusetts. The acceptability categories were defined on the basis of both percentage of specimens taken and the order in which these specimens were taken in the trials. Several behaviors of the birds also were recorded, including whether or not an insect was eaten, and, if eaten, whether it was de-winged prior to being consumed.

Analyses of the data revealed that overall size and wing area/body size ratio were important determinants of acceptability. Bark-like cryptic moths were the most acceptable insects presented, butterflies overall were less acceptable than moths, and mimetic species were among the least acceptable insects presented. A number of presumably warningly colored species were quite acceptable to the birds, and this finding is discussed with reference to the complexities involved in defining this prey defense. Overall, the results are compared with those obtained in earlier studies.

Additional key words: feeding experiments, insect defenses, predator/prey relationships, warning coloration, cryptic coloration, mimicry.

This paper presents the results of over 300 bird-feeding trials involving local butterflies and moths that were carried out from 1982 to 1985 in Leverett, Massachusetts. The major aim of this study was to assess the relative acceptabilities of 162 lepidopteran species to birds selecting from sample arrays presented in discrete trials at a single feeding station.

The most similar prior study was carried out by Jones (1932, 1934) at a feeding station on the island of Martha's Vineyard, Massachusetts. This earlier study, though similar in many respects to mine, involved some inconsistencies in experimental design (e.g., unequal sample sizes and unequal test durations) that precluded rigorous statistical analyses and, therefore, unequivocal interpretations of the results. The present study, while posing some of the design problems inherent in field experiments of this sort, has yielded data that have been subjected to a rigorous discriminant analysis, which some readers may wish to consult (MacLean, Sargent & MacLean 1989). Here I attempt to present results of more specific interest to lepidopterists and persons with primarily behavioral and ecological interests.

A second important aim of the present research was to provide some interpretation of the contributions of various characteristics of butterflies and moths to their relative acceptabilities to birds. Thus, all of the lepidopteran species used were classified within (1) taxonomic, (2) size,

(3) larval hostplant, and (4) appearance categories. While detailed analyses of the relative importance of these characteristics in determining the acceptability of lepidopteran prey to birds were presented in the previously mentioned discriminant analysis, I will here discuss some of the highlights of that work. In particular, I will address the role of appearance (crypsis, warning coloration, and mimicry) in determining prey acceptability to birds. Finally, I hope that a number of questions will emerge from these results that will stimulate further research.

METHODS

All of the moths used in this study were taken at night at 150-watt incandescent spotlights (Westinghouse outdoor projector) at my home in Leverett, Massachusetts. The butterflies were collected by net during the day at several sites up to 10 km from my home. Most of the specimens collected were immediately frozen in small jars in the freezer compartment of a household refrigerator and were thawed just prior to their use in the bird-feeding trials. All of the specimens were utilized within one week of their capture. Thus, as in the studies of Jones (1932, 1934), most of the insects were dead when presented to the birds. However, a few moths were only cooled in the refrigerator and were presented alive in order to determine whether this difference would affect the acceptabilities of the species involved. A total of 213 species of butterflies and moths were used as prey, and 162 of these were tested in two or more trials.

A bird-feeding trial consisted of a 15-minute presentation of six different species (or distinctive morphs) arranged in a circle on a 15.24 cm diameter light blue dish. This dish was set out on an open feeding tray located 1 m from a large glass door through which observations were made. [A photograph of this feeding situation is presented in Sargent (1987).] I observed the feeding tray from approximately 2 m away and recorded the specimens taken, in order, and the bird species taking each insect. In addition other behaviors of the birds were noted when they occurred, as follows: SW = specimen swallowed whole; DWE = specimen taken to perch and there de-winged and eaten; PD = specimen picked up and dropped in place; and TD = specimen taken to perch and dropped. All feeding trials were conducted between 0600 and 0800 h EDST, and no more than four trials were run on any one day.

Two measures of acceptability for each species (or morph) were obtained: the overall percentage of specimens taken, and the average rank of the specimens taken. These two measures were highly correlated (Pearson's correlation coefficient: $r = -0.699$, $P < 0.0001$ for the 69 species tested on more than 10 occasions), indicating that preferred species were both taken more often and taken earlier in the trials than were less-preferred species.

These two measures of acceptability were then utilized to develop a ten-category classification of all of the species that were tested in the feeding trials. The percentage of specimens taken and the average rank of the specimens taken were scored as follows:

Percent Taken	Score	Average Rank	Score
80–100	1	1–1.9	1
60–79	2	2–2.9	2
40–59	3	3–3.9	3
20–39	4	4–4.9	4
0–19	5	5–6	5

An overall score was then obtained by averaging the percent taken and average rank scores. In this way, nine acceptability categories were created with scores ranging from 1, in 0.5 step increments, to 5. In addition, a category 10 was established for those species that were never taken by the birds. The overall classification is:

Category	Score	Description
1	1	very highly acceptable
2	1.5	highly acceptable
3	2	very acceptable
4	2.5	moderately acceptable
5	3	marginally acceptable
6	3.5	slightly unacceptable
7	4	moderately unacceptable
8	4.5	very unacceptable
9	5	highly unacceptable
10	—	totally unacceptable

The G-test of independence (Sokal & Rohlf 1969) was used in analyzing the data.

RESULTS AND DISCUSSION

A total of 2158 individual butterflies and moths, representing 203 species from 21 families, was presented to birds during this study (Table 1). The birds involved were primarily woodland species, with blue jays contributing the majority of the records (Table 1).

A listing by acceptability categories of the 162 lepidopteran species that were presented more than once to the birds is given in Table 2. Over half of the species tested (55.5%) rated as very acceptable or better (categories 1, 2 and 3). Another large group of species (33.3%) ranged

TABLE 1. Summary of the Lepidoptera presented, and those taken by birds, in feeding trials in Leverett, MA (1982–85).

Family	No. species	No. individuals	% taken	Bird species[1]			
				bj	bcc	tt	others
Sesiidae	1	1	0.0	—	—	—	—
Cossidae	2	2	100.0	2	—	—	—
Hesperiidae	2	16	75.0	11	—	1	—
Papilionidae	3	51	52.9	24	2	1	—
Pieridae	3	124	55.6	36	18	15	—
Lycaenidae	1	7	28.6	2	—	—	—
Nymphalidae	14	115	49.6	39	11	6	1
Satyridae	4	42	57.1	20	2	1	1
Danaidae	1	17	35.3	3	1	2	—
Limacodidae	2	10	50.0	5	—	—	—
Pyralidae	1	11	27.3	2	1	—	—
Thyatiridae	2	2	100.0	—	1	1	—
Drepanidae	3	28	46.4	8	1	4	—
Geometridae	22	259	70.7	131	21	28	3
Lasiocampidae	5	79	94.9	56	9	10	—
Saturniidae	3	76	81.6	53	3	6	—
Sphingidae	15	77	93.5	63	3	6	—
Notodontidae	14	53	98.1	40	6	4	2
Arctiidae	14	229	69.9	133	7	16	4
Lymantriidae	3	72	86.1	45	14	3	—
Noctuidae	88	887	93.5	453	235	121	20
Totals	203	2158	79.6	1126	335	225	31
%'s				65.6	19.5	13.1	1.8

[1] bj = bluejay; bcc = black-capped chickadee; tt = tufted titmouse.

from moderately acceptable to slightly unacceptable (categories 4, 5 and 6), while only 18 species (11.1%) fell into the moderately unacceptable to totally unacceptable range (categories 7–10).

Certain subgroups within the 162 species total in Table 2 were singled out and are listed in descending order of their acceptability to birds in Table 3. This ranking indicates that sphingids, notodontids, and noctuids were the most acceptable insects presented, while geometrids and arctiids were less acceptable among the moths. Butterflies, however, were less acceptable than moths overall ($G = 172$, $P < 0.001$). And certain warningly-colored and mimetic insects were among the least acceptable insects presented. This list also includes some well known genera for which there were reasonable samples, and these genera usually fit the generalizations just described (e.g., *Papaipema* and *Catocala* were very highly acceptable like most noctuids). An exception was provided, however, by moths of the genus *Spilosoma* which were far more acceptable than arctiids generally. The high acceptability of these and other supposedly aposematic species will be discussed later.

TABLE 2. Acceptability data on 162 lepidopteran species[1] presented to birds in feeding trials in Leverett, MA (1982–85).

Category	Family Species	N	% taken	Av. rank
1	Sphingidae			
	Ceratomia undulosa (Walker)	15	100.0	1.5
	Ceratomia catalpae (Boisduval)	2	100.0	1.0
	Paonias excaecatus (J. E. Smith)	11	100.0	1.5
	Notodontidae			
	Nadata gibbosa (J. E. Smith)	4	100.0	1.3
	Noctuidae			
	Euparthenos nubilis (Hubner)	10	100.0	1.6
	Catocala epione (Drury)	5	100.0	1.8
	Catocala ilia (Cramer)	4	100.0	1.8
	Catocala coccinata (Grote	2	100.0	1.0
	Acronicta americana (Harris)	45	100.0	1.7
	Acronicta morula Grote & Robinson	2	100.0	1.0
	Apamea amputatrix (Fitch)	7	100.0	1.9
	Papaipema inquaesita (Grote & Robinson)	5	100.0	1.6
	Metaxaglea innulta (Grote)	7	100.0	1.3
	Adita chionanthis (J. E. Smith)	6	100.0	1.8
	Agrotis ipsilon (Hufnagel)	14	100.0	1.9
2	Geometridae			
	Biston betularia cognataria (Guenee)	3	100.0	2.3
	Ennomos magnaria Guenee	16	100.0	2.4
	Lasiocampidae			
	Malacosoma americanum (Fabricius)	46	93.5	2.6
	Saturniidae			
	Actias luna (L.)	9	88.9	2.4
	Sphingidae			
	Sphinx gordius Cramer	2	100.0	2.0
	Lapara bombycoides Walker	9	100.0	2.0
	Paonias myops (J. E. Smith)	8	100.0	2.0
	Laothoe juglandis (J. E. Smith)	7	100.0	2.4
	Darapsa pholus (Cramer)	5	100.0	2.2
	Notodontidae			
	Peridea ferruginea (Packard)	20	95.0	2.7
	Schizura unicornis (J. E. smith)	4	100.0	2.8
	Arctiidae			
	Pyrrharctia isabella (J. E. Smith)	47	93.6	2.6
	Halysidota tessellaris (J. E. Smith)	63	88.9	2.7
	Lymantriidae			
	Dasychira obliquata (Grote & Robinson)	14	92.9	2.6
	Noctuidae			
	Zale horrida Hubner	8	87.5	2.7
	Catocala antinympha (Hubner)	5	100.0	2.0
	Catocala judith Strecker	10	100.0	2.5
	Catocala retecta Grote	14	100.0	2.4
	Catocala ultronia (Hubner)	39	100.0	2.4
	Catocala crataegi Saunders	9	88.9	2.9
	Catocala grynea (Cramer)	9	88.9	2.6
	Catocala amica (Hubner)	30	93.3	2.8

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	Panthea pallescens McDunnough	150	97.3	2.5
	Charadra deridens (Guenee)	35	97.1	2.7
	Macronoctua onusta Grote	5	100.0	2.4
	Papaipema speciosissima (Grote & Robinson)	2	100.0	2.0
	Phlogophora periculosa Guenee	10	100.0	2.2
	Amphipyra pyramidoides Guenee	60	98.3	2.4
	Lacanobia grandis (Guenee)	7	100.0	2.6
	Nephelodes minians (Guenee)	12	100.0	2.4
	Feltia jaculifera (Guenee)	7	100.0	2.0
	Xestia adela Franclemont	14	100.0	2.9
	Xestia bicarnea (Guenee)	7	100.0	2.9
	Anaplectoides prasina (Denis & Schiffermuller)	3	100.0	2.3
3	Nymphalidae			
	Polygonia comma (Harris)	5	80.0	3.8
	Vanessa atalanta rubria (Fruhstorfer)	14	85.7	3.6
	Speyeria cybele (Fabricius)	4	100.0	3.5
	Satyridae			
	Cercyonis pegala (Fabricius)	23	73.9	2.9
	Geometridae			
	Lytrosis unitaria (Herrich-Schaffer)	18	100.0	3.1
	Pero honestaria (Walker)	14	78.6	2.8
	Caripeta angustiorata Walker	3	100.0	3.7
	Prochoerodes transversata (Drury)	37	89.2	3.2
	Hydria undulata (L.)	6	50.0	1.7
	Lasiocampidae			
	Phyllodesma americana (Harris)	11	90.9	3.8
	Saturniidae			
	Dryocampa rubicunda (Fabricius)	56	83.9	3.2
	Sphingidae			
	Darapsa myron (Cramer)	5	100.0	3.6
	Notodontidae			
	Pheosia rimosa Packard	6	100.0	3.0
	Nerice bidentata Walker	2	100.0	3.5
	Furcula modesta (Hudson)	4	100.0	3.0
	Arctiidae			
	Spilosoma congrua (Walker)	34	91.2	3.4
	Spilosoma virginica (Fabricius)	17	94.1	3.7
	Lymantriidae			
	Orgyia leucostigma (J. E. Smith)	7	85.7	3.8
	Lymantria dispar (L.)	51	84.3	3.1
	Noctuidae			
	Panopoda rufimargo (Hubner)	15	93.3	3.4
	Panopoda carneicosta Guenee	10	90.9	3.7
	Caenurgina erechtea (Cramer)	6	88.3	3.0
	Catocala residua Grote	2	100.0	3.0
	Catocala palaeogama Guenee	3	100.0	3.0
	Catocala gracilis W. H. Edwards	4	100.0	3.0
	Catocala andromedae Guenee	13	100.0	3.2
	Catocala praeclara Grote & Robinson	5	100.0	3.0

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	Catocala micronympha Guenee	4	100.0	3.5
	Chrysanympha formosa (Grote)	6	83.3	3.0
	Anagrapha falcifera (W. F. Kirby)	8	100.0	3.6
	Acronicta innotata Guenee	36	83.3	3.3
	Papaipema ptersii Bird	11	100.0	3.4
	Papaipema nebris (Guenee)	4	100.0	3.3
	Phlogophora iris Guenee	11	81.8	3.6
	Lithophane grotei Riley	2	100.0	3.5
	Eucirroedia pampina (Guenee)	14	100.0	3.6
	Sunira bicolorago (Guenee)	8	100.0	3.8
	Polia imbrifera (Guenee)	4	100.0	3.0
	Pseudaletia unipuncta (Haworth)	13	100.0	3.6
	Agrotis venerabilis Walker	16	100.0	3.2
	Anomogyna dilucida (Morrison)	19	100.0	3.3
4	Hesperiidae			
	Epargyreus clarus (Cramer)	15	73.3	3.6
	Nymphalidae			
	Speyeria aphrodite (Fabricius)	5	60.0	3.0
	Limacodidae			
	Euclea delphinii (Boisduval)	7	71.4	3.8
	Geometridae			
	Euchlaena serrata (Drury)	6	66.7	3.8
	Tetracis crocallata Guenee	4	50.0	2.5
	Lasiocampidae			
	Tolype velleda (Stoll)	7	100.0	4.3
	Tolype laricis (Fitch)	2	100.0	4.0
	Malacosoma disstria Hubner	13	100.0	4.2
	Notodontidae			
	Macrurocampa marthesia (Cramer)	4	100.0	4.0
	Arctiidae			
	Apantesis virgo (L.)	2	100.0	4.5
	Noctuidae			
	Scoliopteryx libatrix (L.)	2	100.0	4.0
	Synedoida grandirena (Haworth)	7	57.1	2.5
	Parallelia bistriaris Hubner	42	78.6	3.4
	Crymodes burgessi (Morrison)	3	100.0	4.3
	Achatodes zeae (Harris)	2	100.0	4.0
	Chytonix palliatricula (Guenee)	9	55.6	2.6
	Polia latex (Guenee)	2	100.0	4.0
	Schinia florida (Guenee)	10	90.0	4.2
5	Papilionidae			
	Papilio troilus L.	18	66.7	4.4
	Pieridae			
	Colias eurytheme Boisduval	19	73.7	4.5
	Nymphalidae			
	Polygonia interrogationis (Fabricius)	3	66.7	4.0
	Vanessa virginiensis (Drury)	9	44.4	3.3
	Junonia coenia (Hubner)	8	50.0	3.8
	Basilarchia archippus (Cramer)	29	51.7	3.5

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	Satyridae			
	Enodia portlandia (Fabricius)	2	50.0	3.0
	Drepanidae			
	Oreta rosea (Walker)	11	63.6	4.3
	Geometridae			
	Anacamptodes ephyraria (Walker)	10	60.0	4.2
	Xanthotype sospeta (Drury)	17	70.6	4.6
	Caripeta piniata (Packard)	25	72.0	4.1
	Nemoria mimosaria (Guenee)	3	66.7	4.0
	Eulithis explanata (Walker)	3	66.7	4.5
	Coryphista meadii (Packard)	11	72.7	4.0
	Dyspteris abortivaria (Herrich-Schaffer)	2	50.0	3.0
	Saturniidae			
	Hemileuca lucina Henry Edwards	11	63.6	4.9
	Notodontidae			
	Schizura ipomoeae Doubleday	3	100.0	5.3
	Arctiidae			
	Haploa clymene (Brown)	7	42.9	3.7
	Noctuidae			
	Idia lubricalis (Geyer)	3	66.7	4.0
	Leuconycta diphteroides (Guenee)	6	50.0	3.0
6	Papilionidae			
	Papilio polyxenes asterius Stoll	14	57.1	4.2
	Papilio glaucus L.	19	36.8	3.4
	Pieridae			
	Artogeia rapae (L.)	43	46.5	4.3
	Colias philodice Godart	62	56.5	4.2
	Lycaenidae			
	Satyrium calanus (Hubner)	7	28.6	3.5
	Nymphalidae			
	Clossiana bellona (Fabricius)	3	33.3	3.5
	Euphydryas phaeton (Drury)	12	25.0	3.3
	Pyralidae			
	Desmia funeralis (Hubner)	11	27.3	3.3
	Drepanidae			
	Drepana bilineata (Packard)	7	57.1	4.8
	Geometridae			
	Campaea perlata (Guenee)	41	53.7	4.1
	Ennomos subsignaria (Hubner)	14	42.9	4.3
	Eulithis propulsata (Walker)	8	75.0	5.0
	Sphingidae			
	Hemaris thysbe (Fabricius)	8	37.5	3.3
	Arctiidae			
	Ctenucha virginica (Esper)	7	57.1	4.8
	Noctuidae			
	Agriopodes fallax (Herrich-Schaffer)	8	62.5	5.0
	Callopistria cordata (Ljungh)	4	50.0	4.5

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
7	Nymphalidae			
	Vanessa cardui (L.)	4	50.0	5.0
	Satyridae			
	Megisto cymela (Cramer)	6	50.0	5.3
	Danaidae			
	Danaus plexippus (L.)	17	35.3	4.2
	Geometridae			
	Euchlaena irraris (Barnes & McDunnough)	11	54.5	5.3
8	Nymphalidae			
	Phyciodes tharos (Drury)	11	27.3	5.7
	Satyridae			
	Coenonympha inornata W. H. Edwards	11	27.3	5.0
	Drepanidae			
	Drepana arcuata Walker	10	20.0	5.0
	Arctiidae			
	Cycnia tenera Hubner	3	33.3	5.0
9	Geometridae			
	Itame pustularia (Guenee)	6	16.7	5.0
	Arctiidae			
	Haploa lecontei (Guerin-Meneville)	17	11.8	5.0
10	Nymphalidae			
	Clossiana selene myrina (Cramer)	7	—	—
	Limacodidae			
	Apoda biguttata (Packard)	3	—	—
	Arctiidae			
	Hypoprepia fucosa Hubner	19	—	—
	Holomelina laeta (Guerin-Meneville)	3	—	—
	Cisseps fulvicollis (Hubner)	8	—	—
	Noctuidae			
	Paectes oculatrix (Guenee)	2	—	—
	Lithacodia carneola (Guenee)	2	—	—
	Cerma cerintha (Treitschke)	3	—	—

[1] Species are listed sequentially (after Hodges et al., 1983) within each of the 10 acceptability categories defined in the text.

Prey Size

A previous discriminant analysis (MacLean, Sargent & MacLean 1989) revealed that size was the single most important predictor of acceptability for the moths and butterflies used in this study. A comparison of data obtained for small, medium, and large species (based on the wingspans given in Forbes, 1923, 1948, 1954, 1960) shows that medium and large species were taken more often than small species ($G = 28.5$; $P < 0.001$), despite the fact that medium and large species, if eaten, were more likely to be de-winged before being consumed ($G = 28.9$;

TABLE 3. Selected groups of Lepidoptera arranged in descending order of acceptability to birds.

Groups	No. species	No. individuals	% taken
Sphingids (nocturnal)	13	68	100.0
Papaipema spp.	6	24	100.0
Notodontids	14	53	98.1
Catocala spp.	22	169	97.3
Noctuids	88	887	93.5
Spilosoma spp.	2	51	92.2
Moths	175	1786	85.1
Geometrids	22	259	70.7
Arctiids	14	229	69.9
Colias spp.	2	81	60.5
Butterflies	28	372	53.0
Haploa spp.	2	24	20.8
Batesian mimics (non-lepidopteran models)	4	35	20.0

P < 0.001) (Table 4). This suggests that any handling costs associated with larger lepidopteran prey are not sufficient to offset the gains (presumably caloric) associated with consuming them.

Another line of evidence for an aversion of the birds to smaller prey is the finding that small prey were three times more likely to be picked up and dropped in place than were large prey (G = 17.5; P < 0.001) (Table 4), suggesting that small prey were often rejected on the basis of an assessment of their weight (most of the small species used were cryptic (Table 4), and therefore presumably palatable).

A general preference of birds for larger prey, all else being equal, has often been demonstrated (e.g., Marples 1993). However, the tradeoffs suggested here between the costs and benefits of sampling, handling,

TABLE 4. Data comparisons for small (<38 mm), medium (38.1–53 mm) and large (>53 mm) Lepidoptera species used in this study.

Characteristics	Small	Medium	Large
No. species	71	90	42
No. individuals	592	1164	402
No. cryptic species	55 (77.5%)	71 (78.9%)	33 (78.6%)
No. cryptic individuals	481 (81.3%)	836 (71.8%)	293 (72.9%)
Percent taken	71.8	82.3	82.8
Percent eaten/taken	32.5	23.9	17.4
Percent de-winged/eaten	13.0	31.0	60.3
Percent picked up and dropped	9.5	4.3	3.0

TABLE 5. Comparative acceptabilities of noctuids and geometrids in two cryptic categories.

Moths	No. species	No. individuals	% taken	picked up & dropped
Barklike noctuids	47	613	96.2	0.5
Leaflike noctuids	33	242	90.9	6.6
Barklike geometrids	3	31	87.1	3.2
Leaflike geometrids	12	158	77.2	8.2

and consuming lepidopteran prey of different sizes would seem to warrant more precise quantitative analyses of this matter in the future.

Wing Area/Body Size Ratio

Jones (1932) speculated that another factor contributing to the relative acceptabilities of various Lepidoptera to birds might be the wing area to body size ratio. Thus, he suggested that the higher ratios characterizing certain groups, such as butterflies (as opposed to moths) or geometrids (as opposed to noctuids), might contribute to the lower acceptabilities of these insects to birds. Other studies have yielded results that are consistent with this suggestion. For example, Chai (1986) noted that within butterflies, acceptability was often associated with "short, stout bodies," whereas unacceptability was often associated with "long, slender bodies."

I previously have pointed out the relatively low acceptability of butterflies (compared to moths) in the present study (Table 3), and data on the relative acceptabilities of geometrids and noctuids are presented in Table 5. Geometrids were less acceptable than noctuids overall ($G = 72.5$; $P < 0.001$), and it is interesting to note that leaflike specimens (with generally higher wing area/body size ratios) in both families were significantly less often taken ($G = 27.5$; $P < 0.001$) and significantly more often picked up and dropped ($G = 19.4$; $P < 0.001$) than were barklike specimens (with generally lower wing area/body size ratios).

The general impression conveyed by these data is that wing area/body size ratio is a contributing factor to the acceptability ratings of lepidopteran prey and, as with size alone, further quantitative study is needed.

Warning Coloration and Mimicry

A peculiarity of this study was the finding of a high acceptability of some presumably aposematic species to birds. In fact, MacLean, Sargent and MacLean (1989) found warning coloration to be the third most important single predictor of acceptability (after large size and barklike appearance) for this entire array of butterflies and moths!

TABLE 6. Comparison of acceptabilities of living and dead specimens of several presumably aposematic moth species.

Species	Living			Dead		
	No.	% taken	Rank	No.	% taken	Rank
Dryocampa rubicunda	4	100.0	1.8	52	82.7	3.3
Pyrrharctica isabella	10	100.0	1.9	37	91.9	2.8
Spilosoma congrua	3	100.0	3.0	31	90.3	3.4
Spilosoma virginica	2	100.0	2.5	15	93.3	3.9
Halysidota tesselaris	6	100.0	2.5	57	87.7	2.7
Totals	25	100.0	2.2	192	88.0	3.1

In part, this finding may have resulted from the erroneous assignment of some species to the warning coloration category (e.g., *Pyrrharctica isabella*). In other cases, however, there were prior reports of unpalatability (e.g., *Halysidota tessellaris* to bats (Dunning & Roeder 1965; Dunning 1968), and *Spilosoma* species to birds (Rothschild 1983), or field evidence of very low acceptability to birds (e.g., *Spilosoma congrua* and *Dryocampa rubicunda* (Jones 1932)).

On the other hand, some of these species may show a form of crypsis that has been described as "special resemblance" (Cott 1940), i.e., resemblance to some distinctive part of the environment. Thus, the white *Spilosoma* species may resemble fallen dogwood bracts on the forest floor (Endler 1984), and the pink-and-yellow *Dryocampa rubicunda* may resemble flowers or flower parts, like the similarly colored *Schinia florida* (Sargent 1969).

Whatever the case, I did attempt to control for the fact that these presumably aposematic moths were presented as dead specimens (and so might have lacked some behavioral or biochemical attribute that would otherwise have deterred the birds) by presenting live specimens (cooled in the refrigerator) of six species in several tests. Although the sample sizes were small, birds found the living moths more acceptable than the dead ones in every case (Table 6).

It is clear that designating a species as warningly colored or aposematic is no longer the simple matter it once seemed to be. We know, for example, that individuals of a seemingly aposematic species may vary with respect to the levels of toxins they possess (e.g., the so-called "palatability spectrum" in danaid butterflies (Brower et al. 1968; Brower 1984)), reflecting, at least in part, variations in the chemistry of their hostplants (see references in Bowers 1990). We also know that predators vary, both within and between species, in the extent to which they find particular prey aversive, reflecting motivational (e.g., Swynnerton 1915, Chai 1986), physiological (e.g., Brower et al. 1985), and behavioral (e.g., Brower & Calvert 1985, Brower & Fink 1985) variables in these predators. Further study obviously is needed in order to establish the qualifications that must be applied to any particular case of warning coloration.

Despite these caveats, however, it is important to note that at least a few species that generally are regarded as aposematic were quite unacceptable to the birds in this study. Among these cases were the brightly colored, day-flying saturniid, *Hemileuca lucina* (category 5); the checkerspot butterfly, *Euphydryas phaeton* (category 6), and a number of colorful or boldly patterned arctiids, including *Haploa clymene* (category 5), *Haploa lecontei* (category 9), *Cycnia tenera* (category 8), and *Holomelina laeta* (category 10).

In contrast to the warningly colored insects, Batesian mimics (especially those with non-lepidopteran models) were consistently rejected by the birds in this study. Examples include the bee mimic, *Hemaris thysbe* (category 8); the wasp mimics, *Ctenucha virginica* (category 6) and *Cisseps fulvicollis* (category 10); and the firefly mimic, *Hypoprepia fucosa* (category 10). An unusual case of "special resemblance" (which some might regard as Batesian mimicry (e.g., Edmunds 1974)), involving a noxious element in the environment (bird-droppings) also elicited rejection by the birds (e.g., *Cerma cerintha* (category 10)).

The much-studied mimicry case involving the monarch (*Danaus plexippus*) and viceroy (*Basilarchia archippus*) butterflies, a seemingly inexhaustible source of new insights (e.g., Brower 1969) and new surprises (e.g., Ritland 1991), here yielded equivocal results, with both the putative model and putative mimic being relatively unacceptable to the birds (categories 7 and 5, respectively). This classic relationship will undoubtedly repay yet further investigation.

Comparisons with Jones (1932)

There were a number of similarities between the present study and the earlier one of Jones (1932). The total numbers of lepidopteran species presented on at least two occasions in the two studies were 162 (Sargent) and 118 (Jones). Butterflies made up 15.9% (Sargent) and 7.6% (Jones) of these totals. If Jones' acceptability ratings are converted to 10 categories (10 units each on his 0–100 scale), then 79.1% (Sargent) and 66.1% (Jones) of the species presented were rated as acceptable or better (categories 1–5).

In addition, some of the general findings of Jones were noted here as well. For example, the birds clearly preferred larger to smaller insects in both studies. They also preferred moths over butterflies, noctuids over geometrids, and found large cryptic moths with colorful or boldly patterned hindwings (e.g., *Catocala* and many sphingids) among the most highly acceptable insects presented. I also obtained data to support Jones' suggestion that wing area/body size ratio was an important factor affecting the acceptability of various lepidopteran prey.

There were 40 species presented to birds that were clearly identical in the two studies. If, as noted above, Jones' acceptability ratings are converted to 10 categories, then comparisons with my ten-category classification are possible. Of the 40 species so compared, 8 were placed in the same category, 17 were placed in adjacent categories (+ or −1), and 8 more were placed in categories no more than two steps apart in the two studies. This leaves 7 species that were classified rather differently (3 steps or more apart), 5 of which were far less acceptable in Jones' study (*Artogeia rapae, Dryocampa rubicunda, Euchlaena serrata, Schinia florida*, and *Tetracis crocallata*), and 2 of which were far less acceptable in mine (*Euchlaena irraria* and *Cerma cerintha*). There seems to be no particular overall significance to these differences, and they may represent only the kind of variation to be expected in studies that are separated in time and place and that involve somewhat different arrays of avian predators.

I believe that the present study, while corroborating many of the findings of Jones, provides stronger evidence for these findings due to the utilization here of more precisely defined acceptability categories, the recording of additional behavioral data, and the use of several statistical methods (see also MacLean, Sargent & MacLean 1989). Hopefully, future studies will continue to move in the directions of increased quantification and more rigorous statistical analyses.

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