

## Effectiveness of tiger moth (*Lepidoptera*, *Arctiidae*) chemical defenses against an insectivorous bat (*Eptesicus fuscus*)

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**Summary.** Adult tiger moths exhibit a wide range of palatabilities to the insectivorous big brown bat *Eptesicus fuscus*. Much of this variation is due to plant allelochemicals ingested and sequestered from their larval food. By using a comparative approach involving 15 species from six tribes and two subfamilies of the *Arctiidae* we have shown that tiger moths feeding on cardiac glycoside-containing plants often contain highly effective natural feeding deterrents. Feeding on pyrrolizidine alkaloid-containing plants is also an effective deterrent to predation by bats but less so than feeding on plants rich in cardiac glycosides. Moths feeding on plants containing iridoid glycosides and/or moths likely to contain biogenic amines were the least deterrent. By manipulating the diet of several tiger moth species we were able to adjust their degree of palatability and link it to the levels of cardiac glycosides or pyrrolizidine alkaloids in their food. We argue that intense selective pressure provided by vertebrate predators including bats has driven the tiger moths to sequester more and more potent deterrents against them and to acquire a suite of morphology characteristics and behaviors that advertise their noxious taste.

**Key words.** Allelochemicals – cardiac glycosides – pyrrolizidine alkaloids – iridoid glycosides – biogenic amines – *Arctiidae* – bats

### Introduction

Moths of the family *Arctiidae* possess an impressive array of chemical, morphological and behavioral adaptations that contribute to their defense against both vertebrate and invertebrate predators (Blest 1964; Rothschild 1985). While a wide variety of chemical compounds have been identified in arctiids (Teas *et al.* 1966; Hesbacher *et al.* 1995) the most prevalent are the biogenic amines (BAs), iridoid glycosides (IGs), pyrrolizidine alkaloids (PAs) and cardiac glycosides (CGs) (Weller *et al.* 1999; Nishida 2002). The accumulation and maintenance of secondary chemicals in the different life stages of arctiids occurs in a number of ways. Defensive compounds can be produced *de novo* by either larvae or

adults. This is assumed to be the case for the biogenic amines since moths contain the necessary biochemical pathways to produce them (Rothschild 1985). The IGs, PAs and CGs are sequestered from plants as the larvae feed on allelochemically laden tissues (Rothschild *et al.* 1970; Black 1976; Conner *et al.* 1981; Bowers 1991; Nickisch-Rosenegk & Wink 1993; Wink & Nickisch-Rosenegk 1997; Eisner & Meinwald 2003). Some PAs are collected by adults through plant visitation (Beebe 1955; Pliske 1975; Goss 1979; Boppré 1990; Conner *et al.* 2000). Defensive chemicals may also be transferred between the sexes, male to female and transovarially from mother to offspring (Dussourd *et al.* 1988; González *et al.* 1999; Conner *et al.* 2000; Rossini *et al.* 2001; Bezzerides & Eisner 2002; Hartmann *et al.* 2004). Sequestered defense compounds may be altered to special insect forms (Hartmann *et al.* 2003; Hartmann *et al.* 2004). Once procured the defensive chemicals are stored in the eggs (Hare & Eisner 1993; Eisner *et al.* 2000; Eisner 2002; Bezzarides *et al.* 2004), in larval setae (Rothschild 1985) in larval integument and hemolymph (Nickisch-Rosenegk *et al.* 1990; Nickisch-Rosenegk & Wink 1993), in the cocoon (Hartmann *et al.* 2004), or in adult integument, scales, hemolymph, and reproductive structures (Dussourd *et al.* 1988; Rossini *et al.* 2003). In many of these locations they are likely to be encountered by an attacking predator. Surprisingly data on the relative effectiveness of chemical defenses notably the pyrrolizidine alkaloids and cardenolides on vertebrate predators are rare (Nishida 2002 but see Rowell-Rahier *et al.* 1995 for studies of their relative effectiveness in chrysomelid beetles against birds).

Beyond defense the PAs are frequently involved in the reproductive behavior of arctiids (Eisner & Meinwald 2003; Conner & Weller, 2004). The alkaloids or their derivatives are used as precursors to male courtship pheromones (Conner *et al.* 1981; Schneider *et al.* 1982) which advertise the ability of their possessors to transfer defensive material to the opposite sex as nuptial contributions (Dussourd *et al.* 1991; Iyengar *et al.* 2001). Dietary PAs also trigger dramatic polyphenisms in the adult scent structures that release the courtship pheromones (Schneider *et al.* 1982; Boppré & Schneider 1985; Nickisch-Rosenegk *et al.* 1990; Davenport & Conner 2003) and in scent dissemination behavior (Jordan & Conner 2005) intimately tying pheromone release to availability.

Defensive compounds can vary between two extremes in their modes of action and effects on the predator.

Chemicals that are noxious by virtue of their capacity to irritate, damage, poison and/or drug potential predators have a direct and rapid negative effect. Other chemicals are acutely innocuous and exert their cumulative effects over relatively longer periods of time. The latter rely on foul taste and associative learning by the predator (Brower 1984). Both types can be combined with aposematic signals in the form of visual, acoustic, and tactile stimuli for the totality of their effects (Rothschild 1985).

Adult arctiid moths are visually striking as a group with a diversity of color patterns whose perception by visual predators can range from crypsis (in this study *Halysidota tessellaris*, *Euchaetes egle*) and mimicry (in this study *Cosmosoma myrodora*; *Empyreuma affinis*) to aposematism (in this study *Hypoprepia fucosa* and *Utetheisa ornatrix*). Many combine their bright colors with reflex bleeding, copious and colorful froth production from prothoracic glands, as well as the exposure of deimatic abdominal and hindwing coloration (Blest 1964). These displays are frequently accompanied by high frequency sound production in the form of trains of tymbalar clicks. Sound production can be triggered tactilely or by the echolocation cries of insectivorous bats (Fullard & Fenton 1977) and can be considered aposematic (Hristov & Conner 2004). The arctiid gestalt is consistent with a group of chemically defended prey.

The effectiveness of these defensive strategies have been tested through whole animal feeding bioassays with a variety of predators: arthropods, spiders, frogs and lizards (Beebe & Kenedy 1957; Eisner & Eisner 1991; Eisner & Meinwald 2003); bats (Frazer & Rothschild 1960; Dunning 1968; Dunning *et al.* 1992), monkeys (Carpenter & Eltringham 1938; Blest 1964) and especially birds (Jones 1932, 1934; Blest 1964; Collins & Watson 1983; Brower 1984). In all of these studies the authors found that arctiids were consumed by the predators less often in relation to other sympatric and less colorful moths. Nevertheless a number of gaps exist in our understanding of the roles of individual chemical constituents in the overall tiger moth defensive repertoire. The majority of these studies investigated the combined effects of chemical, visual and behavioral defenses, while the specific palatability of the moths without their other lines of defense remains untested and unresolved. The question is further complicated by the possible existence of chemical and visual Müllerian and Batesian mimics (Weller *et al.* 2000; Simmons & Weller 2002).

Because of these considerations it seems appropriate and important to consider the separate effects of chemical defenses in arctiid moths against one of their most significant predators – bats. In the following experiments we survey the palatability of arctiids of a variety of dietary backgrounds to big brown bats (*Eptesicus fuscus*). We manipulate the diet of the moths to control the levels of their defensive compounds and determine the relative potency of PAs and CGs to these predators in the absence of visual or acoustic cues.

## Materials and methods

To assess the palatability of arctiid moths to sympatric insectivorous bats tiger moths were collected from locations in the south-eastern US (NC to FL) or reared and presented to big brown bats (*Eptesicus fuscus*) according to two separate experimental

protocols. Over the course of the experiments, a total of 883 arctiid moths representing 15 different species were presented to 21 big brown bats – 9 males, of which 3 were juveniles and 12 females of which 5 were juveniles.

Adult big brown bats were captured at several natural roosts in Forsyth County, NC in early May and brought to the lab at Wake Forest University as part of a resident colony established for the purposes of this research. Juvenile bats were born in the lab from pregnant females. The bats were housed in wooden cages (53 × 28 × 28 cm) on a 16:8 L:D cycle in the animal facility in Winston Hall on the Reynolda campus of Wake Forest University according to ACUC protocols #A98-080 and #A01-186. The bats were maintained on nutrient-rich mealworm diet (medium sized *Tenebrio* larvae) with unrestricted access to water placed in small (10 cm diameter), glass, culture dishes placed on the bottom of their cages (W. Mitch Masters, pers. comm.; Barnard 1995).

In the first experimental protocol, equal numbers of experimental (arctiid) or control (noctuid) moths were presented to the bats in the feeding dishes on the bottom of their cage on alternate days. The bats were allowed to feed on the moths overnight. The palatability of the moths (experimental or control) was scored the next morning. Control noctuids included but were not restricted to the following genera: *Anagrapha*, *Anaplectoides*, *Cerma*, *Heliothis*, *Himella*, *Metaxaglaea*, and *Spodoptera* (Covell 1984).

In the second experimental protocol, bats were trained to feed in larger (20 cm diameter) glass, culture dishes outside of their cages, and experimental and control moths were provided in equal proportions at the same time. To train the bats for this protocol, over the course of one week the feeding of the bats was gradually moved from the interior of their housing cages to large (20 cm diameter) glass culture dishes. Following the successful learning of this task the mealworm diet of bats was slowly replaced with a moth diet by gradually introducing adult wax moths (*Galleria mellonella*) and field-collected geometrid moths to the regular diet of mealworms. The wax moths were selected because they are readily available and highly palatable moths which were suitable for training purposes. Since *Galleria mellonella* moths are acoustic (Jang & Greenfield 1996; Greenfield & Weber 2000), their tegular, sound-producing structures were removed before presentation to the bats. The geometrid moths, also highly palatable, were captured in ultraviolet traps at several locations in Forsyth County, NC and were used to introduce variety in body size and shape to the palatable food during the training procedure. Over time the proportion of mealworms was reduced while the proportion of wax moths and geometrids was increased until the bats were fed exclusively on a moth diet. The bats learned quickly to traverse the floor of the dish and pick out the moths they found acceptable.

Arctiid moths were captured at ultraviolet light traps, collected at bait traps, or raised in the lab when their natural diet was known and sufficiently large numbers could not be collected from the wild. The plant diets of some species were manipulated in order to produce high, medium and low CG lines and high, medium, and low PA lines (CG++, CG+, CG– and PA++, PA+, PA– respectively; Brower 1969; Cohen & Brower 1983; Conner *et al.* 1990; Duffey & Scudder 1972). In a few cases the moths were reared on commercially available insect diets and adult male *Cosmosoma myrodora* were offered 2.5 mg of the pyrrolizidine alkaloid monocrotaline N-oxide suspended in 5% sucrose solution (Conner *et al.* 2000). The specific species tested and their respective diets are as listed below. The chemical designations (CG, PA, IG) refer to the relative availability of these materials in their diet.

### Arctiidae

#### Lithosiinae

*Hypoprepia fucosa* Hbn.–field-collected

#### Arctiinae

*Apantesis nais* (Dru.)–field-collected

*Cisseps fulvicollis* (Hbn.)–raised on *Digitaria sanguinalis* leaves (Poaceae)

*Cosmosoma myrodora* Dyar–raised on *Mikania scandens* (Asteraceae; fed 2.5 mg MNO)

- Cosmosoma myrodora* Dyar—raised on *Mikania scandens* (Asteraceae; PA-free)  
*Cynia tenera* Hbn.—raised on *Apocynum cannabinum* (Apocynaceae; CG)  
*Empyreuma pugione* L.—raised on *Nerium oleander* (Apocynaceae; CG)  
*Euchaetes egle* (Dru.)—raised on *Apocynum cannabinum* (Apocynaceae; CG++)  
*Euchaetes egle* (Dru.)—raised on *Asclepias curassavica* (Asclepiadaceae; CG+)  
*Euchaetes egle* (Dru.)—raised on *Asclepias tuberosa* (Asclepiadaceae; CG-)  
*Halysidota tessellaris* (J.E. Sm.) – field collected  
*Haploa contigua* (Wlk.)—raised on *Eupatorium purpurea* (Asteraceae; PA)  
*Pyrrharctia isabella* (J.E. Sm.)—raised on *Plantago rugelii* (Plantaginaceae; IG)  
*Spilosoma congrua* (Wlk.)—raised on *Plantago rugelii* (Plantaginaceae; IG)  
*Spilosoma virginica* (F.)—raised on *Plantago rugelii* (Plantaginaceae; IG)  
*Syntomeida ipomoeae* (Harr.)—raised on *Ipomoeae* leaves (Convolvulaceae)  
*Syntomeida melanthus* (Cram.)—raised on *Ipomoeae* leaves (Convolvulaceae)  
*Utetheisa ornatrix* (L.)—raised on *Crotalaria spectabilis* seeds (Fabaceae; PA++)  
*Utetheisa ornatrix* (L.)—raised on *Crotalaria spectabilis* leaves (Fabaceae; PA+)  
*Utetheisa ornatrix* (L.) – raised on PA free pinto bean diet (PA-)

On experimental days equal proportions ( $n = 5$  individuals) of wax moths, experimental arctiids and the wild-caught, palatable, control noctuid moths (same genera as in protocol 1) were prepared for presentation by gently squeezing their thoraces to partially immobilize them. Thus prepared, the moths were intact and alive but could not fly and it was easier for the bats to capture them. The sound producing ability of arctiids was tested by manual manipulation in front of a Minibat-2 bat detector (Ultrasound Advice, London, UK), and sound producing species were silenced by gently cutting the tymbal longitudinally with the tip of a stainless steel pin with the aid of a dissecting microscope.

The experiments were always carried out during the scotophase of the day/night cycle for the colony at about the same time (usually 2-3 hours after the onset of scotophase). A small 20 W fluorescent bulb, wrapped with a deep red gel filter was the main source of light in the room during the experiments. The three groups of moths (5 individuals each; 15 total) were placed in a glass culture dish and a single big brown bat was released into the dish. A mesh screen was placed on top of the dish to prevent the escape of crawling moths or the bat while still allowing observation of the experiment. The bat was allowed to traverse the dish and feed on the moths until either all moths were consumed, or the bat showed no further interest in the moths for 5 minutes. At that point the bat was removed from the dish and the palatability of the moths was recorded.

The palatability of individual moths was scored on a scale from 0 to 1. Moths that had no visible bite marks were scored as 0. Moths, which were completely consumed (except for the wings, which bats generally cull), were scored as 1. Partial palatability was scored by dividing the length of the moth body into 6 parts and assigning 1 part for the head, 2 for the thorax and 3 for the abdomen. A partial consumption of 3/6 for example could be recorded as either ( $3/6 = 1/1 + 1/2 + 1/3$ ) or ( $3/6 = 0/1 + 0/2 + 3/3$ ) among several of the possibilities. In the first case, the head, half of the thorax and a third of the abdomen were consumed by the bat, in the second, only the abdomen was consumed to yield the same overall consumption of 50 % of the moth. This method allowed an overall palatability score and also a record of whether certain body regions were differentially consumed by the bats. Since more than one experimental moth was presented to each bat over time the order of presentation of palatable and unpalatable moths was varied.

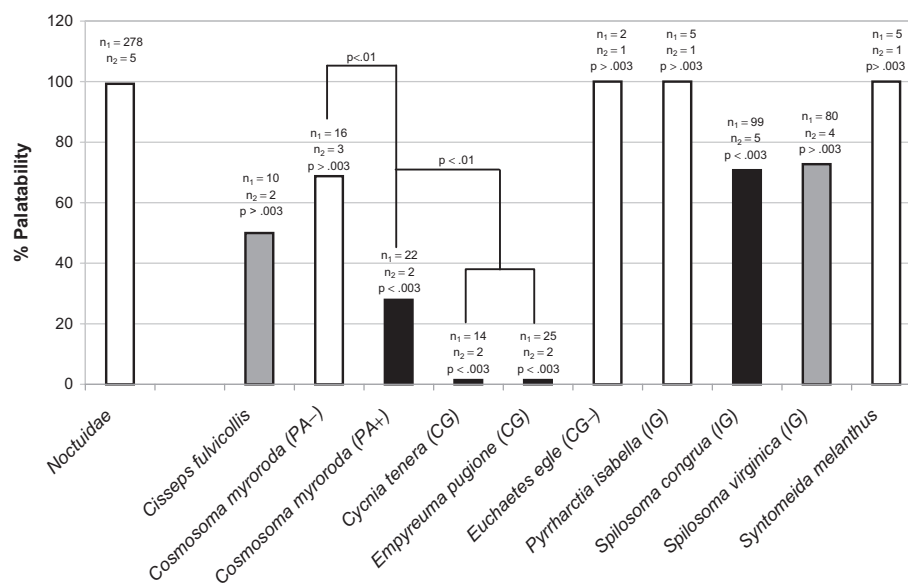
Within each dataset, the presence of an overall difference in the palatability between species was tested with a non-parametric Kruskal-Wallis test at an  $\alpha$ -level of 0.05 (Siegel & Castellan 1988). Post-hoc, pair-wise comparisons of specific palatabilities between moth species or chemical types were tested with a two-sample Kolmogorov-Smirnov Z test (Siegel & Castellan 1988). Since multiple comparisons were made the  $\alpha$ -levels were corrected according to the false discovery rate method (Benjamini & Hochberg 1995; Curran-Everett 2000).

## Results

Differences in the experimental protocols during the collection of the data necessitated separate analyses of the palatabilities of arctiid moths for the dataset from 1999–2000 and that from 2001–2003. In addition, since not all species of moths were presented to all bats and not always in the same numbers within each set, a non-parametric Kruskal-Wallis H test was used to test the acceptability of the few species with high representation among the different bats. Two species were selected for this test: the highly palatable *Apantesis nais* and *Utetheisa ornatrix*, one of the least acceptable species. *Apantesis nais* was presented to 11 of the 21 bats and there was no significant difference in the palatability of that species among the 11 bats (Kruskal-Wallis;  $p > 0.05$ ). Likewise, *U. ornatrix* (PA+ and PA++) was presented to 10 of the 21 bats and there was no difference in the palatability of that moth to these bats (Kruskal-Wallis;  $p > 0.05$ ). As a result of this consistency, the palatabilities of the different species of moths within each dataset were analyzed together.

Within the first dataset a Kruskal-Wallis test showed an overall difference in the palatability among the species of moths and their respective diets ( $p < 0.05$ ). In a series of two-sample Kolmogorov-Smirnov Z tests, the palatability of each of the 10 species and diets of arctiid moths was tested against the palatability of their matched sets of control noctuid moths. Significant differences were found for 4 of these species: *Cosmosoma myrodora* (PA+); *Cynia tenera* (CG), *Empyreuma pugione* (CG) and *Spilosoma congrua* (IG), species with low palatability to bats (Fig. 1). No significant difference was found for *Cosmosoma myrodora* (PA-), *Euchaetes egle* (CG-), *Pyrrharctia isabella* (IG) and *Syntomeida melanthus*, indicating that they were highly acceptable (Fig. 1). Three species of moths *Cisseps fulvicollis* and *Spilosoma virginica* were not significantly different from controls as well, but showed lower proportions of acceptability with higher underlying variation, reflecting an intermediate palatability to bats (Fig. 1).

A similar analysis in the second dataset (2001–2003) showed an overall difference in palatability among the variety of 15 species and diets of tiger moths (Kruskal-Wallis H test,  $p < 0.05$ ). Post hoc two-sample Kolmogorov-Smirnov tests indicated significant difference for 6 of these species (Fig 2). *Cynia tenera* (CG), *Euchaetes egle* (C++), *Halysidota tessellaris*, *Haploa contigua* (PA), *Spilosoma congrua* (IG) and *Utetheisa ornatrix* (PA++) were found to be unpalatable relative to controls. *Hypoprepia fucosa* should likely be included in this category. It was not eaten but because of the small sample size it was not significantly different from controls. The palatability of a second group of moths was not significantly different from that of



**Fig. 1** Tiger moth palatability 1999–2000 relative to noctuid controls using experimental protocol 1.  $n_1$  = moth sample size;  $n_2$  = bat sample size. P-values above each column indicate significance level relative to noctuid controls and reflect adjustment according to the false discovery rate method (see Materials and methods). The critical p value is 0.003. Values less than 0.003 indicate species that are significantly different from noctuid controls. Black columns designate moth species considered highly unpalatable. White columns designate moth species considered highly palatable. Stippled columns indicate moth species of intermediate palatability. PA ± and CG ± indicate presence of absence of pyrrolizidine alkaloids (PA) and cardiac glycosides (CG) in diet. ++, +, – indicate relative levels of defensive compounds in diet. The percent palatability of *Cycnia tenera* and *Empyreuma pugione* are both zero and have been exaggerated slightly in the figure to make their bar-color visible. P-values associated with brackets indicate pair-wise comparisons between indicated groups

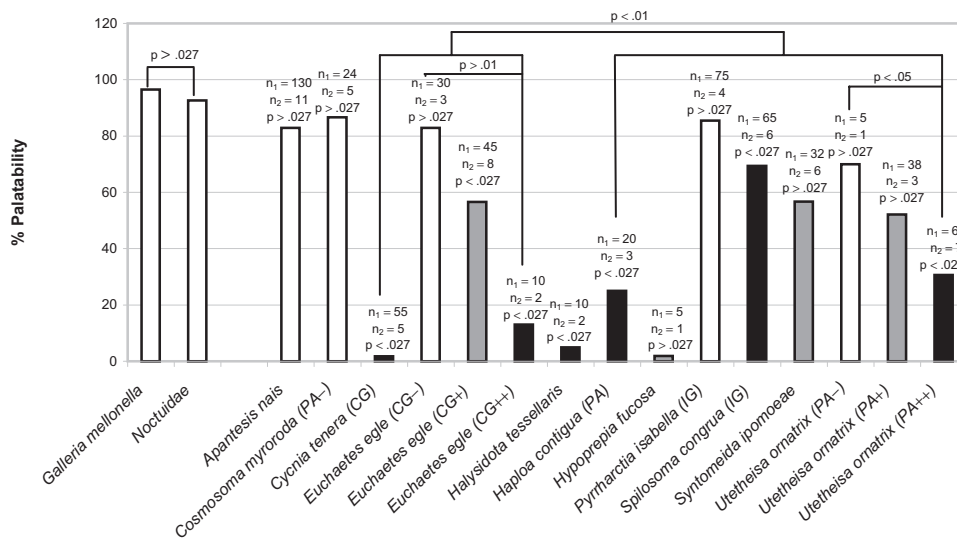
control noctuid moths. *Apantesis nais*, *Cosmosoma myrodora* (PA–), *Euchaetes egle* (CG–), *Pyrrharctia isabella* (IG), and *Utetheisa ornatrix* (PA–) were found to be palatable. Three species of moths *Euchaetes egle* (CG+), *Syntomeida ipomoeae* and *Utetheisa ornatrix* (PA+) were not significantly different from the controls but again showed lower proportions of acceptability with higher underlying variation reflecting an intermediate palatability to bats (Fig. 2).

The effect of diet on the palatability of arctiids was tested in three pair-wise comparisons between groups of moths reared on diets with high and low defensive chemical compositions. Two of these species with PA-based defense, *Cosmosoma myroroda* and *Utetheisa ornatrix*, showed a greater palatability to bats when reared on plants or diets devoid of PAs than when reared on PA-rich diets (Fig. 1 and 2). *Cosmosoma myroroda* (PA–) reared on *Mikania scandens* were significantly more palatable to bats (Fig. 1;  $p < 0.01$ ) and were rejected only when allowed to feed on a PA source (PA+) as an adult. Similarly, *Utetheisa ornatrix* fed on a PA-free diet (PA–) were also apparently quite palatable when compared to animals fed on their naturally occurring PA-rich (PA++) hostplants (Fig. 2;  $p < 0.05$ ). The third species, *Euchaetes egle*, a moth with CG-based chemical defense, also showed a difference in palatability between moths reared on CG-rich and CG-poor hostplants. When *Euchaetes egle* was reared on the CG-poor (GG–) *Asclepias tuberosa* it was found significantly more palatable to bats ( $p < 0.01$ ) than when reared on the leaves of CG-rich (CG++) *Apocynum cannabinum* (Fig. 2).

A comparison of the palatability of moths with PA-based chemical defense (*Cosmosoma myrodora* (PA+) in Fig. 1

and *Utetheisa ornatrix* (PA++), *Haploa contigua* (PA) in Fig. 2) vs. moths with CG-based chemical defense (*Cycnia tenera* (CG) and *Empyreuma pugione* (CG) in Fig. 1 and *Cycnia tenera* (CG) and *Euchaetes egle* (CG++) in Fig. 2) indicated a significant difference between the two types of defense in each case (Kruskal-Wallis,  $p < 0.01$ ). Species with CG-based defenses were consumed in smaller proportions than PA-defended species.

A qualitative review of the feeding behavior of the bats in the dishes revealed several observations. Bats randomly approached the three groups of moths in the dish. If a sample moth was found palatable, the bat proceeded with eating it by manipulating the moth so that the head and thorax were eaten first and the abdomen last. If a moth was found unpalatable, it was rejected and a new one selected. Two of the three moths with CG-based defense (*Cycnia tenera* and *Empyreuma affinis*) were never eaten by bats. Upon presentation, interactions were limited to a one time, very brief bite, and release of the moths without the consumption of any part of their bodies. Such bites were usually accompanied by the violent shaking of the head, salivating and wiping of the mouth. In contrast to these two moths, *Euchaetes egle*, a moth raised on either the CG-rich *Asclepias curassavica*, or CG-poor *A. tuberosa*, were sampled extensively by the majority of the bats and can be considered palatable. These moths were rendered unpalatable only when raised on the leaves of the *Apocynum cannabinum*, the same plant that renders *Cycnia tenera* unpalatable. Moths with PA-based chemical defense were consistently rejected by bats as well but only after tasting and chewing on parts of the body of the moths which resulted in relatively higher



**Fig. 2** Tiger moth palatability 2001–2003 relative to noctuid controls using experimental protocol 2.  $n_1$  = moth sample size;  $n_2$  = bat sample size. P-values above each column indicate significance level relative to noctuid controls and reflect adjustment according to the false discovery rate method (see Materials and methods). The critical p value is 0.027. Values less than 0.027 indicate species that are significantly different from noctuid controls. Black columns designate moth species considered highly unpalatable. White columns designate moth species considered highly palatable. Stippled columns indicate moth species of intermediate palatability. PA± and CG± indicate presence of absence of pyrrolizidine alkaloids (PA) and cardiac glycosides (CG) in diet. ++, +, - indicate relative levels of defensive compounds in diet. The percent palatability of *Cynia tenera* and *Hypoprepia fucosa* are both zero and have been exaggerated slightly in the figure to make their bar-color visible. P-values associated with brackets indicate pair-wise comparisons between indicated groups

proportions of consumption than for moths with CG-based defenses. In several species, the bats ate the head and the thorax but left the abdomen uneaten. This behavior was most apparent with female moths (e.g. *Spilosoma congrua*) whose egg-filled abdomen were clearly found unpalatable, as well as with flocculent-containing males of *Cosmosoma myrodora* whose PA-laden flocculent bearing abdomen was usually rejected.

## Discussion

### The palatability spectrum

We have assessed the palatability of different species of arctiid moths to sympatric insectivorous bats and evaluated the importance of diet on the relative palatability of each species. Although some arctiids are considered diurnal, it must be emphasized that they also fly during the night (Fullard *et al.* 2000; Fullard & Napoleone 2001), especially courting males (Acharya 1995), and thus they are exposed to predation by insectivorous bats. While not moth specialists *Eptesicus fuscus* routinely include moths in their diet (Black 1972). It is clear from our results that arctiids are not uniformly palatable or unpalatable to big brown bats, rather they span a spectrum of palatability.

The relative palatability is highly dependent on the nature of the larval food of each species. The highest degree of unpalatability is associated with feeding on cardiac-glycoside containing plants. *Cynia tenera* and *Empyreuma affinis* are known to sequester cardiac glycosides from their larval food (Black 1976; Cohen & Brower 1983) and this appears to be an extremely effective strategy for repelling

bats. Both of these species are also day-flying and rest in the open. Apparently birds and other visual predators quickly learn to avoid them through the association of their unpalatability with distinct color patterns. *Euchaetes egle*, on the other hand, also a cardiac glycoside feeding insect, is only moderately unpalatable to bats when raised on hostplants with significant amounts of cardiac glycosides. It is likely that this insect metabolizes or excretes the majority of the cardiac glycosides that it consumes. Only when reared on plants with very high levels of cardiac glycosides does it become even mildly noxious. The wings of this species render it cryptic in vegetation, and it may rely on a flash of orange on its abdomen for its protection against day-active predators.

Although not as potent as moths feeding on CGs, PA-feeding insects are also highly unpalatable to bats as illustrated by the brightly colored *Utetheisa ornatix*, *Haploa contigua* and *Cosmosoma myrodora*. *Utetheisa ornatix* is a specialist on legumes of the genus *Crotalaria* and its degree of unpalatability depends on the relative proportion of high PA seeds and low PA leaves available its diet (Conner *et al.* 1990). *Haploa contigua* feeds on PA-containing plants only during its early larval instars (Tietz 1972; Covell 1984). It switches to a more generalist feeding strategy in its later instars but retains its PA content to adulthood (Davidson *et al.* 1997). Male *Cosmosoma myrodora* are pharmacophagous and only become unpalatable when they imbibe PAs as adults. Females must obtain alkaloids as nuptial gifts from the male (Conner *et al.* 2000). It is also possible that the rejection of field-collected *Halysidota tessellaris* in our experiments is based on PAs ingested by the adults since both sexes are well know visitors to PA baits (Goss 1979). Thus it appears that tiger moths have evolved multiple strategies for acquiring these effective deterrents

and utilizing them. The level of distastefulness of the PA possessors in this study is quite sufficient to aversively condition free-flying bats to these insects after a small number of trials (Hristov & Conner 2005).

The arctiids that fed on *Plantago rugelii*, a species containing iridoid glycosides, were for the most part palatable or only mildly unpalatable. This is not surprising given that iridoid glycosides are sequestered by the larval stages but are not thought to be carried over to the adult stage (Bowers & Stamp 1997). It is interesting that the least palatable of the plantain feeders in our work *Spilosoma congrua* is also the best sequesterer of iridoid glycosides as a larva (Bowers & Stamp 1997). The mildly unpalatable nature of *Spilosoma congrua* in this study may be due to some carry over to the adult stage or to biogenic amines which can reach high concentrations in some species of *Spilosoma* (Rothschild 1963). Regardless they were only marginally different from control moths.

The most palatable arctiids were generalist feeders *Apantesis nais* and *Pyrpharctia isabella* (Weller *et al.* 1999). It should be noted however that our methods did not allow *P. isabella* to sample multiple hostplants as they do in nature. Generalist feeding is thought to be associated with the spread of Arctiini out of the tropics into more northern climes (Krasnoff & Roelofs 1990). This spread is accompanied by a decrease in overall exposure to bat predation (Morrill & Fullard 1992; Lewis *et al.* 1993) and perhaps by an overall increase in palatability.

#### Evolutionary trends

There is a general trend in the evolution of chemical defenses in arctiine (including Arctiini, Callimorphini, Pericopini, Phaegopterini, Ctenuchini, and Euchromiini (Weller *et al.* 1999)) arctiids toward compounds of greater effectiveness against vertebrates such as bats. The less effective biogenic amines are considered a primitive trait of arctiids. Based on phylogenetic evidence the PAs were added to the chemical arsenal later followed by the addition of cardenolides (Weller *et al.* 1999). It should be noted that the ability to sequester iridoid glycosides is less well known and was not mapped on the phylogeny. However, based on the data presented here, the addition of pyrrolizidine alkaloids and the later acquisition of cardenolides clearly represent escalations in a chemical arms race and may have been part of a suite of characters that allowed arctiids to fly during the day and develop their bright aposematic coloration and behavioral characteristics that serve as a warning to predators. Note that Rowell-Rahier *et al.* (1995) argue the opposite relationship for pyrrolizidine alkaloids and cardiac glycosides present in beetles and tested against birds. Further studies using purified compounds will be necessary to determine whether birds and bats have differential sensitivity to these broad classes of compounds. It also seems that a second lineage the lithosiines (Lithosiinae) have evolved feeding habits that protect them from predators. Lichen-feeding and the sequestration of polyphenolic compounds from the algal portion of the lichen (Hesbacher *et al.* 1995) appears to be an effective strategy. Although not yet proven, this is likely what renders the brightly colored *Hypoprepia fucosa* unpalatable.

There is general agreement between the findings presented here and those of other experiments assessing the

effectiveness and variation of arctiid defenses against different invertebrate and vertebrate predators. However information about the relationship between arctiids and vertebrate predators is fragmented and inconsistent across predator groups. Birds (Jones 1932, 1934; Collins & Watson 1983) and monkeys (Blest 1964) are generally known to reject arctiids with suspected PA and CG-based defenses (however see Kassarov 2001 for an alternative view) but apparently some *Peromyscus* species (Glendinning 1990; Glendinning *et al.* 1990) and the Loggerhead shrike (Yosef *et al.* 1996) can tolerate them. While surveying the sound production of neotropical arctiids Blest (1964) presented different species to monkeys and birds and observed that a large proportion of the arctiid species were rejected by these predators. However lack of detailed quantitative information on the interactions and knowledge of the hostplants makes further analysis difficult.

The best assessment of the palatability of arctiids was provided by the extensive work of Jones (1932, 1934). Using birds as model predators, he showed that among 11 lepidopteran families, arctiids, represented by 7 different species had the lowest overall palatability. Five of the seven tested species (or genera) were the same ones included in our experiments. *Cisseps fulvicollis*, and *Hypoprepia* sp. received the lowest acceptability scoring, followed by *Utetheisa* sp. and *Euchaetes egle*. The polyphagous *Apantesis nais* received the highest palatability score. These results are in agreement with our findings which indicate that *Hypoprepia fucosa* and *Utetheisa ornatrix* moths are generally rejected while *Cisseps fulvicollis* (note these did not have access to PAs as adults as they do in nature) and *Euchaetes egle* assume a more intermediate palatability. Both studies agree that *Apantesis nais* was one of the more palatable arctiid species.

Taken together, this information leads to the conclusion that arctiids, largely as a result of their diet, are found unpalatable to a variety of predators when they possess chemical defenses in the form sequestered allelochemicals. While CGs were found to be the most potent deterrent to bat attacks PAs clearly rendered the species possessing them unacceptable. This information contradicts early suggestions that the protective function of pyrrolizidine alkaloids is questionable (Brower 1984; Robinson 1979) and is consistent with growing experimental evidence that PAs are effective proximate deterrents to predator attack (Rowell-Rahier *et al.* 1995; Cardoso 1997). It should also be noted that other insect groups utilize PAs in defense, most notably two lineages of chrysomelid beetles (Pasteels and Hartmann, 2004). Since some bats are beetle specialists it is possible that they may also be exposed to PAs through this channel.

#### Mimicry and acoustic aposematism

The variation in palatability among species may have encouraged another striking aspect of arctiid biology. Tropical arctiids are superb mimics of wasps, bees, blister beetles, hemipterans, chemically protected roaches as well as of each other (Blest 1964). In most cases it is not yet clear to what extent these represent Müllerian or Batesian mimicry (Simmons & Weller 2002). Our results would suggest that both are likely. The two relatively palatable species

*Syntomeida ipomoeae* and *S. melanthus* may rely on wasp mimicry for survival. In addition female *Cosmosoma* which only receive PAs after mating with an alkaloid endowed male (Conner *et al.* 2000) may benefit from intersexual Batesian automimicry (Brower 1968) through their resemblance to males that have obtained alkaloids through pharmacophagy.

The most relevant mimicry *vis-à-vis* bats is acoustic mimicry. There is considerable evidence for acoustic aposematism in tiger moths (Dunning 1968; Acharya & Fenton 1992; Dunning *et al.* 1992; Dunning & Krüger 1995). Tiger moths answer the echolocation cries of bats with intense trains of clicks (Fullard & Fenton 1977). While naïve bats do not respond to the acoustic signals they quickly learn to associate the sounds with unpalatable prey and thereafter avoid sound-producing prey (Hristov & Conner 2005). Acoustic aposematism sets the stage for acoustic mimicry. Palatable species may benefit from mimicking the sounds of PA and CG laden models and unpalatable species may benefit from sounding alike. Additional experiments will be necessary to determine whether acoustic mimicry exists in nature.

#### Odors

Pyrazines have been suggested to function as warning odors stimulating neophobic "alerting" reactions in birds (Guilford *et al.* 1987). The role of the odors of arctiids (some of which are quite strong) on their relative acceptability to bats is unknown. The importance of prey odor to bats needs further investigation.

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