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**THE DEFENSIVE ROLE OF ULTRASONIC MOTH CLICKS AGAINST
BAT PREDATION: A MATHEMATICAL MODELING APPROACH**

By

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Abstract

Some moths emit ultrasonic clicks in response to bat echolocation calls. These clicks are believed to serve as a defence mechanism against bat predation by means of jamming, aposematism or startle. By assessing the characteristics and variation of the ultrasonic moth clicks it was possible to define the most likely function of the ultrasonic clicks by moths from sites in South Africa. Additionally, this study used Schaefer based mathematical models informed by field data on moth diversity and abundance, moth click parameters and bat population numbers and diversity, from these same sites in South Africa, to gain insight into the conditions that are required for each of these functions to work. The Jamming hypothesis proposes that moth clicks function by interfering with the bat's perceptual system, which is believed to be most effective in the terminal phase of the bat's attack were the clicks have been shown to be the most similar to the bats echolocation calls. This would place functional constraints on the clicks, decreasing the variation in the clicks. This was shown not to be the case, as a high level of variation was found between species' clicking parameters (e.g. peak frequency, inter pulse interval and intensity). A high level of individual moth variation was also found, with numerous patterns being produced by the same moths. Clicking variation was created both by manipulation of individual tymbals (e.g. changes in modulation cycle rate and durations) and between tymbals (e.g. timing of tymbal alternation). Furthermore the moth clicks are too different to bat echolocation calls to allow them to be mistaken by the bat as echoes from its own calls. The aposematic hypothesis suggests that the

clicks function as a warning signal to inform the predator of the prey's unpalatability. As in visual based aposematism, the cost of predator learning on the prey population would exert selective pressure towards higher densities of clicking moths and convergence in warning signals. This would allow one species to benefit from the predator learning induced by another species. This strategy is thus density dependent and would require a minimum proportion of clicking moths to work. Both the data from the ultrasonic moth clicks and mathematical modelling does not support this hypothesis as there is no signs of convergence and the mathematical modelling suggests that the low proportion of clicking moths (2.3%) in the natural moth population does not allow bats to form the association between moth clicks and noxiousness of the moth. In the case of jamming, the low proportion of clicking moths also does not reflect the competitive advantage supposedly gained from jamming. The startle hypothesis proposes that moth clicks confuse the bat by altering the normal sequence of expected events during the bat's attack. However, bats will habituate to these sounds if they are encountered regularly. Both the low proportions of clicking moths and the extreme variability of the click patterns hinder habituation and are consistent with the startle hypothesis, which suggest that the most likely function of ultrasonic moth clicks in these South African sites is startle. On the other hand, the aposematic and startle models do suggest that the existence of both noxiousness and clicking create the initial conditions for the evolution of an aposematic function for moth clicks. If the clicking moth is noxious the startle effect of the clicking could allow the population to grow to high enough numbers to make the aposematic function of the clicks viable.

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CHAPTER 1

Bats, Moths and Mathematical Models

Insectivorous bats are considered to be one of the main predators of nocturnal insects (Fullard 1982; Triplehorn and Yager 2001) and are believed to be the major selective force behind the evolution of tympanal organs (ears) in nocturnal insects, especially moths (Roeder 1967; Fullard 1982, 1987; Surlykke 1988; Surlykke and Fullard 1989). Evidence in support of this view includes the fact that many moth families have evolved tympanal organs with auditory characteristics that match the echolocation parameters of sympatric bat assemblages (Fullard 1982, 1987, 1992; Fullard and Dawson 1996). For example, the dominant frequency range used by aerial insectivorous bats in North America is between 20 kHz and 50 kHz, corresponding to the range of highest auditory sensitivity of moths (Fullard 1982; Surlykke 1988; Surlykke and Fullard 1989). In tropical West Africa, on the other hand, moths are exposed to more diverse bat assemblages using a wider range of echolocation frequencies and here the hearing sensitivity of moth's ranges from 20 kHz to 60 kHz (Fullard and Thomas 1981; Fullard and Belwood 1988). Lastly, day-flying moths, no longer exposed to bat-predation, have been shown to display advanced auditory degradation (Fullard 1994; Fullard *et al.* 1997; Surlykke 1988).

Hearing allows moths to detect echolocating bats and to execute evasive manoeuvres to escape predation (Roeder 1967; Fullard 1987; Waters and Jones 1996; Speakman and Rydell 2000). These manoeuvres vary from moving in the opposite direction to the bat at low sound intensities of echolocation (i.e. when the bat is far from the moth), to extreme twists, loops and power dives at higher intensities (i.e. when the bat is close to the moth) (Roeder 1967; Fullard 1987; Waters and Jones 1996). Studies have shown that moths with tympanal organs are up to 40% more successful at evading bat predation than moths without tympanal organs (Roeder 1967; Hickey and Fenton 1990; Rydell 1992; Acharya and Fenton 1999). Furthermore, bats that use echolocation frequencies outside the hearing range of moths (<20 kHz or >50 kHz) have higher proportions of moths in their diet than bats that use frequencies that are within the hearing range of moths (between 20 kHz and 50 kHz) (Jones 1992; Bogdanowicz *et al.* 1999; Jacobs 2000; Schoeman and Jacobs 2003).

In addition to evasive flight, some moths produce brief, broadband, high-frequency clicks in response to bat echolocation. These clicks often cause an incoming bat to break off its attack (Blest, Collet and Pye 1963; Dunning and Roeder 1965; Dunning 1968; Fullard and Fenton 1977; Dunning *et al.* 1992). Most moths generate these rapidly repeated clicks by the buckling action of the microtymbals (striated bands) on the surface of the tymbals, which are swollen air-filled katapisternal sclerites (Blest, Collet and Pye 1963). Three hypotheses, not necessarily mutually exclusive, have been advanced to explain the function of these ultrasonic clicks; these are the jamming, aposematism, and startle hypotheses.

Jamming

The jamming hypothesis proposes that moth clicks interfere with the bat's echolocation, disorientating the bat and causing it to abort its attack (Fullard, Fenton and Simmons 1979; Fullard *et al.* 1994; Tougaard *et al.* 1998). Two mechanisms have been put forward to explain how jamming could occur. Jamming, as defined by Fullard *et al.* (1994), is "the creation of false (phantom) echoes of sufficient quality to create the perception of objects in the path of an attacking bat". For the moth clicks to act as phantom echoes, the acoustic structure of the clicks should resemble that of bat calls (Fullard *et al.* 1994). The high rate at which moth clicks are produced is most similar to rate of calls emitted by the bat during the terminal phase of its echolocation sequence (Fullard 1984; Fullard *et al.* 1994).

The echolocation sequences of bats during an attack can be divided into three phases: search, approach and terminal (Griffin *et al.* 1960, Acharya and Fenton 1992). These three phases are distinguished by the differences in duration and interpulse interval. During the search phase the bat emits echolocation calls of relatively long duration, and low repetition rate (Schnitzler and Kalko 1998). The approach phase starts once the bat has detected a target. The bat reacts to the target by turning towards it and increasing the repetition rate (shorter interpulse interval) of its echolocation calls. During the approach phase the bat gathers information about target size, shape, texture and distance (Schnitzler and Kalko 1998, Kalko and Schnitzler 1998). The terminal phase is characterised by a group of short pulses (echolocation calls) at a very high repetition rate called a "feeding buzz" (Griffin 1958, Griffin *et al.* 1960). The feeding buzz is used to collect final and precise information on the exact position of the prey, taking

into account any last-minute manoeuvres performed by the prey (Griffin 1958, Griffin *et al.* 1960, Schnitzler and Kalko 1998).

Moth clicks resemble the frequency modulated call in the feeding buzz of an echolocation sequence (Fullard 1987; Fullard *et al.* 1994) in terms of interpulse interval, frequency and general shape (i.e. steep downward sweep), but not duration. The duration of the clicks is shorter, but the rapid repetition of clicks suggests that this may affect the integration time of the bat's hearing by producing a ringing effect in the bat's ear that causes clicks to stretch into subsequent clicks, giving the clicks durations similar to echoes from the bat's call (Fullard *et al.* 1994).

The second form of jamming suggests that clicks disrupt the neural mechanism that encodes the time of occurrence of the echo (Miller 1991, Tougaard *et al.* 1998). Neurons may still be recovering from a click-evoked spike when an echo from the bat's call arrives back at the bat, numbing the neurons responsiveness toward the echo and increasing the latency ambiguity (Tougaard *et al.* 1998). The nuclei of the lateral lemniscus is the auditory pathway that conveys information about the time relationship between sounds and is strongly linked to the output of the motor systems (Covey and Casseday 1986, 1991; Covey 1993). By recording the responses of single neural units in the nuclei of the lateral lemniscus to combinations of broad-band clicks and test signals, it was shown that 77% of the test units suffered neural interference (Tougaard *et al.* 1998). If the clicks occurred just before (0 - 3 ms) the test signal, latency and even suppression of the test signal (i.e. echo) was observed.

In both mechanisms, for jamming to be most effective, it would need to occur during the most vulnerable phase of attack when the high repetition rate of the clicks is most similar to the bat's echolocation calls. The bat is probably most vulnerable to disorientation and confusion during the terminal phase due to the high level of information being received in a short period of time (Wohlgenant 1989; Miller 1991; Fullard *et al.* 1994). It has been shown that a bat's ranging performance at these critical times deteriorates by up to 4000% (i.e. from 6 mm to 240 mm) (Miller 1991; Fullard *et al.* 1994). This deterioration, together with the perceived delay value assigned by the bat, increases the amount of time a click has to produce an interference effect on the bat's perception of echoes (Fullard, Fenton and Simmons 1979; Fullard *et al.* 1994; Tougaard *et al.* 1998). The distance at which the moth starts emitting clicks is between 0.5m and 1 meter (Fullard *et al.* 1994). This is relatively late in a bat's attack and falls well within the terminal phase of the echolocation sequence (Acharya and Fenton 1992; Fullard *et al.* 1994). The evolution of a jamming function for moth clicks should also result in convergence in the acoustic parameters of moth clicks since these clicks must match the calls in the terminal phase of the most common bat's echolocation sequence.

Aposematism

The Aposematism hypothesis proposes that the moth clicks provide information to the bat about the unpalatability of the moth allowing the bat to make a decision about whether or not to abort its attack (Dunning and Roeder 1965; Dunning 1969).

Aposematism is the correlation between a conspicuous warning signal, such as a bright colour, and prey unpalatability (Rowe 1999). In this case the moth's warning signal

comes in the form of sound (rapid repeated clicks), and apparently serves to inform the bat of the moth's noxiousness. However, the unpalatability of clicking moths has been assumed and few studies have confirmed the correlation between noxiousness and clicking (Hristov and Conner 2005).

The ability of the bat to learn to associate moth clicks with unpalatability plays an important role in aposematism. Dunning (1969) and Bates and Fenton (1990) showed that bats were capable of associating clicks with bad taste. Moreover, bats needed to encounter the clicks regularly to maintain the association between the noxious taste and clicks (Bates and Fenton 1990). On this basis one would assume that the aposematic function of moth clicks would be more successful when the densities of clicking moths are high in the moth population. Aggregation behaviour in aposematic signalling is believed to be an important factor for the success of such a strategy (Vulinuc 1990; Gegliardo and Guilford 1993; Speed 2001). The higher numbers of prey using the same warning signal dilutes the cost, to the prey, of the predator learning the association, and slows the rate of forgetting in the predator. Desert locusts, *Schistocerca gregaria*, for example change from a cryptic colour in low densities to a conspicuous black and yellow aposematic colouration in high densities (Key 1957; Sword and Simpson 2000). At low locust densities the predator rarely encounters this aposematic prey, preventing the predator from effectively associating the warning signal with the negative stimulus, making any conspicuous signal too costly. At high locust densities the higher encounter rate between the predator and prey allows for efficient aposematic signal association by the predator, decreasing the cost of conspicuous signalling. However clicking moths are

known not to be found in large groups and apparently constitute less than 1% of the total moth population (Bates and Fenton 1990).

In diurnal aposematism, where predators are reliant on vision (e.g. birds and butterflies), the prey's warning signal (usually colour) is constantly advertised, giving the predator an early indication of the prey's unpalatability (Edmunds 1974; Rowe 1999). Fullard *et al.* (1994) thus predicted that if aposematism occurs in bat/moth interactions, the moths should emit the clicks at an early phase of attack to allow the bat time to make the association between the clicks and the negative stimuli. However, clicking too soon may be costly to moths. Despite being capable of learning the association, it has been shown that bats have short memory retention and do not associate moth clicks with unpalatability after a certain period of time has elapsed (Bates and Fenton 1990). If the densities of clicking moths are low, bats probably forget and have to relearn this association often. Bat learning places a high cost on moths due to sampling by naïve bats that are attracted to conspicuous clicking moths. Evidence of such sampling can be inferred from the fact that it is mostly unpalatable species that are found with damaged wings in lepidopteron collections rather than palatable species (Rothschild 1985; Scoble 2002). Apparently unpalatable species will be attacked and then released, while palatable ones will be consumed (Brower 1984; Rothschild 1985; Scoble 2002). Thus a moth that clicks later in the bat echolocation attack sequence, i.e. when it is certain that it is the focus of the bat's attack, is less likely to be sampled by a naïve bat. Clicking too soon will attract the bat's attention (Masters 1979).

This kind of controlled timing of warning signal emittance cannot occur in visually-based predator/prey interactions due to the fixed nature of visually based signals. On the other hand, the sound-based echolocation system of bats provides the hearing moths with conspicuous cues, such as sound intensity and interpulse interval, which the moths can use to determine the distance and level of threat a bat represents. This allows the prey to temper its response accordingly. For example, it has been shown that some moths use the interpulse interval of the bat's echolocation to time the emittance of their clicks (Fullard *et al.* 1994). This is unlike the visual-based aposematic interaction in which the prey may become aware of the predator's presence only once it has been attacked. Thus, contrary to Fullard *et al.*'s (1994), prediction, moths should emit the warning signal later rather than sooner, if the densities of naïve bats in the population is high.

Startle

The startle hypothesis proposes that the moth clicks startle the bat by altering the normal sequence of expected events during an attack (Fullard 1977, 1987; Fullard, Fenton and Simmons 1979; Fullard *et al.* 1994). For maximum effect, the clicks should be emitted late in the bat's attack echolocation sequence, as for jamming. Bats are known to be sensitive to unexpected sounds during the approach and terminal phase of their attack (Stoneman and Fenton 1988; Bates and Fenton 1990).

In contrast to jamming, the clicks do not have to be confined to certain parameters (intensity, interpulse interval, duration, and bandwidth) to function. The click has only to

surprise the bat and does not need to mimic the echo of the bat's call or fall within the integration time of the bat's hearing to interfere with the bat's perceptive processes. Furthermore, variability of moth clicks may be advantageous because it may hinder habituation. It is thus proposed that if the moth's clicks function as a startle effect then one should expect a high level of inter-and intra-specific variation between the clicks and secondly, the parameters (e.g. duration, intensity, interpulse interval) of the clicks may differ from echo of the bat's call.

Bats are capable of habituating to moth clicks if no negative stimulus is associated with the sound (Bates and Fenton 1990). This suggests that the startle effect would be less effective with experienced bats, but still plays an important role in naïve bats (Bates and Fenton 1990). Even though bats in general are capable of habituating to moth clicks there is some evidence that this is not the case in all bat species (Stoneman and Fenton 1988). Furthermore, for bats to maintain their habituation towards moth clicks they would have to encounter moth clicks on a regular basis. This may be unlikely if clicking moths constitute less than 1% (Bates and Fenton 1990) of the total moth population.

Unlike the other two hypotheses, the startle function would be more effective at low densities of clicking moths. Increased survival would increase the percentage of clicking moths in the population. This in turn would increase the habituation rate of bats to the clicks and would lower the number of naïve bats making the defence less effective. More experienced bats would decrease the survival of clicking moths and their densities in the population would decline.

The startle function can occur in conjunction with either one or both of the other two functions. It is also possible that moth clicks are used against other predators and no single hypothesis may therefore explain the role of moth clicks (Fullard 1987; Bates and Fenton 1990; Fullard *et al.* 1994). For example in Bates and Fenton (1990) bats were put through two setups when exposed to moth clicks. Firstly they were exposed to moth clicks without a bad taste linked to it and secondly with a bad taste associated with the clicks. At first bats were startled by the moth clicks, but after three trials they habituated to the moth clicks and proceeded to feed. When exposed to moth clicks linked to bad tasting food the bats again took on average three trials to habituate to the startle effect of the moth clicks after which they proceeded to feed on the bad tasting food. It then took an average of seven trials of eating bad tasting food linked to moth clicks for the bats to make the association between the bad taste and moth clicks. This suggests that the startle and aposematic functions can both be present sequentially.

Mathematical Modelling

It is extremely difficult to observe bat/moth interactions in their natural situation because they are nocturnal species that use inaudible (to humans) high-frequency sounds, and rapid, erratic flight behaviour. It is therefore, difficult to quantify or even identify the components involved in the interaction between bats and moths (Fullard *et al.* 1994). To overcome these problems researchers have resorted to experimental approaches, which simulate bat/moth interactions to infer the natural function of moth

clicks. An alternative approach to this problem is to model bat/moth interactions using mathematical models.

Mathematical models are widely used to predict the behaviour of predator/prey systems, in particular their stability and the outcome of different strategies (Edelstein 1988, Varley *et al.* 1973, Pielou 1977). Mathematical models start by simplifying the complex natural system in question by including only the basic fundamental factors thought to influence the system. It also adopts sets of assumptions that allow for a simpler mathematical interpretation of the system (Edelstein 1988, Varley *et al.* 1973). This approach usually passes through an interactive process in which the assumptions and simplifications are repeatedly revised so that the mathematical model has significant biological interpretations, with complexity being introduced in a step by step fashion. In short modelling is thus a synthesis of observations and ideas, with the objective of identifying the fundamental factors influencing the system, to gain insight into the question being asked.

Aims

The aim of this study was to test the predictions and assumptions of the three hypotheses advanced to explain the functioning of ultrasonic moth clicks. Field data on moth and bat populations was used to construct a basic mathematical model in which each of the hypotheses were ran independently under different conditions and then compared in terms of their effect on the steady state equilibrium (stable point) of moth population sizes.

Jamming is independent of the level of experience of the bat. This makes the advantage of the strategy constant as bats do not require learning nor can bats habituate to this strategy. The advantage of jamming coupled with hearing should cause this strategy to have the highest population stable point of the three strategies (see chapter three). However, for this strategy to be successful, it has to fulfil certain functional constraints. The clicks would have to occur late in the bat attack sequence and evoke a spike in the neural mechanism (encodes the time occurrence of an echo) of the bat similar to that evoked by an echo from one of the bat's calls. Secondly, moth clicks should have a high repetition rate (clicks per unit time) and duty cycle (average number of clicks times average click duration per unit time) to maximize the chance that some clicks will fall within the narrow interference window. This should place constraints on the level of variation in the moth clicks (see chapter two).

For aposematism the ability to develop the association between noxiousness and clicking is vital. Therefore clicks should facilitate learning by being conspicuous (distinguishable from the array of other benign sounds), reliable (linked to negative stimulus) and low in variation (convergence by sharing the cost of predator learning) (see chapter two). Aposematic moths should have a higher population steady state equilibrium (stable point) when compared to earless moths and similar or higher population stable point when compared eared moths (see chapter three) as the higher numbers dilute the costs, to aposematic moths, of bat learning.

Startle is more effective with naïve bats than with experienced bats that have habituated to the moth clicks. Therefore to keep the number of experienced bats low this strategy should have a lower population stable point than the other strategies (aposematism and jamming) so that bats rarely encounter clicking moths and are startled by the unexpected sound (see chapter three). Unlike jamming, startle sounds do not need to mimic bat echoes. This places fewer functional constraints on the structure of the clicks, thus increasing variation. The increased variation of the clicks should also hinder the bats ability to habituate (see chapter two). I therefore also test the startle hypotheses against the other two, both of which predict low variability, by determining the degree of variability associated with moth clicks.

The aim of my study is therefore to use mathematical models to investigate the parameters of moth populations that are likely to be important for testing the three hypotheses that have been advanced for why moths click. I also test some of the predictions of these hypotheses associated with the density of clicking moths and the degree of variability of moth clicks by sampling a temperate bat and moth community in South Africa. These data from a real bat/moth community were also used in my mathematical models to make them as realistic as possible.

CHAPTER 2

Variation in ultrasonic moth clicks in the context of bat predation

Ultrasonic moth clicks are believed to serve as an additional defense mechanism in hearing moths against bat predation by means of jamming, aposematism or startle (Dunning and Roeder 1965; Dunning 1968; Fullard *et al.* 1979, 1994). Predictions currently set up under these three hypotheses based on when moths produce clicks relative to the echolocation sequence of an attacking bat, are not mutually exclusive (Surlykke and Miller 1985; Fullard *et al.* 1994). However, it may be possible to set up mutually exclusive predictions based on the characteristics and variability of moth clicks rather than on their timing.

Jamming

The Jamming hypothesis proposes that moth clicks function by interfering with the bat's perceptual system. If the clicks function as phantom echoes (chapter 1) the clicks should resemble a bat's echo i.e. they should have low intensities, correct duration and similar inter-pulse intervals. If the clicks disrupt the functioning of the neural pathways of

the bat's auditory system (chapter 1) moths would need to produce click trains with a large number of clicks of short duration and short inter pulse intervals to maximize the probability of one click falling within the critical time window (Miller 1991, Tougaard *et al.* 1998). The high diversity of bat echolocation assemblages and the varied inter pulse intervals would make it virtually impossible for a moth to predict the next bat echolocation pulse and to place a click in the narrow interference window (Simmons *et al.* 1989: 1 ms; Miller 1991: 1.5 ms; Tougaard *et al.* 1998: 3 ms) just before the bat receives the echo from that pulse. Furthermore, the response time for producing clicks (*Cygnia tenera*: Fullard 1982: 25 -35 ms; Fullard 1992: 80 -150 ms) prevents the moth from hearing a specific echolocation pulse and then placing clicks before the returning echo.

Aposematism

Aposematism is the use of a conspicuous warning signal (such as moth clicks), to inform the predator of the prey's unpalatability (Rowe 1999). Extensive research has been done on visually based warning signals, which has served as the basis for understanding aposematism (Müller 1879; Cott 1940; Brower 1958; Recorla and Wagner 1972; Endler 1988; Speed *et al.* 2000; Kapan 2001; Sherratt and Beatty 2003; Beatty *et al.* 2005). However, the basic principles of visual aposematism are applicable to auditory based aposematism. For example, the signal has to be distinguishable (Guilford 1988; Endler 1991; Mallet and Joron 1999) from the array of other benign sounds that the bat receives such as the returning echo from its echolocation call. This is contrary to the greater similarity between clicks and bat calls predicted by the Jamming Hypothesis. Furthermore, to aid the predator's learning of the association

between the signal and unpalatability, the signal has to be reliable (Sherratt and Beatty 2003).

Distinguishable and conspicuous signals have been shown to aid in predator learning (Guilford 1988; Endler 1991; Mallet and Joron 1999). For example, predators learn to avoid conspicuous, unpalatable prey more quickly than cryptic, unpalatable prey (Gittleman and Harvey 1980; Gittleman *et al.* 1980; Roper and Wistow 1986). In addition, conspicuousness increases the chance of being detected by a predator, making conspicuous signals among the least exploitable by palatable “cheats” (Sherratt and Beatty 2003). However, proportionally rare “cheats” can occur and are referred to as Batesian mimics (Brower 1960). For example Dunning (1968) found that one species of North American tiger moth could be using its clicks in a mimetic fashion. In predator populations that retain their learning (i.e. retain the association between the signal and unpalatability) the proportion of naïve predators can be relatively low. This reduces the costs of false advertising and can increase the chance of Batesian mimics evolving.

In the same manner that Batesian mimics benefit from using the signal of aposematic species, aposematic species also benefit from signal convergence by sharing the cost of predator learning. This is referred to as Müllerian mimicry and has been shown to be the most common form of mimicry (Cott 1940; Wickler 1968; Edmunds 1974). Müllerian mimics are not cheats per se, as it is an unpalatable species mimicing another unpalatable species. A large number of unpalatable sympatric species share common conspicuous warning signals often rendering them indistinguishable (Kapan 2001). The adaptive advantage in sharing a warning signal is that individuals of two or more

species share the local cost of predator learning (Müller 1879) and assumes that a predator has to attack a fixed number of prey before it learns the association between a signal and unpalatability (Müller 1879; Poulton 1890). It's been shown that predators that avoid a particular aposematic species will avoid its mimics (Brower 1958; Brower *et al.* 1963; Platz *et al.* 1971).

One of the best examples of the cost of predator learning and the advantage of shared reliable signals is provided by an experiment on heliconid butterflies (Kapan 2001). In this study unpalatable individuals were moved to areas where they matched or contrasted with the locally abundant monomorphic model species. Survival rates were significantly lower for translocated butterflies when they didn't match the local abundant monomorphic unpalatable model species than when they did. The survival rates were the lowest when translocated butterflies that didn't match the local abundant monomorphic model species, were released in low densities. In this case the cost of learning was shared among a smaller number of individuals increasing the cost per individual. Thus Müllerian mimicry can be highly advantageous and pattern convergence in visual aposematic signaling is striking (Cott 1940; Wickler 1968; Edmunds 1974). Using the same logic one should expect a similar pattern of convergence in the clicks of moths if the function of such clicks is aposematic. Furthermore, one would predict that moth clicks should be distinguishable (i.e. conspicuous) and reliable (linked to a negative stimulus) to aid learning and avoid confusion with benign signals.

Startle

The Startle hypothesis proposes that moth clicks confuse the bat by altering the normal sequence of expected events during the bat's attack (Edmunds 1974). This unexpected sound startles the bat giving the moth time to escape or causes the bat to abort its attack. Unlike aposematism, where learning is beneficial and required for the success of the strategy, the startle strategy is hindered by learning because the predator can become habituated to the clicks (Bates and Fenton 1990). Bats are capable of habituating to moth clicks when encountered regularly, causing the bat to ignore the clicks (Bates and Fenton 1990). This suggests that low densities of clicking moths would benefit the startle function of moth clicks. Clicks should also have a high level of inter- and intra-specific variation preventing predator habituation. In visual based learning it has been shown that predators take longer to learn (i.e. to become habituated) when presented with an array of signals (Beatty *et al.* 2004).

Aims

In this chapter I test predictions of the jamming, aposematic and startle hypotheses associated with the relative density of clicking moths and the variability of moth clicks. Both the jamming and aposematism hypotheses predict that clicking moths should occur in relatively high densities, whereas the startle hypothesis predicts that clicking moths should occur in low densities. If clicking functions as an aposematic signal, the clicks from different species should converge and interspecific variation in clicks should be low. In this case the clicks may or may not be similar to the calls in the terminal phase of a bat's echolocation sequence. If clicks function by jamming a bat's

echolocation, they should resemble the terminal phase of the bats echolocation sequence in terms of timing, duration and structure (e.g. be broadband). This constraint would also predict a low level of intra- and interspecific variation in the clicks. If clicks function by startling the bat, interspecific variation should be high (to retard habituation) and the clicks should not resemble bat calls so that they are easily distinguishable from the echoes from bat calls. I test the above predictions by investigating the relative abundance of clicking moths and the pattern and variation of moth clicks in a temperate moth community in the southwestern region of South Africa.

Materials and Methods

This study was done at Algeria Forestry Station in the Cederberg mountain range, in the Western Cape Province of South Africa during October (3rd - 7th) 2004 and November (11th – 17th) 2004. The two sites sampled were along the Rondegat River in the same large valley. The first site was referred to as the camp site (CS, 32°34'S; 19°02'E) and the second site was referred to as the swamps (SW 32°37'S; 19°06'E). The vegetation is predominantly natural mountain fynbos (medium to low laying shrubs and bushes), but one of the sites (CS) had the last remaining plots of cultivated *Pinus* spp. The climate is characterized by cool, wet winters and dry, hot summers, with an average annual rainfall of 500 mm to 1000 mm and summer diurnal temperatures ranging between 4.6 and 35.7°C (Koeberg Weather Station, South African Weather Service).

This study was located at Algeria Forestry Station because both the moth and bat fauna have been extensively sampled (e.g. Schoeman and Jacobs 2003; Schoeman 2006) during the last 5 years, allowing a reasonable understanding of both the bat and moth fauna. Thus the species compositions and diet of the bats are well known and a reference collection of 200 or more moth morpho-species for Algeria Forestry Station already exists.

Moth capture

Moths were passively captured using a 22-watt battery-operated black-light trap (BioQuip Products, 1320 East Franklin Avenue, El Segundo, California) with ethyl acetate. The trap was placed on the ground and emptied regularly (every 1 to 2 hours). Dead moths were placed in containers labeled with the time, date and site. This method allowed one to obtain the proportions of each moth family caught as well as the number of individual moths caught per hour effort.

Moths were actively caught by hand and/or insect nets directly off four white cotton sheets (180mm X 120mm) hung vertically between two poles. Each of two sheets were illuminated by a mercury vapour light (Osram 80w mercury vapour bulb, HQL-MBFU, München, Germany) and the other two were each illuminated by an ultraviolet light (Lohuis 30W ultraviolet black fluorescent tube, FT18/T8-BLB 0603, South Africa). The four sheets were placed at least 20 meters apart and erected half an hour before dusk and checked regularly until mid-night (24h00). These live moths were placed in netted boxes (25cm X 25cm X 40cm) and lightly sprayed every few hours with diluted sugar

water. They were only used in experiments and not included in determining the total morpho-species richness or relative abundance because I searched for specific morpho-species.

Moths were classified to family and morpho-species, with clicking moths being identified to species level when possible. This was done using Scholtz and Holm (1996) and then later confirmed using the reference collection of the Iziko Museum (25 Queen Victoria Street, Cape Town, South Africa). Identification of problematic moths was confirmed by either Dr Mike Picker (Department of Zoology, University of Cape Town) or Dr Martin Krüger (Transvaal Museum, Lepidopteron Department, Transvaal Museum). Where species identification was difficult, the moths were classified into morpho-species, which has proven to be useful as surrogates for species (Oliver and Beattie 1993, 1996).

The number of morpho-species in each family caught during the two fieldtrips were calculated and used as the indication of the moth population diversity. The number of individuals caught per hour trapping and the abundance per family for each fieldtrip and site were also calculated. Families were divided into hearing and non-hearing families based on Scoble's (1992) classification of families composed mostly of species which can hear ultrasound (i.e. hearing). This method is biased towards the classification of moths as non-hearing because some hearing families have few hearing species and unstudied families are classified as non-hearing.

Clicking moths and sound recordings

Species new to science were described and assigned a provisional species name by Dr Martin Krüger of the Transvaal Museum, Pretoria. The body length and wingspan was measured for all clicking moths. Body length was taken from the furthest tip of the head excluding antennae to the furthest point on the abdomen. Wingspan was taken from wing tip to wing tip with the wings held at a right angle to the central axis of the moth's body.

Moths were tested for clicking within five hours of capture and taken directly from the moth box to be recorded. During recordings, the moths were placed perpendicular to the ground at a height of 10 cm with wings fixed above the abdomen to eliminate wing beats. The microphone was placed at the same height, parallel to the moth at a distance of 10cm from the moth pointing to the ventral side of the moth. Care was taken to handle each moth in the same way. Moths respond similarly whether restrained or tethered (Fullard *et al.* 1994). Attempts were made to sample at least three individuals of each morpho-species, but this was not always possible with rare forms. Recording only commenced when the moth showed no sign of movement (e.g. legs and abdomen), and was not producing any sounds, for more than 30 seconds. Moths were stimulated by one single light touch with a soft brush on the ventral side of the thorax and the reaction was recorded for 20 seconds using a condenser microphone capsule CM16 (Avisoft Bioacoustics, Berlin, Germany) linked to an Avisoft multi-channel ultrasoundgate 416 (Avisoft Bioacoustics, Berlin, Germany) connected (via USB 2.0) to a notebook computer (HP Pavilion v1050, 1.6 Centrino, USA) set at 500 kHz sampling rates (16 bit,

mono). Harder touches and prodding was used when moths didn't react to the soft brush as some moths require stronger stimulus to react (Fullard and Fenton 1977; Barber and Conner 2006). However, all the clicking moths reacted to the soft brush and the stronger stimulus did not expose any new clicking species.

Data analysis

All recorded files were analyzed using BatSound Pro software (version 3.20; Pettersson Elektronik AB, Uppsala, Sweden) set at a sampling rate of 500 kHz. Duration of clicks, inter-pulse interval (IPI, interval between the end of one click and start of the next click) including maximum and minimum IPI of each set as well as inter-set and inter-cycle intervals (Figure 3) were measured from the oscillogram. Peak frequency (frequency of maximum intensity measured from the power spectrum) and bandwidth (15 dB above and below peak frequency) were taken from the FFT power spectrum using FFT sizes between 512 and 1024. A Hanning filter window was used to reduce effects of any unexpected background noise and to keep the protocol the same as in previous studies. Only high quality clicks, selected on the basis of the signal-to-noise ratio (unmistakable and clearly distinguishable peaks relative to the background noise on the oscillogram) were measured. At least 10 clicks from each individual were analysed and used to calculate averages. The most representative click based on the calculated average was then chosen as the single data point for that individual in statistical analyses. This was done to avoid pseudoreplication and to ensure that one was using real rather than statistical values.

I calibrated the intensity (i.e. peck equivalent Sound Pressure Level) of the moth clicks by playing a low-frequency 3 kHz sine signal through the speaker (the Avisoft ultrasonic scanspeak speaker has a flat response from about 2 kHz to over 100 kHz at intensities equal or below 100 dB at 1 meter, Avisoft Bioacoustics, Berlin, Germany) and recorded it with the ultrasound microphone with the same volume and amplitude settings as in our experiments. Simultaneously I measured the intensity of the sound using a sound level meter (Brüel and Kjaer 2231, Denmark, Copenhagen) at the same distance used in the experiments. This was repeated for 20 kHz, 40 kHz and 60 kHz sine signal at the same volume and amplitude as the 3 kHz sine signal. These sine signals were produced using Avisoft-SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). Even though the microphone is referred to as having a flat response in the relative frequencies analyzed there are usually small variations. The use of more than one frequency (i.e. four) allowed for a more precise calibration of the peck equivalent SPL throughout the frequency range as it compensates for any non flat response of the microphone. I obtained peck equivalent SPL, which Avisoft SASLab Pro software automatically calculates, by placing the sound meter results, play back settings and distances, including the distance between the microphone and moth (i.e. 10 cm) used in the experiments, into the command "Tools/Calibration" option of the software, which incorporated atmospheric attenuation and spreading loss under the standard condition of 18 C° and 50% humidity (Griffin 1971 and Stapells *et. al.* 1982).

The number of clicks produced by the active buckling of the tymbal organ ('on' set) and the passive return buckle ('off' set) were counted because of the occurrence of both smooth (usually one click per buckle and return buckle) and striated tymbals (usually multiple clicks per buckle and return buckle). The set repetition rate (number of clicks produced within a set per ms) was measured as well as set duration and inter-set gap. The buckle and return buckle was called a modulation cycle (i.e. a cycle included both an 'on' set and an 'off' set) and the inter-cycle gap was the time between the end of one modulation cycle and the beginning of the next modulation cycle in the sequence (Blest *et al.* 1963). When the clicks of one tymbal were mixed with those from the other tymbal the inter-cycle gap was not clear and the joint cycle of both tymbals was used (referred to as repetition unit) and the gap between the repetition units was used instead of the inter-cycle gap.

I was able to distinguish the 'on' and 'off' sets because the amplitude of the sound waves in the two sets was in opposite directions (Skals and Surlykke 1999). In this case the 'on' set starts with a very slight oscillation downwards followed by a strong upward oscillation. The 'off' set does the reverse with a very slight oscillation upwards followed by a strong downward oscillation (Skals and Surlykke 1999). This information is obtained by expanding the time axis so that the wave structure of the click can be seen. However this is only possible on extremely clear recordings and was one of the main causes of decreased sample sizes because clear recordings were not obtained for all individual moths.

For every click analyzed the number of clicks within 50 ms to each side of the click was counted to obtain a repetition rate. The percentage of time occupied by the clicks was calculated for each species and was referred to as duty cycle (Barber and Conner 2006). This was done to obtain the probability of any given click, within a train of clicks, falling within the narrow time window required for the click to have a jamming function. The maximum duty cycle (i.e. percentage of time) was obtained by multiplying the average duration of the clicks by the maximum average number of clicks in a 100 ms time bin. The maximum average number of clicks for each species was taken by calculating the average number of moth clicks in the two 100 ms time bins with the highest number of clicks (Barber and Conner 2006).

Results

Moth population diversity

At Algeria Forestry Station moths dominated (73%) the insects captured in the size groups most commonly taken by bats (>5 mm body length). In total 872 moths were collected comprising 219 morpho-species belonging to 16 families, 7 of which were known to have eared species. Even though insects were collected during two field trips and only during summer, a robust insect collection based on three years of collecting during all season already exists for the area (Schoeman and Jacobs 2003; Schoeman 2006). All seven of the hearing moth families present in the reference collection were caught and only two of the non-hearing moth families were not caught, but two new non-hearing families that were not present in the reference collection were caught (Pyraustidae and Pterophoridae) resulting in the same total number of moth families.

More importantly for the main group of interest, Arctiidae, I collected a higher number of morpho-species than was in the reference collection. The main reason why I was able to do so was probably my use of both ultraviolet and mercury vapor lamps and an increased trapping effort (3 to 4 times more light traps per night trapping and active searching for new morpho-species and families). However, the three year (all seasons) reference collection (Schoeman and Jacobs 2003; Schoeman 2006) still had a higher total number of morpho-species (278 vs. 219) than I collected. Most of the additional morpho-species in reference collection were from field trips taken earlier in the three year collection period and belonged mainly to rare non-hearing moth families. The missing non-hearing moth families and missing morpho-species has no correlation with season. The higher morpho-species in the reference collection may be due to the longer collection period, but could also be due to the removal of most of the pine plantations during the last few years, which could explain why the main differences occur during the early phases of the reference collection when the pine plantations were still present.

There was no significant difference between the two field trips in this study with regards to the number of individual moths caught per hour trapping (Two-way independent T-Test: $F_{(1, 7)} = 2, P > 0.08$) nor in the diversity of moth morpho-species caught during the two field trips (Matched T-Test: $F_{(1, 16)} = - 0.7 P > 0.4$).

The relative abundance of the 7 eared families was Arctiidae (20.7%), Geometridae (14.3%), Lymantriidae (9.2%), Noctuidae (39.7%), Notodontidae (3.5%), Pyralidae (2.3%) and Sphingidae (3%). The eared families thus comprised 92.7% of all moths captured at Algeria Forestry Station despite our sampling bias to earless families. The

relative abundance of the remaining 9 families that supposedly do not have eared species was Chrysopolmidae (0.6%), Crambidae (0.75%), Eupterotidae (2.85%), Limacodidae (0.9%), Pterophoridae (0.35%), Pyraustidae (0.6%), Saturniidae (0.35%), Thyretidae (0.6%) and Tortricidae (0.2%).

Even though there were fewer eared families than earless families the morpho-species richness showed a similar pattern to that of relative abundance of moth families, with 87% of the morpho-species belonging to eared families. However, Arctiidae had lower relative species richness (13.7%) than expected from their relative abundance (20.7%), whereas Geometridae had higher relative species richness (31.5%) than expected from their relative abundance (14.3%). If one translated these data into species richness indices (Menhinick index = species richness divided by the square root of abundance; Menhinick 1964), the Geometridae would have species richness almost three times higher than Arctiidae (7.68 vs. 2.78 respectively). The relatively low species richness of Arctiidae was mainly due to one very dominant Arctiidae morpho-species, which was found to be always one of the 4 most dominant morpho-species overall and constituting around 68% of all Arctiidae caught.

Clicking diversity

I tested 308 moths comprising 174 morpho-species from 13 families for the ability to produce clicks. Clicking moths were found to be rare with only four Arctiidae morpho-species and one Sphingidae morpho-species found to produce clicks. Thus, only 1.8% of the total morpho-species richness clicked. In terms of relative abundance, clicking

moths constituted only 2.3% (i.e. 13 of the 564 caught in the bucket black-light traps with ethyl acetate).

The Sphingidae morpho-species was identified as *Marcopoliana natalensis*, a relatively large moth with average wingspan of 113.8 ± 2 mm and body length of 45.4 ± 0.3 mm. Only three males were caught and tested, with only two of them producing clicks (Figure 1). Unlike most moth families where clicks are produced by the buckling of tymbal organs, in the Sphingidae clicks are produced by air passing from the proboscis into the pharyngeal cavity, causing a flap-like epi-pharynx to vibrate (Scoble 1992). In addition to these clicks a high frequency noise is produced when air is expelled from the pharyngeal cavity. No clicks are produced, when air is thus expelled, because the flap-like epi-pharynx is raised so air flow is not impeded. The click duration ranged between 0.3 – 0.8 ms with a mean of 0.5 ± 0.2 ms and click trains of 85 – 414 ms at a mean click rate of 21.3 ± 11.4 clicks per 100 ms resulting in a maximum duty cycle of 11.3%. Peak frequency averaged at 23 ± 2.8 kHz with a range of 18.9 kHz – 26.7 kHz and a mean intensity of 83.1 ± 1.5 dB. The mean bandwidth was 56.9 ± 15.9 KHz with an average minimum frequency of 6.2 ± 4.5 kHz and an average maximum frequency of 63.1 ± 20.1 kHz.

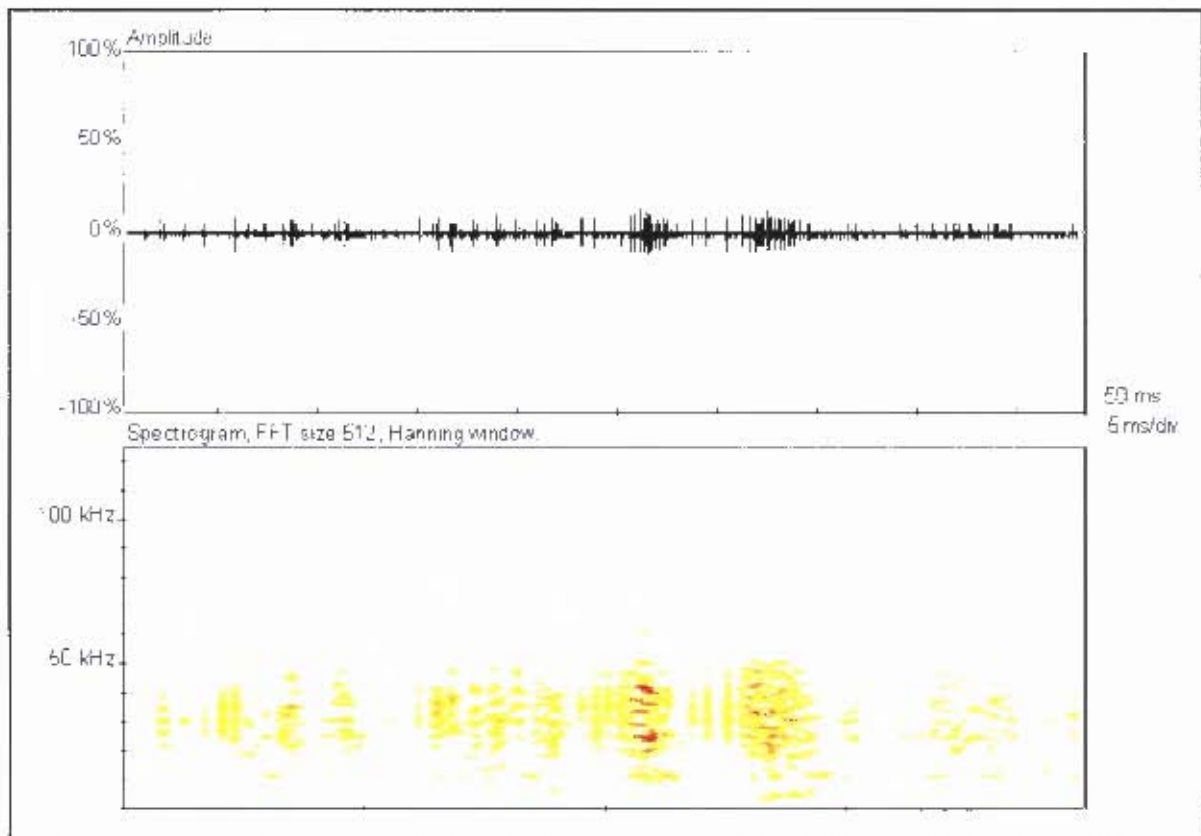


Figure 1: A 50 ms section recording of clicks emitted by *M. natalensis*. The top graph gives the amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks. *Marcopaliana natalensis* has a long silent period (+/- 30 – 50 ms) after each active clicking phase.

The four clicking Arctiidae morpho-species are undescribed species from the sub-family *Lithosiinae* and are at present being described and registered by Dr Martin Krüger (Lepidoptera Department, Transvaal Museum, Pretoria). Here provisional manuscript names are used, *Eilema brunneotinctum* (Figure 2A), *Ctenosia psectriphora* (Figure 2B), *Sozusa montana* (Figure 2C) and *Pasteosia tephriata* (Figure 2D). All

four species produced clicks by the active and passive buckling of the tymbal found on each side of the metathorax.

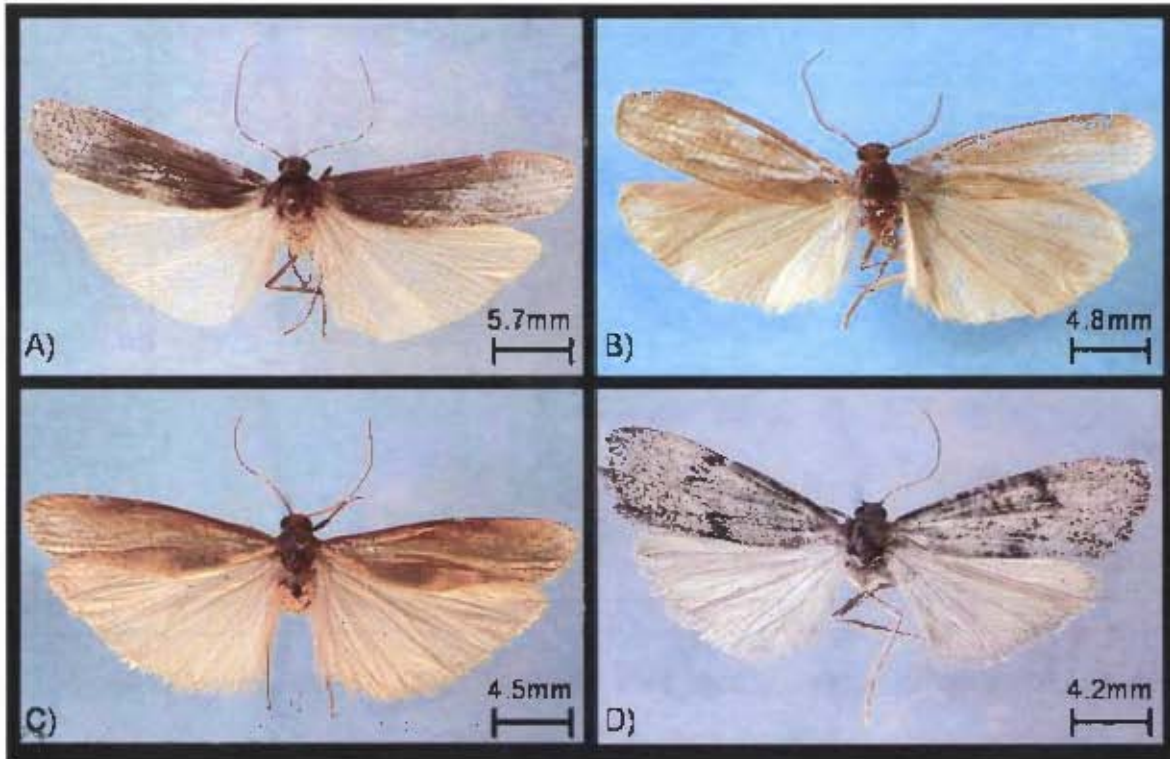


Figure 2: A dorsal view of the four clicking arctiid moths from the sub-family Lithosiinae. A) *E. brunneotinctum*, $n = 2$, wingspan 42.5 ± 0.28 mm, body length 12.85 ± 1 mm, B) *C. psectriphora*, $n = 1$, wingspan 35.6 mm, body length 8.4 mm; C) *S. montana*, $n = 34$, wingspan 34.8 ± 3.12 mm, body length 11.2 ± 2.1 mm; and D) *P. tephriata*, $n = 19$, wingspan 31.2 ± 2.78 mm, body length 9.8 ± 0.95 mm.

Eilema brunneotinctum is the largest of the four clicking Arctiidae and was rare with only one female and one male caught. The female had an average wing span of 42.3 mm and a body length of 12.1 mm and the male an average wing span of 42.7mm and a body length of 13.6 mm. Both male and female produced clicks consisting of repeated cycles (84 ± 46) of 3 to 6 clicks in each active and passive buckling of the tymbal (Figure 3), with click trains of 20 – 572 ms at a mean click rate of 27 ± 18 clicks per 100 ms. The click duration ranged between 0.1 – 0.3 ms with a mean of 0.2 ms resulting in a

maximum duty cycle of 5.4%. The peak frequency in the clicks varied from 30 – 36.4 kHz with a mean of 34 ± 3.8 kHz at a mean intensity of 78.1 ± 3 dB. The mean bandwidth was 38.8 ± 18.7 KHz with an average minimum frequency of 17 ± 5.8 kHz and an average maximum frequency of 55.8 ± 14.7 kHz.

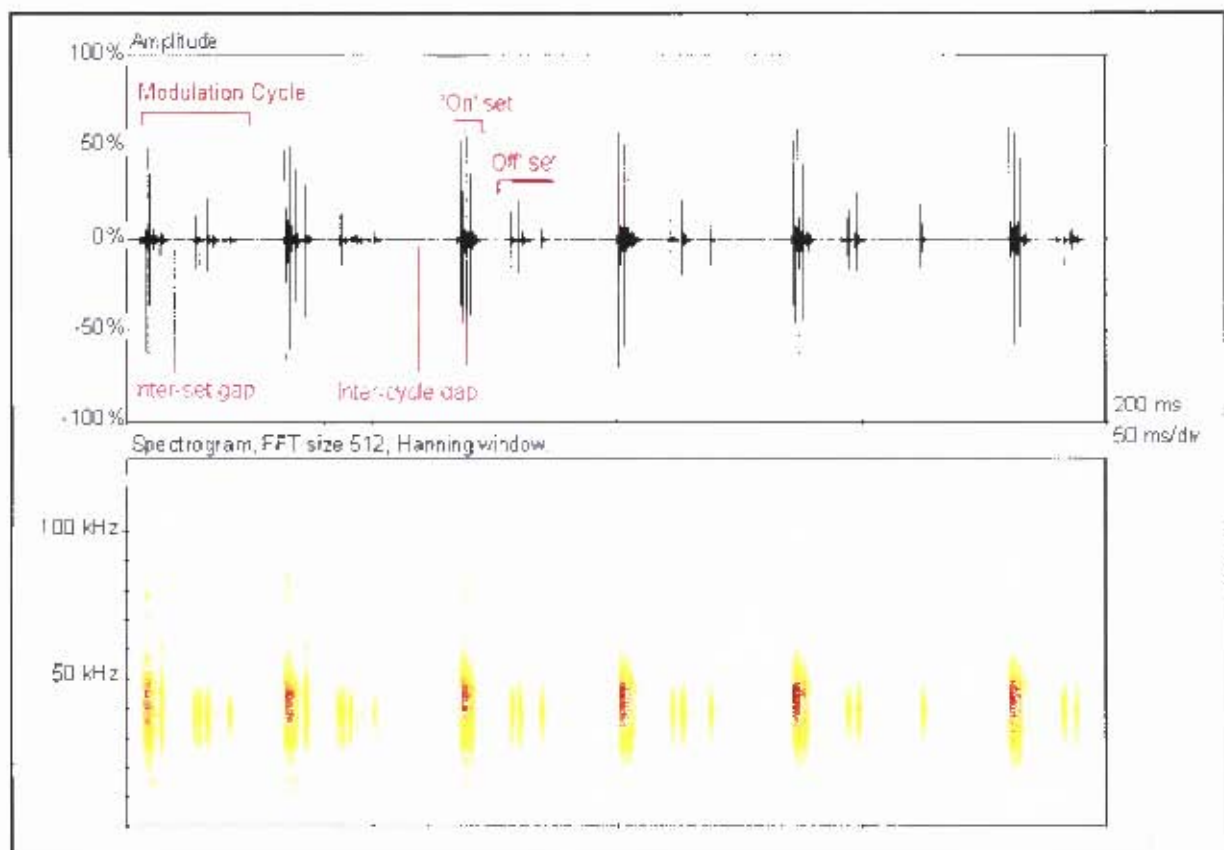


Figure 3: A 200 ms section recording of clicks emitted by *E. brunneotinctum* showing a clear active buckle ('on' set), and a less intense passive buckle ('off' set). The top graph gives the amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

Ctenosia psectriphora was the rarest of the four clicking arctiids species with only one female caught with a measured wingspan of 35.6 mm and body length 8.4 mm. This individual produced 2 clicks in each active and passive buckling of the tymbal (Figure 4). A single click train was 1541 ms in duration and consisted of 297 clicks resulting in a click rate of 19.2 ± 11.3 clicks per 100 ms and a maximum duty cycle of 3.5%.

The most representative click with the best signal-to-noise ratio had a duration of 0.2 ms and a peak frequency of 25.2 kHz at the maximum intensity of 71.9 dB. The bandwidth was 62.6 kHz with a minimum frequency of 12.1 kHz and a maximum frequency of 74.7 kHz. Due to the low sample sizes of *E. brunneotinctum* and *C. psectriphora* it was not possible to perform statistical test on these species.

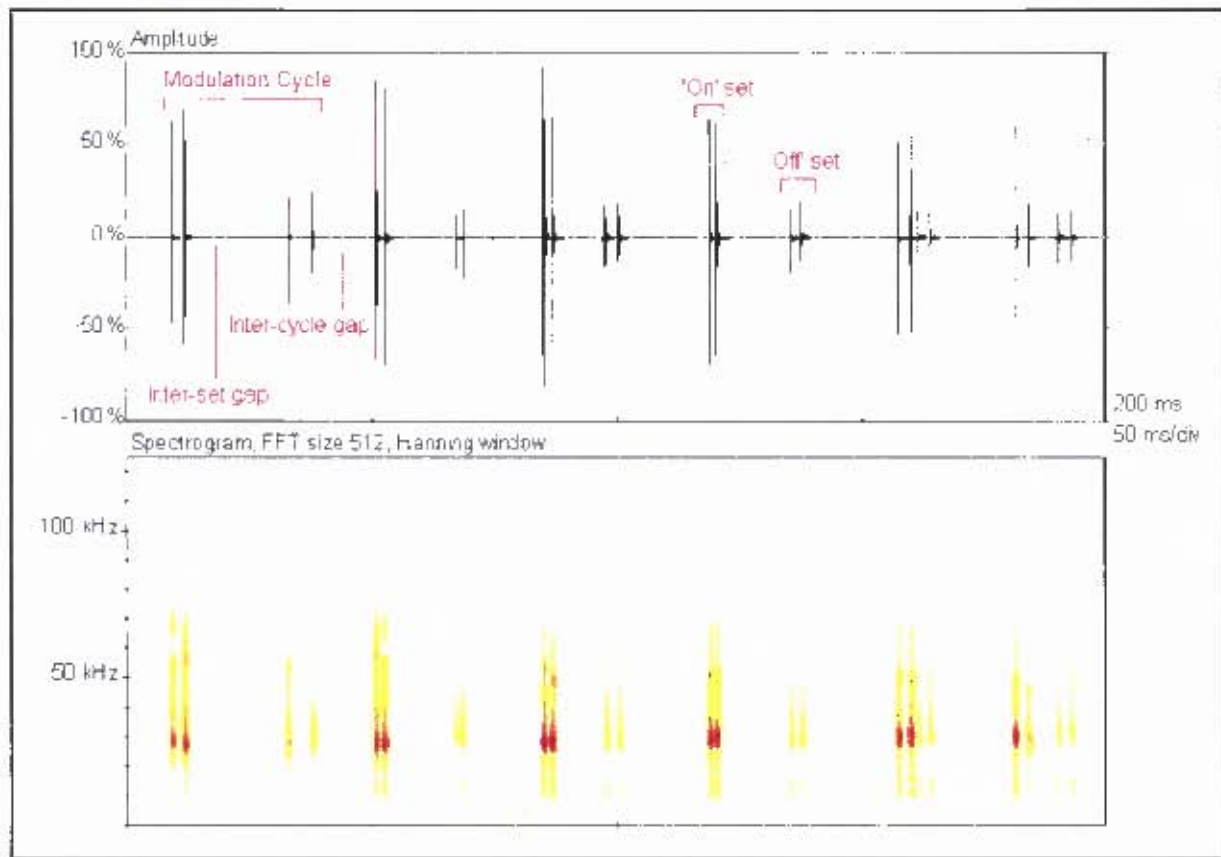


Figure 4: A 200 ms section recording of clicks emitted by *C. psecriphora* showing the irregular inter-set gap and inter-cycle gap, which was common throughout the recording. The top above graph gives the amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

In total *S. montana* and *P. tephriata* were the two most common clicking moths, constituting 57.6% (34 individuals) and 32.2% (19 individuals) of clicking moths. Both species showed no significant differences in abundances between field trips (Two-way independent T-Test: *S. montana*, Mean 1st 3.1 ± 2.3 and 2nd 4.5 ± 2.2 , $T = -0.1$, $DF = 9$, $P > 0.9$; *P. tephriata*, Mean 1st 2.2 ± 1.4 and 2nd 1.8 ± 1.2 , $T = 0.6$, $DF = 9$, $P > 0.5$), between trapping areas (Two-way independent T-Test: *S. montana*, Mean CS 4.2 ± 2.7

and SW 3.5 ± 1.9 , $T = 0.5$, $DF = 11$, $P > 0.6$; *P. tephriata*, Mean CS 2.7 ± 2.1 and SW 2 ± 1.5 , $T = 0.1$, $DF = 11$, $P > 0.9$) or between sexes (Two-way independent T-Test: *S. montana*, Mean M 4.1 ± 1.2 and F 3.6 ± 1.6 , $T = -0.7$, $DF = 16$, $P > 0.4$; *P. tephriata*, Mean M 2.4 ± 1.1 and F 1.2 ± 0.5 , $T = 0.5$, $DF = 16$, $P > 0.4$). The same was true for click parameters within each species with no significance found between field trips (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 1.1$, $P > 0.4$; *P. tephriata* Wilks $F_{(1, 10)} = 2.9$, $P > 0.4$), between trapping areas (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 2$, $P > 0.2$; *P. tephriata* Wilks $F_{(1, 10)} = 46.9$, $P > 0.1$) or between sexes (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 3.8$, $P = 0.1$; *P. tephriata* Wilks $F_{(1, 10)} = 1.4$, $P > 0.5$). As no significant differences were found in abundances and clicking parameters each individual of a specific species was considered as one data point independent of the field trip, trapping area or sex.

There were significant differences in the click parameters between *S. Montana* and *P. tephriata* (One-way ANOVA: Wilks $F_{(12, 18)} = 8.2$, $P < 0.001$). *Sozusa montana* had a lower average intensity than *P. tephriata* (74.7 ± 8.4 and 85.7 ± 4.3 dB, respectively; post hoc Tukey test: $P < 0.001$) as well as a lower peak frequency than *P. tephriata* (42.4 ± 4.8 kHz compared to 49.4 ± 5.7 kHz, respectively; post hoc Tukey test: $P < 0.002$), whereas, the inter pulse interval (IPI) for *S. montana* was significantly higher than *P. tephriata* (1.6 ± 1.6 and 0.5 ± 0.2 ms, respectively; post hoc Tukey test: $P < 0.001$).

Sozusa montana clicks consisted of repeated cycles of 3 - 11 clicks in each active and passive buckling of the tymbal, with click trains of 241 – 1091 ms at a mean click rate of 21.8 ± 12.5 clicks per 100 ms (Figure 7, 8 and 9). The click duration ranged

and SW 3.5 ± 1.9 , $T = 0.5$, $DF = 11$, $P > 0.6$; *P. tephriata*, Mean CS 2.7 ± 2.1 and SW 2 ± 1.5 , $T = 0.1$, $DF = 11$, $P > 0.9$) or between sexes (Two-way independent T-Test: *S. montana*, Mean M 4.1 ± 1.2 and F 3.6 ± 1.6 , $T = -0.7$, $DF = 16$, $P > 0.4$; *P. tephriata*, Mean M 2.4 ± 1.1 and F 1.2 ± 0.5 , $T = 0.5$, $DF = 16$, $P > 0.4$). The same was true for click parameters within each species with no significance found between field trips (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 1.1$, $P > 0.4$; *P. tephriata* Wilks $F_{(1, 10)} = 2.9$, $P > 0.4$), between trapping areas (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 2$, $P > 0.2$; *P. tephriata* Wilks $F_{(1, 10)} = 46.9$, $P > 0.1$) or between sexes (One-way ANOVA: *S. montana* Wilks $F_{(1, 12)} = 3.8$, $P = 0.1$; *P. tephriata* Wilks $F_{(1, 10)} = 1.4$, $P > 0.5$). As no significant differences were found in abundances and clicking parameters each individual of a specific species was considered as one data point independent of the field trip, trapping area or sex.

There were significant differences in the click parameters between *S. Montana* and *P. tephriata* (One-way ANOVA: Wilks $F_{(12, 18)} = 8.2$, $P < 0.001$). *Sozusa montana* had a lower average intensity than *P. tephriata* (74.7 ± 8.4 and 85.7 ± 4.3 dB, respectively; post hoc Tukey test: $P < 0.001$) as well as a lower peak frequency than *P. tephriata* (42.4 ± 4.8 kHz compared to 49.4 ± 5.7 kHz, respectively; post hoc Tukey test: $P < 0.002$), whereas, the inter pulse interval (IPI) for *S. montana* was significantly higher than *P. tephriata* (1.6 ± 1.6 and 0.5 ± 0.2 ms, respectively; post hoc Tukey test: $P < 0.001$).

Sozusa montana clicks consisted of repeated cycles of 3 - 11 clicks in each active and passive buckling of the tymbal, with click trains of 241 – 1091 ms at a mean click rate of 21.8 ± 12.5 clicks per 100 ms (Figure 7, 8 and 9). The click duration ranged

between 0.1 – 0.5 ms with a mean of 0.2 ± 0.1 ms resulting in a maximum duty cycle of 7.8%. The mean bandwidth was 39.1 ± 13.4 KHz with an average minimum frequency of 25.6 ± 7.8 kHz and an average maximum frequency of 64.7 ± 11.3 kHz. The average set duration was 5.3 ± 2 ms followed by an average inter-set gap of 12 ± 6.1 ms.

Pasteosia tephriata had modulation cycles which ranged between 2 to 12 clicks, with click trains of 89 – 1582 ms at a mean click rate of 33.2 ± 18.1 clicks per 100 ms (Figure 5 and 6). The click duration ranged between 0.1 – 0.2 ms with a mean of 0.1 ± 0.1 ms and a maximum duty cycle of 5.4%. The mean bandwidth was 43.2 ± 8.5 KHz with an average minimum frequency of 29.5 ± 9.4 kHz and an average maximum frequency of 72.7 ± 6.9 kHz. The average set duration was 3.9 ± 1.4 ms and the average inter-set gap was 10.6 ± 2.4 ms.

Clicking patterns

While analyzing the clicks of *S. montana* and *P. tephriata* I observed several different modulation cycle patterns (sequence of modulation cycles, Table 1). The combination of an active buckle ('on' set) and a passive return buckle ('off' set) is referred to as a modulation cycle. Both the right and the left tymbal can produce modulation cycles, which can occur in synchrony or alternately (Skals and Surlykke 1999). Theoretically the active buckling is produced by the coxal branch of the basalar muscle contracting and causing the tymbal to buckle (Blest *et al.* 1963, Fullard and Fenton 1977, Heller and Fullard 1990) releasing a set of 'on' clicks. When the muscle relaxes the tymbal return buckles, releasing a set of 'off' clicks, which can be

distinguished from the 'on' set by the opposite direction in amplitude of the sound waves in the two sets (Skals and Surlykke 1999).

Table 1: Means and standard deviations for the main click parameters for the five most common patterns produced by *S. montana* and *P. tephriata*. Due to the low quality of the recording of *P. tephriata* for pattern three, four and five they could not be used. The parameter "Gap" represents the gap or interval following the set in question. From pattern one to three the gap following the 'on' set would be the inter-set gap while the gap following the 'off' set would be the inter-cycle gap. For pattern four and five the gap following the first two sets would be the inter-set gaps whereas the gap following the last set would be the gap between the repetition units. Note: The values for each of the patterns may vary from the species averages due to some individuals that did not produce a specific pattern or due to the higher quality required for identifying a pattern excluding the specific individual from the average.

	Pattern 1		Pattern 2		Pattern 3	Pattern 4	Pattern 5
	<i>S. montana</i>	<i>P. tephriata</i>	<i>S. montana</i>	<i>P. tephriata</i>	<i>S. montana</i>	<i>S. montana</i>	<i>S. montana</i>
	N=13	N=8	N=10	N=6	N=5	N=4	N=4
	On' set		On' set		On' set	On' set	On' set
Intensity	75.8 ±10.0	83.9 ±7.7	72.6 ±7.0	81.7 ±7.4	70.2 ±4.6	75.7 ±2.4	78.5 ±4.1
Peak Frequency	45.5 ±10.4	49.4 ±6.4	43.3 ±6.2	51.5 ±4.9	43.1 ±3.4	42.1 ±3.2	43.4 ±4.2
Click Duration	0.2 ±0.1	0.1 ±0.1	0.2 ±0.2	0.1 ±0.1	0.1 ±0.1	0.1 ±0.0	0.1 ±0.0
Bandwidth	43.2 ±22.1	44.7 ±8.5	40.0 ±14.7	42.1 ±9.2	33.3 ±5.7	45.4 ±11.4	50.1 ±18.3
IPI	0.0 ±0.5	0.5 ±0.2	1.5 ±1.2	0.4 ±0.1	1.2 ±0.5	0.8 ±0.2	1.1 ±0.7
Clicks per msec	1.1 ±0.4	1.9 ±0.5	0.9 ±0.3	2.2 ±0.6	0.9 ±0.3	1.2 ±0.4	1.2 ±0.4
Set Duration	6.4 ±1.7	3.0 ±1.6	4.5 ±2.0	2.8 ±1.6	5.2 ±0.5	6.1 ±1.3	4.0 ±1.4
Gap	10.1 ±5.0	10.6 ±2.2	17.2 ±5.3	11.7 ±3.2	7.5 ±3.4	5.4 ±1.6	5.6 ±3.8
Clicks in set	6.6 ±3.0	6.9 ±3.0	3.7 ±1.9	5.7 ±2.7	4.6 ±1.3	7.3 ±0.5	5.0 ±2.2
	Off' set		Off' set		Off' set	Mixed set	On' set
Intensity	66.4 ±7.1	69.0 ±7.5	64.3 ±6.0	67.9 ±7.1	68.8 ±5.5	78.4 ±6.5	78.1 ±5.3
Peak Frequency	44.4 ±12.3	44.6 ±5.0	44.1 ±3.3	49.9 ±5.2	43.1 ±4.7	41.1 ±0.6	44.8 ±5.1
Click Duration	0.1 ±0.1	0.1 ±0.1	0.2 ±0.1	0.1 ±0.0	0.1 ±0.1	0.1 ±0.00	0.1 ±0.0
Bandwidth	54.6 ±23.7	57.3 ±11.1	48.3 ±14.4	56.7 ±10.2	41.3 ±13.8	35.3 ±2.1	42.0 ±15.2
IPI	1.6 ±0.9	1.9 ±3.3	4.6 ±3.7	1.7 ±1.7	1.1 ±0.3	1.0 ±0.2	1.2 ±0.8
Clicks per msec	0.7 ±0.4	1.0 ±0.5	0.6 ±0.6	1.1 ±0.5	1.0 ±0.4	1.3 ±0.2	1.2 ±0.4
Set Duration	9.5 ±3.3	6.6 ±2.3	6.6 ±4.1	6.0 ±3.3	5.0 ±1.1	9.4 ±0.3	4.8 ±1.5
Gap	37.6 ±20.1	31.6 ±9.7	8.8 ±2.8	4.4 ±0.8	0.4 ±5.2	3.8 ±1.1	9.1 ±8.8
Clicks in set	6.2 ±2.6	6.0 ±2.8	2.9 ±1.4	5.3 ±2.0	4.6 ±1.3	12.3 ±1.7	6.0 ±2.9
						Off' set	Off' set
Intensity						64.5 ±10.3	71.7 ±5.6
Peak Frequency						38.6 ±1.5	40.9 ±4.3
Click Duration						0.1 ±0.1	0.1 ±0.1
Bandwidth						47.2 ±6.0	57.8 ±33.0
IPI						1.3 ±0.5	1.2 ±0.6
Clicks per msec						0.9 ±0.2	0.8 ±0.4
Set Duration						7.8 ±0.6	13.6 ±3.7
Gap						42.1 ±8.5	47.4 ±38.3
Clicks in set						7.3 ±2.1	10.5 ±4.5

Pattern one (Figure 5) was produced by all four species of clicking Arctiidae, comprising from 40% to 80% (depending on the species) of all clicks produced and found at least once in every recording sequence analyzed (Table 1). Pattern one consisted of repeated cycles of active buckling of the tymbal organ ('on' set) followed by a short inter-set gap and the passive return buckle ('off' set). The return buckle was followed by a pause (inter-cycle gap) before the next active buckle (Figure 5). Pattern one had a significantly longer inter-cycle gap (at least 3 times longer, Table 1) than the inter-set gap (*S. montana*, Mann Whitney U-Test: $Z = -4.1$, $DF = 13$, $P < 0.001$; *P. tephinata*, $Z = -3.4$, $DF = 8$, $P < 0.001$). The 'on' clicks also had a higher intensity (around 10 dB higher, Table 1) than 'off' clicks (Two-way independent T-Test: *S. montana*, $T = 2.6$, $DF = 24$, $P < 0.02$; *P. tephinata*, $T = 3.9$, $DF = 14$, $P < 0.002$). The 'on' sets also had a significantly higher click repetition rate (clicks per ms) than 'off' sets (see Table 1; Two-way independent T-Test: *S. montana*, $T = 2.6$, $DF = 24$, $P < 0.02$; *P. tephinata*, $T = 3.1$, $DF = 14$, $P < 0.01$), which was partly due to the significantly shorter set duration (Table 1; Two-way independent T-Test: *S. montana*, $T = -2.9$, $DF = 24$, $P < 0.01$; *P. tephinata*, $T = -2.7$, $DF = 14$, $P < 0.02$) of 'on' sets.

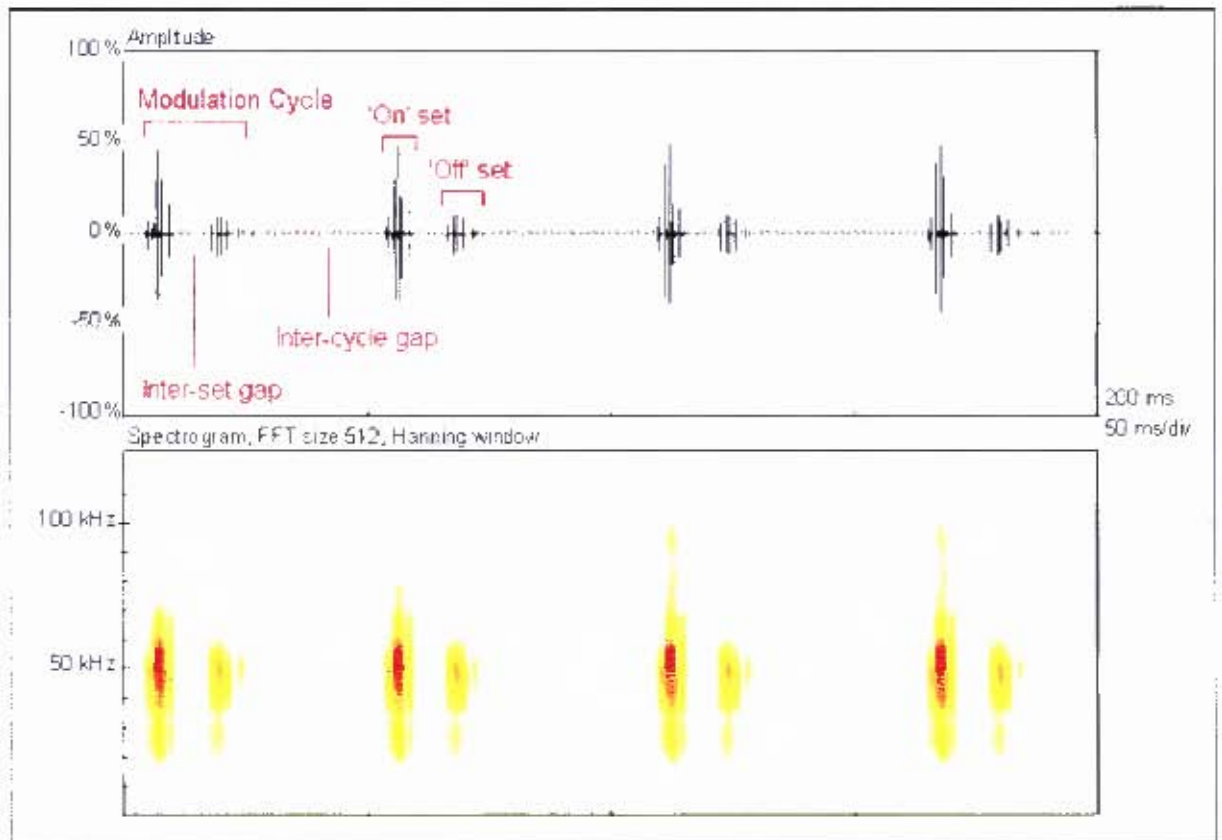


Figure 5: A 200 ms section recording of clicks emitted by *P. tephinata* consistent with pattern one. The top graph gives the amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Note. All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

The intensity difference between 'on' and 'off' clicks combined with spacing patterns caused by the short inter-set gap and long inter-cycle gap could be interpreted as loud click, soft click, space, loud click, soft click, space. The difference in click repetition rate between the two sets makes them even more distinguishable, reinforcing the different

phases of the pattern. In addition to pattern one, more than eight other patterns were identified, but only five of which were common, i.e. produced more than three times in at least three individuals.

Pattern two (Figure 6) was also found in all four species of clicking Arctiids, but was not as abundant as pattern one (only 5 – 15% depending on species) and it was not found in all individuals. Pattern two differed from pattern one by having a significantly larger inter-set gap (at least double, Table 1) than inter-cycle gap (Two-way independent T-Test: *S. montana* $T = 4.4$, $DF = 18$, $P < 0.001$; *P. tephinata*, Mann Whitney U-Test: $Z = 2.9$, $DF = 10$, $P < 0.005$). In pattern one the inter-set gap was significantly smaller than the inter-cycle gap. In pattern two it is the reverse. The quick succession from active to passive buckling with longer inter-cycle gap in pattern one relative to pattern two could be explained by pattern one being produced by the buckling of a single tymbal and pattern two being produced by the two tymbals on either side buckling alternately. If so, then in pattern two either the moth is alternating between tymbals quicker than the transition between active buckle ('on' set) to passive return buckle ('off' set); or after the active buckle ('on' set) the coxal branch of the basalar muscle remains contracted for a short while before it is relaxed to produce the passive return buckle ('off' set) (Skals and Surlykke, 1999). This gives a pattern of buckle ('on' set), pause (inter-set gap), passive return buckle ('off' set), short inter-cycle gap and buckle ('on' set) (Figure 6). The ability to produce pattern two by one of the tymbals or by alternating between the left and right tymbal alters the density of the pattern, adding a further component of variation.

Pattern two produced by *P. tephriata* varied slightly to pattern two produced by *S. montana*. With *P. tephriata* the inter-set gap was of similar duration to that of pattern one, but had a much shorter inter-cycle gap (Table 1), which suggests that pattern two was produced mainly by quick alternation between the two tymbals. In the case of *S. montana* the inter-set gap was almost double the average duration, while the inter-cycle gap was around a third of the average duration to that found in pattern one (Table 1), which suggest pattern two was produced by both quick alternation between tymbals and basalar muscle contraction. In addition to this difference between the two species, pattern two in *P. tephriata* had a significantly higher (more than double, Table 1) click repetition rate for the 'on' set compared to the 'off' set (Two-way independent T-Test: *P. tephriata*, $T = 3.5$, $DF = 10$, $P < 0.01$), while *S. montana* showed no such difference (Two-way independent T-Test: *S. montana*, $T = 1.3$, $DF = 18$, $P > 0.2$)

The period of time that a moth produced pattern two was significantly shorter than that of pattern one (*S. montana*, mean of 252.3 ± 137.6 and 475 ± 249.8 ms, respectively; Two-way independent T-Test: $T = 2.7$, $DF = 23$, $P < 0.02$; *P. tephriata*, mean of 178.6 ± 59.6 and 522.4 ± 373.5 ms, respectively; Two-way independent T-Test: $T = 2.57$, $DF = 14$, $P < 0.03$). This could be due to the higher energetic cost of pattern two, causing the moth to tire quicker which would shorten the sequence duration. When pattern two is produced by a quick transition from one tymbal to the next the number of clicks per unit time increases (i.e. increased number of muscle contractions).

When pattern two is produced by one tymbal the moth has to keep the coxal branch of the basalar muscle contracted to allow for the long inter-set gap. Both methods of producing pattern two have higher energetic cost than pattern one. This would also explain the high number of individuals (80% i.e. 24 of the 30 tested) shifting between pattern one and two within a single click train, with the most common setup being between pattern one and a high density pattern two. This can occur by decreasing the alternation time between the two tymbals changing pattern one into pattern two; or if pattern one is being produced by one tymbal and pattern two by the introduction of the second tymbal in a quick succession to the passive return buckle ('off' set) of the other tymbal.

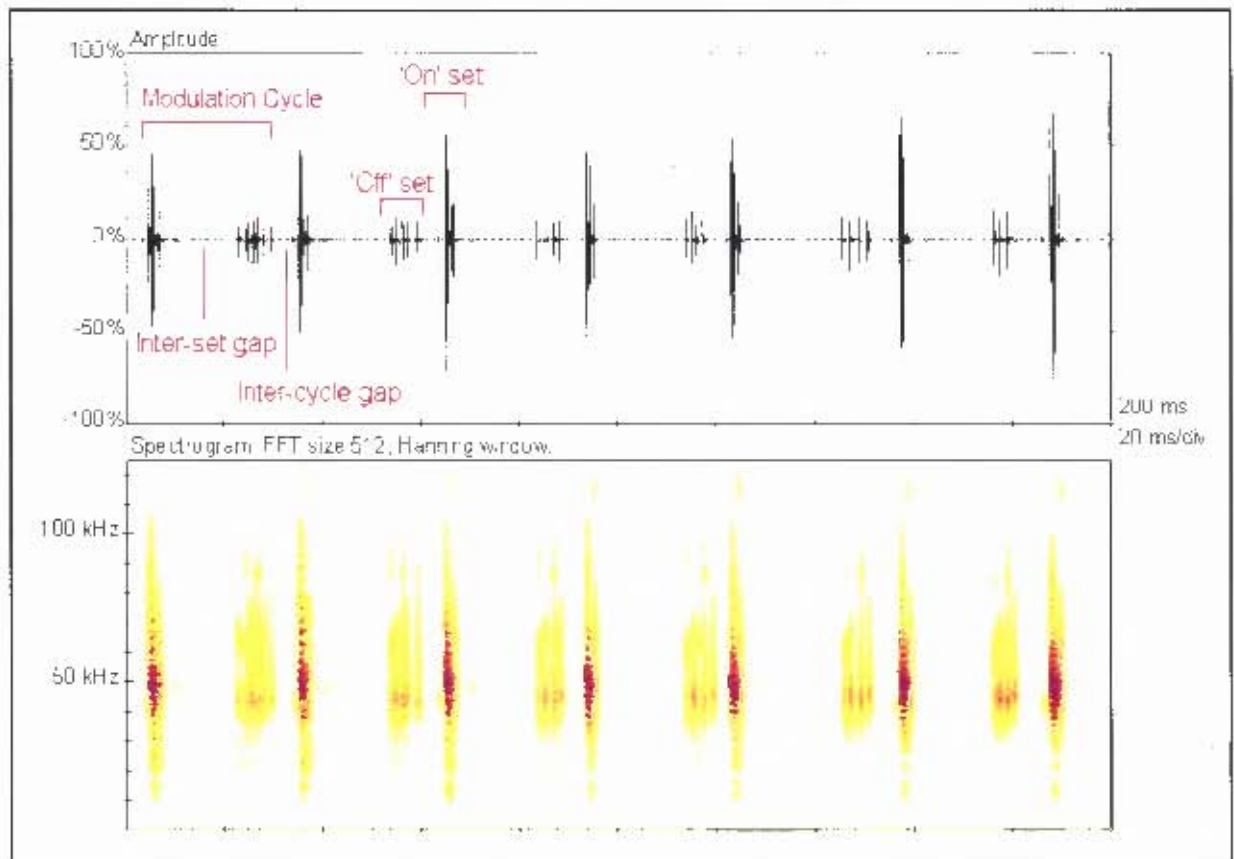


Figure 6: A 200 ms section recording of clicks emitted by *P. tephinata* consistent with pattern two. The top graph is amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks, therefore, any direct data taken from this graph may show small variations relative to the results.

As in pattern one the 'on' clicks had a higher intensity (around 10 dB or higher, Table 1) than the 'off' clicks (Two-way independent T-Test: *S. montana*, $T = 2.9$, $DF = 18$, $P < 0.02$; *P. tephinata*, $T = 3.3$, $DF = 10$, $P < 0.01$). This intensity difference combined with spacing patterns caused by the long inter-set gap and short inter-cycle gap could be interpreted as loud click, space, soft click, loud click, space, soft click. Using the biggest space (silent phase) as the starting point, the intensity pattern of pattern one would be silence, loud click ('on' set), soft click ('off' set), silence (inter-cycle gap), whereas the

intensity pattern of pattern two would be silence, soft click ('off' set), loud click ('on' set), silence (inter-set gap). If intensity is an important factor in the bats perceptual analysis, then pattern two would be distinct from pattern one.

Only eight individuals from *S. montana* and three from *P. tephriata* produced pattern three (Figure 7). I obtained good quality recordings for five individuals of *S. montana* and one of *P. tephriata*. Pattern three is the most homogenous of all the patterns I observed with no significant differences between inter-set gap and inter-cycle gap (Table 1; Two-way independent T-Test: *S. montana*, $T = 0.4$, $DF = 8$, $P > 0.6$) or in intensities between 'on' clicks and 'off' clicks (Table 1; Two-way independent T-Test: *S. montana*, $T = 0$, $DF = 8$, $P > 0.9$). In other words, the cycle patterns progress from active buckle ('on' set) to passive return buckle ('off' set) with no clear differences between the sets or timing of the pattern (Figure 7). The only method to identify a set is by expanding the time axis to show the wave pattern of a click within a set i.e. whether amplitude starts with a downward ('on' set) or upward ('off' set) oscillation.

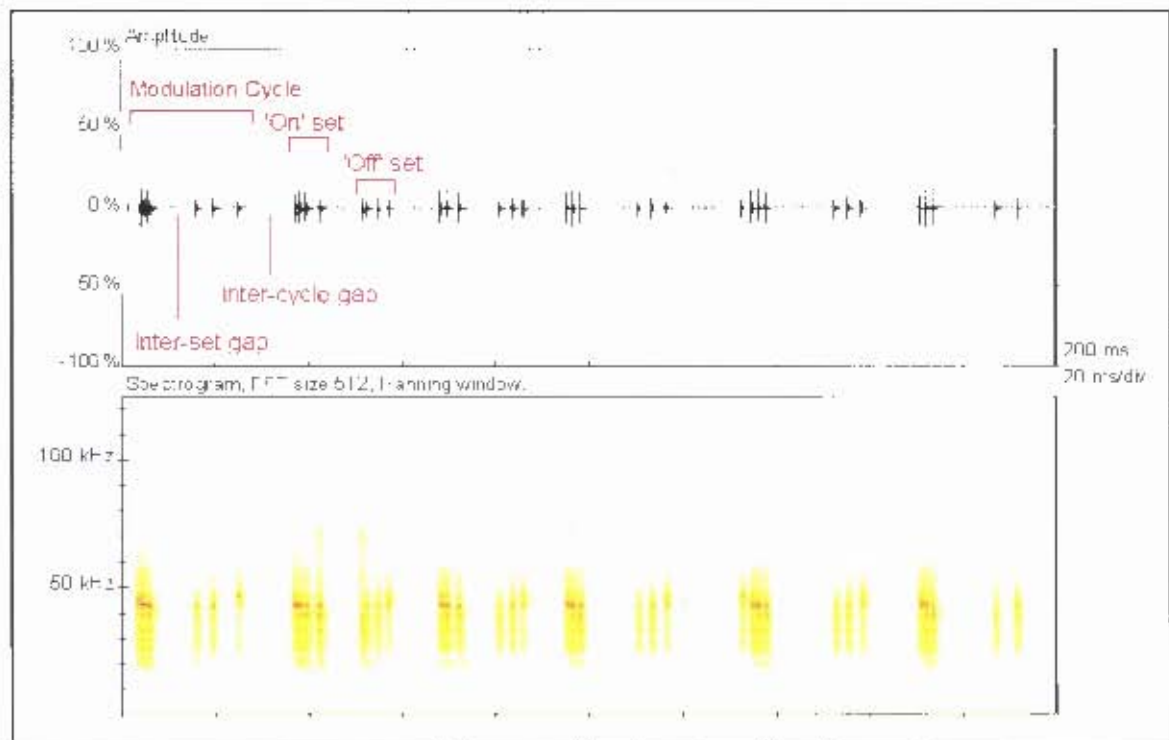


Figure 7: A 200 ms section recording of clicks emitted by *S. montana* consistent with pattern three. The top graph is amplitude in percentage and the bottom graph is a spectrogram with frequency as the y-axis and time on the x-axis. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

One can regard patterns one and two as having a two set cycle, whereas pattern three would have a single set cycle because the 'on' sets are the same as the 'off' set (Figure 7). If one compares the intensities of 'on' clicks of pattern one to 'on' clicks of pattern three one observes that pattern three has a significantly lower intensity (see Table 1; Two-way independent T-Test: *S. montana*, $T = 3.1$, $DF = 16$, $P < 0.008$). However, no significant difference is found between 'off' clicks from pattern one to 'off' clicks from pattern three (Table 1; Two-way independent T-Test: *S. montana*, $T = 0.7$, $DF = 16$, $P > 0.5$). This means that the intensities of 'on' clicks are lowered to a similar level to that of 'off' clicks to produce this single set cycle.

Pattern four (Figure 8) was relatively rare, occurring in only six individuals from *S. montana* and two from *P. tephinata*, with only four individuals of *S. montana* providing us with calls of sufficient quality to be able to use with confidence. If one regards patterns one and two as having a two set cycle and pattern three as a single cycle, then pattern four would have a three set cycle, because there are three distinct sets (Figure 8). The first 'on' set from the active buckle is followed jointly by the passive return buckle coupled with active buckle of the opposite tymbal forming a mixed 'on'/'off' set. In other words, the moth relaxes the coxal branch of the basalar muscle of one tymbal at the same time it contracts the other tymbal. This is then followed by the passive return buckle of the remaining tymbal, hence the three set cycle (Figure 8A). As would be expected the mixed set had significantly more clicks, on average twice the number of clicks (Table 1 and Figure 8A) than the first set ('on' clicks) (*S. montana*, Two-way independent T-Test: $F_{(1,6)} = -5.6$, $P < 0.002$) and third set ('off' clicks) (*S. montana*, Two-way independent T-Test: $T = -3.7$, $DF = 6$, $P < 0.01$). The set duration of the mixed set was also significantly longer than both the other two sets (*S. montana*, First set: Two-way independent T-Test: $T = -5.1$, $DF = 6$, $P < 0.003$; Third set: Two-way independent T-Test: $T = -5$, $DF = 6$, $P < 0.003$).

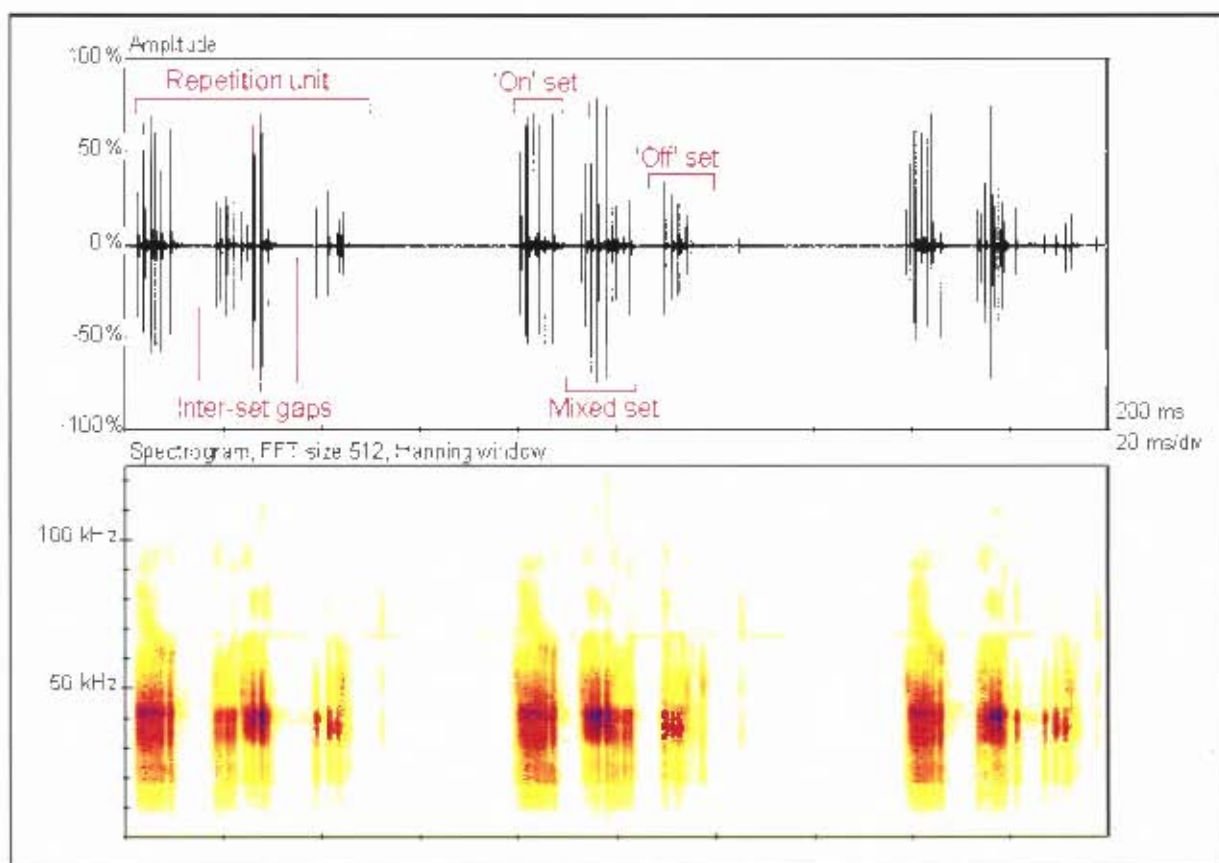


Figure 8: A 200 ms section recording of clicks emitted by *S. montana* consistent with pattern four. The top graph shows amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Notice the existence of a mixed set: causing pattern four to have a three set repetition unit. The inter-cycle gap now occurs only once for every two active buckles and passive return buckles (i.e. left and right tymbal) due to the mixed set. The modulation cycle is not labeled because it is interrupted by the formation of the mixed cycle caused by the 'off' set of one tymbal being interrupted by the 'on' set of the other tymbal. Note: All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

The repetition unit was used instead of the modulation cycle (set of 'on' clicks and a set of 'off' clicks that is produced by the same tymbal) because the passive return buckling ('off' set) (Figure 8A) fuses with the active buckling ('on' set) of the other tymbal eliminating the modulation cycle. This occurs once every two cycles, which is referred to

as a repetition unit (Figure 8A). The significantly longer gaps between the repetition units than between the inter-set gaps (Table 1; *S. montana*, Inter-set gap one: Two-way independent T-Test: $T = -8.5$, $DF = 6$, $P < 0.001$; Inter-set gap two: Two-way independent T-Test: $T = -8.9$, $DF = 6$, $P < 0.001$) help distinguish the repetition unit.

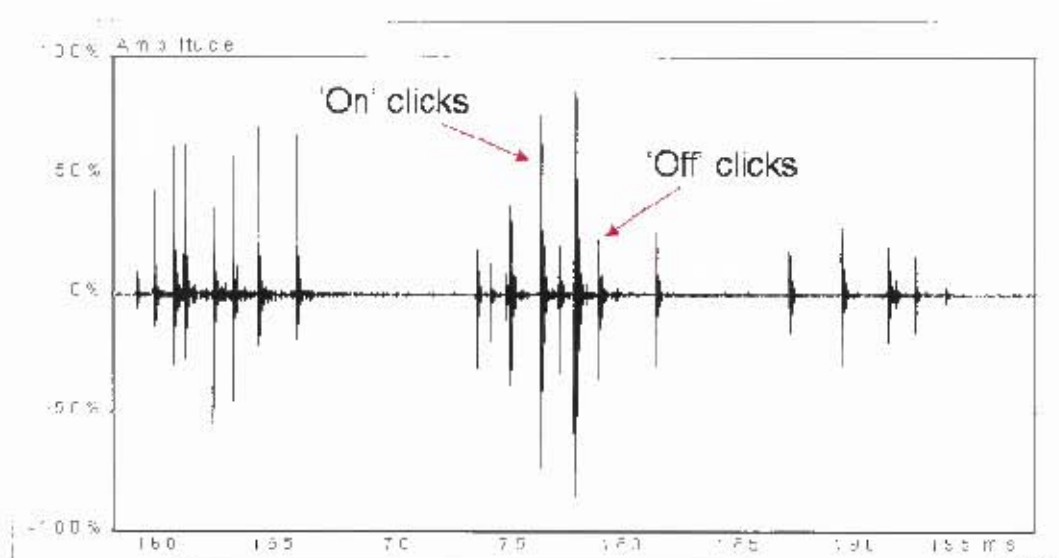


Figure 8A: A 30 ms section recording of clicks emitted by *S. montana* consistent with pattern four. This represents a single repetition unit showing the middle set of clicks which is composed of both 'on' clicks and 'off' clicks.

Pattern five (Figure 9) was produced by eight individuals of *S. montana* and two individuals of *P. tephriata*. Unfortunately only four individuals of *S. Montana* produced clicks of high enough quality to be used in the statistical analyses. As with pattern four, pattern five is a three set pattern, with the active buckling of one tymbal, shortly followed by the active buckling of the opposite tymbal. This produced two 'on' set clicks before the passive return buckling of the two tymbals, which occurred in immediate succession forming one large 'off' set (Figure 9A). Due to the consecutive passive return buckling of the two tymbals one large 'off' set is formed with no inter-set gap.

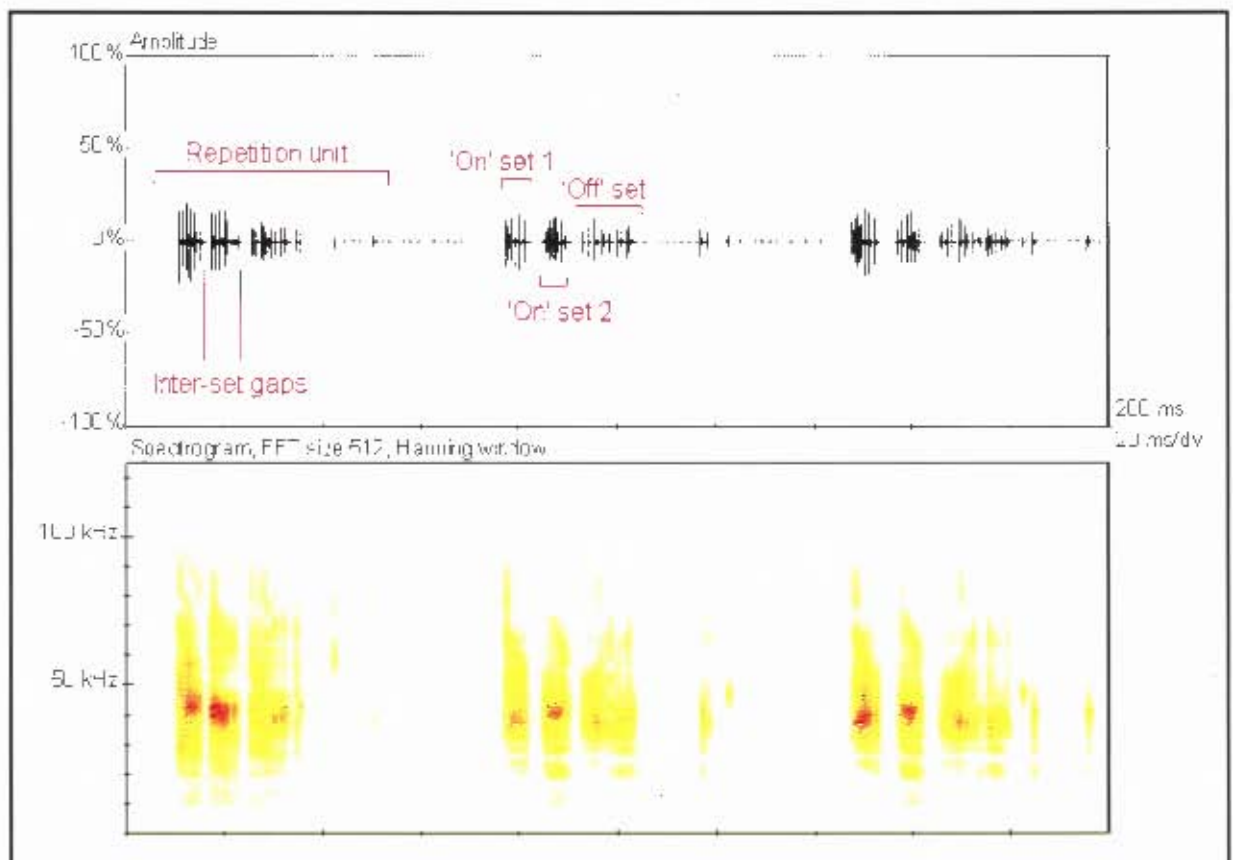


Figure 9: A 200 ms section recording of clicks emitted by *S. montana* consistent with pattern five. The top graph is amplitude in percentage and the bottom graph is a spectrogram with frequency on the y-axis and time on the x-axis. Notice the existence of two 'on' sets caused by the successive active buckling of the two tymbals. The large 'off' set is due to the passive return buckle of both tymbals. The modulation cycle is not labeled because it is interrupted by the 'on' set of the opposite tymbal. Note: The lower apparent amplitude relative to the other patterns is due to lower recording levels and is not characteristic of pattern five. All the recordings and analysis of the clicks were done with a sampling rate of 500 kHz. However, this spectrogram is presented with a sampling rate of 125 kHz to remove the empty space of the unused higher frequencies allowing for a larger and clearer representation of the clicks.

As expected the single 'off' set was significantly longer than any of the two 'on' sets (Table 1; *S. montana*; 'On' set one: Two-way independent T-Test: $T = -4.89$, $DF = 6$, $p = 0.00273$; 'On' set two: Two-way independent T-Test: $T = -4.41$, $DF = 6$, $P = 0.00452$). The number of clicks in the single 'off' set was also significantly higher than in the two

'on' sets (Table 1; *S. montana*; 'On' set one: Two-way independent T-Test: $T = -4.1$, $DF = 6$, $P < 0.008$; 'On' set two: Two-way independent T-Test: $T = -3$, $DF = 6$, $P < 0.03$). As for intensity both the 'on' sets had intensities that were on average 6 dB higher than the long joint 'off' set (Table 1). However, this difference is smaller than usual and was not significant (Table 1; *S. montana*; 'On' set one: Two-way independent T-Test: $T = 1.7$, $DF = 6$, $P > 0.1$; 'On' set two: Two-way independent T-Test: $T = -1.5$, $DF = 6$, $P > 0.1$).

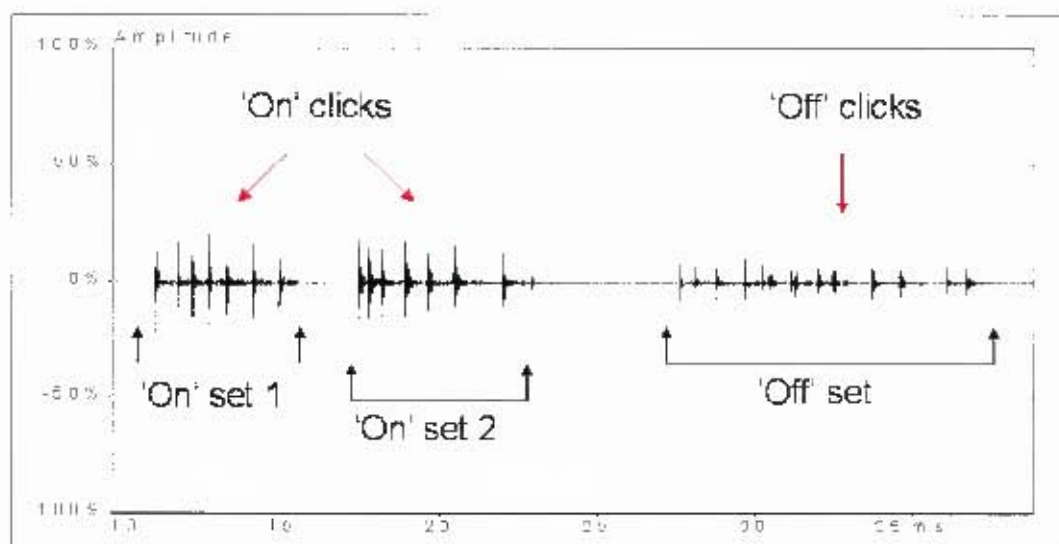


Figure 9A: A 30 ms section recording of clicks emitted by *S. montana* consistent with pattern four. This represents a single repetition unit showing the two 'on' sets and the large 'off' set.

In addition to these five patterns, other less common patterns were observed (Figure 10). Three of these patterns were found in both *S. montana* and *P. tephriata*, but the recordings were of too poor a quality to allow the identification of 'on' or 'off' sets with confidence. These three patterns were variations on pattern five (Figure 10), the most common being found in 4 individuals of *S. montana* and 5 individuals of *P. tephriata*; and the rarest found in 3 individuals of *S. montana* and 2 individuals of *P. tephriata*.

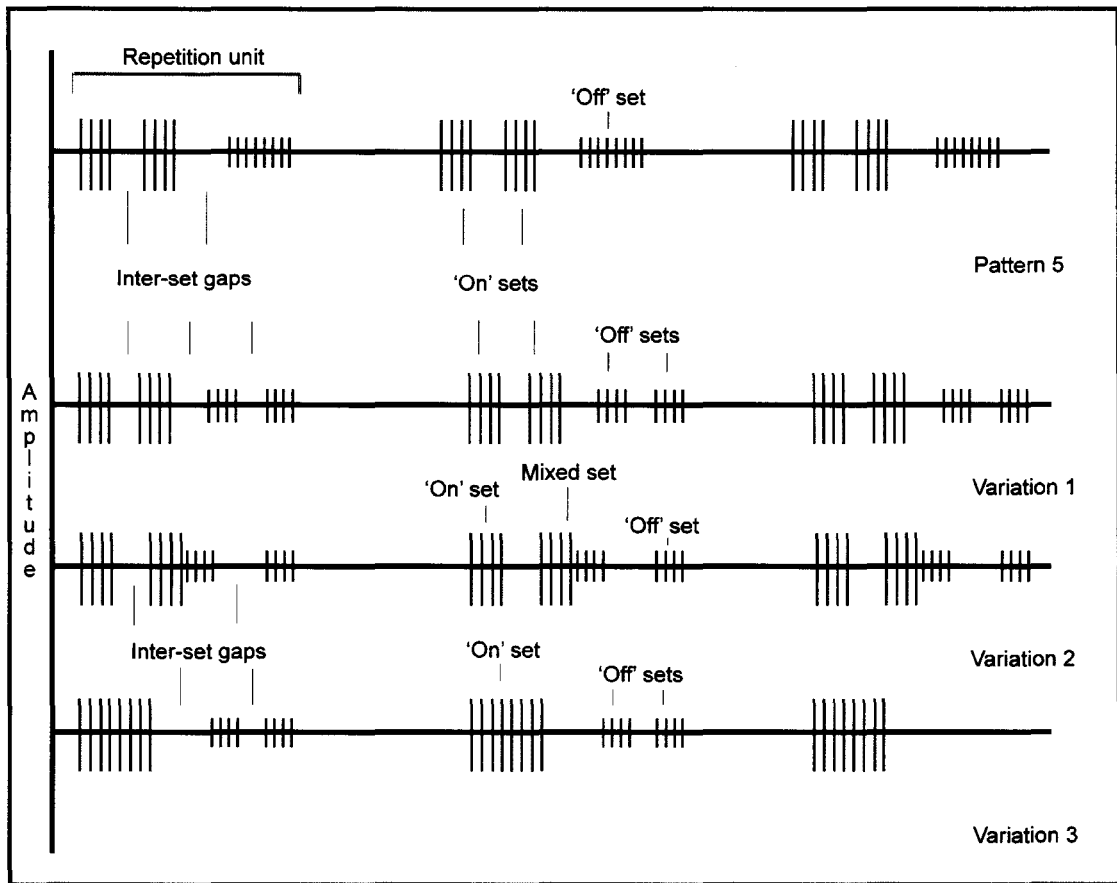


Figure 10: Diagram of pattern five with three variations that were observed in both *S. montana* and *P. tephinata*. Variation 1 differs by have two “off” set instead of one large ‘off’ set. Variation 2 has the passive return buckle of one tymbal directly follow without a gap by the active buckle of the opposed tymbal. Variation 3 has the two active buckles joined to form one large ‘on’ set.

The remaining patterns often occurred in one or two individuals only and were composed of two or three cycles. Not only do the low sample sizes make it impossible to do any statistics, but there is also too much variation and lack of any apparent structure. These clicks could be pattern transition clicks or fatigue clicks as they occurred more often toward the end of long recordings. One type of click that was common throughout all individuals, but can’t be considered a pattern, was a single loose click found in-between click trains. It’s still unclear how these clicks are produced, because striated tymbals should produce multiple clicks per buckle whereas smooth

tymbals should produce single clicks. Microscopic examination of the tymbals of these two species show that that the tymbals are striated. This is supported by the fact that all of the sets in the different patterns were composed of multiple clicks. The intensities of the single loose 'on' clicks were significantly lower than the intensity of the 'off' clicks in pattern one (*S. montana*, 59.1 ± 7.5 dB and 66.4 ± 7.1 dB respectively: Two-way independent T-Test: $T = -3$, $DF = 26$, $P < 0.006$, *P. tephinata*, 60.1 ± 5.97 dB and 69 ± 7.5 dB respectively: Two-way independent T-Test: $T = -3$, $DF = 18$, $P < 0.008$). One possibility is that these clicks are produced indirectly through extreme body movements while being held during the sound recording. Extreme abdomen movements were noted while recording. This could cause light buckling of the tymbals, hence the low intensity and high random inter click gaps. Unfortunately the scientific literature is silent on this matter. However, if these clicks are produced in flight then this further increases the variation of clicks produced by these moths.

Discussion

Moths were one of the most abundant food sources available to echolocating, insectivorous bats at Algeria Forestry Station (73%). Previous studies have suggested that the higher survival rate of hearing moth families have allowed hearing moths to out-compete earless moths in areas with high bat predation (Fenton and Fullard 1979; Fullard 1990; Pavey and Burwell 1998; Schoeman and Jacobs 2003). The data from this study supports this view. At Algeria Forestry Station hearing moth families constituted 92.7% of all moths caught. Even though this study was done during two summer months and for a relatively short period the study site has been sampled for moth diversity for the past 5 or more years and in different seasons (e.g. Schoeman and

Jacobs 2003; Jacobs *et al.* 2005; Schoeman 2006). My data on the relative abundance of clicking moth families is supported by data from these studies and differences are confined to morpho-species that are in rare non-hearing families, which are very unlikely to produce clicks, and constitute a very small proportion of the morpho-species richness at Algeria Forestry Station. I therefore am confident that the relative abundance of clicking species reported here are unlikely to change appreciably with more extensive sampling.

Proportions of clicking moths

If moth clicks jammed bat echolocation through interference with the bat's perceptual system it would be a highly successful strategy conferring maximum selective advantage on moths that clicked over moths that did not click. One would expect this trait to spread through the population rapidly and clicking moths should therefore occur in higher proportions than moths that could hear but did not click. The former would enjoy the protection of both early warning of a bat's attack as well as the disruption of the bat's perceptual system. The latter, on the other hand, would only be protected by early warning of a bat's attack and would still have to behave appropriately to avoid being taken. However, I found that clicking moths constituted only a small proportion (2.3%) of the total moth abundance, even less than non-hearing moths.

Aposematism requires that the conspicuous signal be associated with a negative stimulus such as unpalatability. Many moths from the family Arctiidae have been shown to be unpalatable (Dunning 1968, Coutts *et al.* 1973, Rothschild 1985, Dunning and Kruger 1995), and considering that colour is not an effective signal at night, sound

would be a viable mechanism to advertise unpalatability to a predator that uses hearing as its main sense for detecting prey. The possibility that moth clicks function as an aposematic signal is supported by the fact that four of the five species caught were of the family Arctiidae. However, in the case of aposematism the increased survival advantage is only achieved once the bat population has learned to associate moth clicks with unpalatability. Presumably even if a moth survived an attack by a naïve bat, its survival and reproduction would be sufficiently adversely affected so that predator learning involved some cost to the moth. Thus, for aposematism to become established, the moth population would have to be large enough to withstand the initial cost of bat learning. Once learning has occurred, aposematism would have similar dynamics as jamming. That is, moths will have increased survival from hearing as well as from being unpalatable. Studies on visually-based aposematism have shown that high densities of clicking and unpalatable moths are vital to the effectiveness of this strategy (Gegliardo and Guilford 1993; Kapan 2001; Speed 2001). However, the proportion of clicking moths (i.e. 2.3%) may not be large enough to overcome the cost to the moths of predators learning the association between moth clicks and unpalatability because bats would encounter clicking moths very rarely. Furthermore, there is evidence that some clicking moths do not perform evasive flight maneuvers in response to a bat attack as do moths that rely solely on hearing (Evans 1983; Dunning and Kruger 1995). The cost of the aposematic strategy at the initial low densities when the strategy first arises would be higher than that for hearing moths, preventing the establishment of an aposematic strategy.

The Startle Hypothesis proposes that moth clicks surprise the bat because they are unexpected sounds during the bat's attack. However, bats will habituate to these sounds if they are encountered regularly (Bates and Fenton 1990). When just a few moths are using this strategy they are at a selective advantage, increasing the survival rate and the relative proportion of moths using this strategy. Once the strategy becomes common, the bats habituate and aren't startled by the sound because it occurs so often. The clicks' conspicuousness now becomes a cost and decreases the survival of these clicking moths, decreasing their proportions within the population. The startle strategy is therefore density dependent, being advantageous when in low proportions but detrimental when in high proportions. This density dependence would keep the strategy fluctuating at low proportions and the startle hypotheses may therefore explain the low proportions of clicking moths I found at Algeria Forestry Station.

Clicking parameters, diversity and variation

In the case of jamming the duration of the moth clicks are too short for the clicks to resemble echoes (Fullard *et al.* 1994). However, Fullard *et al.* (1994) hypothesized that the clicks may produce a ringing effect in the internal ear of the bat, lasting as long as the integration time of the ear and therefore increasing the effective duration of the clicks (Fullard *et al.* 1994). Due to the short inter-pulse intervals of the clicks (means as low as 0.5 ms), the ringing effect would cause one click to merge into another creating a sound with a total duration equivalent to the set duration, which averaged between 6.5 - 9.5 ms (*S. montana*) and 3.5 – 6.5 ms (*P. tephriata*). If this does occur, the increased duration would exceed the integration time of the ear (Fullard *et al.* 1994) and the clicks

would no longer resemble an echo from one of the bat's terminal phase calls. The manner that the clicks are delivered also differs to a bat's terminal phase. A bat's terminal phase is a continuous sequence of pulses, while the moth's clicks are sets of clicks with large gaps between each of the cycles and sometimes even between the active buckle and passive return buckle of the tymbal. The inter-pulse interval of the clicks, the set cycles and general patterns are also very variable and do not resemble the terminal phase of a bat's echolocation sequence. For example *T. aegyptiaca*, the most common bat at Algeria forestry station, has an average pulse duration during the terminal phase of the feeding buzz of 2.0ms (± 0.3 ms, n = 12 randomly selected) and an average interpulse interval of 5.1ms (± 0.8 ms, n = 12 randomly selected). The moth with the highest click duration (*M. natalensis*) has an average of 0.5ms, while all four clicking arctiids have click duration averaging around 0.2ms (Table 1). The differences are also clear with the inter-pulse interval with the values averaging almost always below 2.0ms. These differences and the manner that the clicks are delivered would most likely not create a neural response similar to that evoked by an echo. This is supported by Tougaard *et al.* (1998) who found that the neural response evoked by moth clicks is different to the neural response evoked by echoes from the bat's call.

Click trains produced by *Marcopoliana natalensis* (Sphingidae) were long with average to high numbers of clicks at a high repetition rate and a high maximum duty cycle of 11.29%, all of which would maximize the probability that some of the clicks would fall within the critical time window of 1 to 3 ms before onset of the returning echo (Simmons *et al.* 1989; Tougaard *et al.* 1998). However, I only caught males of this species and it is unknown if females also click. If females do not click then it is possible

that the clicks produced by this species does not function in the context of bat predation but rather in the context of mate attraction.

With the exception of *E. brunneotinctum*, where only one female was caught, I recorded clicks from both males and females for the remaining clicking moth species. In these species the maximum duty cycle ranged from 3.46% to 7.84%, which is below the 10% or above predicted to be a reasonable duty cycle to support jamming (Barber and Conner 2006). Furthermore, the proviso that for clicks to function in jamming they must be emitted in the terminal phase of the bat's attack sequence, which is common to both versions of the Jamming Hypothesis, is apparently not met by most clicking arctiid moths. This has led to the conclusion that it is unlikely that moth clicks function by jamming bat echolocation (Barber and Conner, 2006).

One of the central predictions of the aposematic hypothesis is that of signal convergence and low intra- and interspecific variation in the clicking parameters. All five species that were found to click had different mean peak frequencies and click intensities. In terms of intraspecific variation each species had at least 3 patterns, with some individuals having as many as 5 patterns, in one recording. These differences are marked and contradict the prediction of convergence.

The extreme variation in clicks within the same moth, between moths of the same species and between species, supports the prediction of the startle hypothesis that clicks should be highly variable. Such variable signals will hinder habituation by the predator to the signals, ensuring that the signals remain novel. It is possible that using

tactile rather than acoustic stimulation which is easier to standardize and is the stimulus that clicking moths are most likely to respond to in a natural situation, may have introduced some variability into the moths' response. However, I took care in standardizing the tactile stimuli and the way I handled all moths. It is unlikely therefore that the high level of variability in moth clicks reported here was caused by changes in the stimulus.

Furthermore, insectivorous bats repeatedly capture insects in their membranes then transfer them to their mouths (Webster and Griffin 1962; Bell and Fenton 1984). Tactile stimulation is therefore probably as relevant to the interaction between bats and moths as is acoustic stimulation. Dunning and Krüger (1995), also working in South Africa, reached the same conclusion after testing nine clicking species (125 individuals in total) all of which reacted to both ultrasound and tactile stimulation in the same way. In a study by Barber and Conner (2006) during which 130 species of arctiids were surveyed for sound production, 84 species produced ultrasonic clicks in response to tactile or both tactile and acoustic stimulation. Only 3 species reacted solely to ultrasonic stimulation.

It is possible that moth clicks have other functions besides startle. For example, if moths are toxic, startle may be the main function at low abundance and aposematism the main function at high abundance. It is also possible that moth clicks are used against other predators and no single hypothesis may therefore explain the role of moth clicks (Fullard 1987; Bates and Fenton 1990; Fullard *et al.* 1994).

In conclusion, the low proportions of clicking moths and the extreme variability of the clicking patterns, appear to argue against the aposematic and jamming hypotheses, but appear to be consistent with the startle hypothesis. An important caveat, however, is that this study was done at only one site. It is possible that the function of clicks may differ depending on the habitat, the species diversity and abundance of clicking moths and the community structure of echolocating bats. The general applicability of my results will therefore depend on whether similar results are obtained at different sites and in different habitats.

CHAPTER 3

Modelling bat predation on moths

The ability of hearing moths to detect the ultrasonic echolocation of bats that prey upon them has given these moths a selective advantage over non-hearing moths. This selective advantage, resulting in reduced predation, should be reflected in the higher numbers of species or abundance of hearing moths in the total moth population inhabiting an area. Fullard (1990) reported that up to 95% of moths in both temperate and tropical climates were hearing. Pavey and Burwell (1998) sampled tropical and subtropical sites throughout Australia and found that at least 80% of moths were hearing. In Southern Africa Fenton and Fullard (1979) estimated that 85% of moths are hearing, while Schoeman and Jacobs (2003) showed that hearing moths constituted 90% of the total moth population at a site in South Africa.

Even though many species of hearing moths produce ultrasonic clicks in response to bat echolocation (Blest *et al.* 1963; Blest 1964; Dunning and Roeder 1965) few studies have looked at the actual proportions of clicking moths in moth populations and how ultrasonic moth clicks function at reducing bat predation. The realized selective advantage from ultrasonic clicks is dependent on whether these clicks have a jamming,

aposematic or startle function and could be reflected in the higher proportions of clicking moths in moth populations.

Aims

In this chapter mathematical models are used to explore the selective advantage of each of the proposed functions of clicking under different scenarios and are then compared to results obtained from field data. Initially, the dynamics of each model was independently tested. Secondly, a steady state equilibrium (stable point) of the moth population abundance was used as an indicator of the effects of the different parameters (e.g. reproductive and predation rates) on the model outputs. Moreover, for the different parameter settings the level of success/stability was compared between each of the models.

Materials and Methods

Moth and Bat Sampling

Bats were caught using mist nets placed around forest edges, across and along the riverbed (the Rondegat River) and across suspected roost entrances. Mist nets were placed half an hour before dusk and checked regularly with each net allocated a code so that the type of habitat in which each bat was caught was tracked. The bats caught were kept in cotton bags (12 cm x 20 cm) for a maximum period of 24 hours. Only adult bats were used in the analyses. Adults were distinguished from the sub-adults by the absence of cartilaginous epiphyseal plates in the finger bones, detected by transilluminating the wings (Anthony 1988).

Bats were marked by the holes left after taking biopsy punches (to be used as tissue samples in a separate genetics study) from the wing membrane nearest to the body. Bats were marked to avoid pseudoreplication. Body mass to the nearest 0.5g and forearm length to nearest 0.1mm were measured on each bat caught. Bats were identified using the taxonomic keys in Skinner and Smithers (1990) and Taylor (2000). When echolocation behaviour of a species was known, it was used to confirm the species identification. Echolocation calls were obtained using a Pettersson bat detector D980 (Pettersson Electronik AB, Uppsala, Sweden) with an anti-aliasing filter (F2000, Pettersson Electronik AB, Uppsala, Sweden). The Pettersson bat detector was linked to a HP nx7010 notebook computer via a DAQCardtm – 6062E highspeed soundcard (National Instruments, Austin Texas).

Mathematical Modelling

Modelling a biological system mathematically reduces the system to its basic parameters. More complex parameters are only added if it is essential to a meaningful biological interpretation. Differential equations were used to model moth population sizes as a function of time under the assumption that moths were all earless and a separate model under the assumption that they could all hear. These were compared with the three main models for startle, aposematism and jamming. This allowed one to distinguish the effect of hearing ability from the effect of moth clicks on moth population size in comparison to bat predation. The models also allow for the determination of conditions under which each of the functions of moth clicks lead to stable moth population sizes and at what numbers. The function that led to stable moth populations,

under model parameters that mimicked a real life situation, was assumed to be the most likely biological function of moth clicks.

The most common starting point for modelling population dynamics (i.e. population size, population rate of change, stable points and parameter interaction) is the Schaefer model (Krebs and Davis 1993) and is mathematically expressed as:

$$DN/DT = R N (1 - N / K) - P$$

Equation 1.0

Where:

- DN/DT — is the (instantaneous) change in moth population size over time.
- R — is defined as the “maximum rate per capita of growth” i.e. growth or net reproductive rate which is assumed constant.
- N — is the moth population size at time T.
- K — is the carrying capacity and is defined as the maximum number of moths that a specific environment can sustain if left undisturbed.
- P — is the fixed number of moths removed from the population by bat predation. This predation rate is calculated using a moth population that does not have any defence strategies.

Note: The integration method used was Runge-Kutta and all parameters are in Appendix I and all equations are in Appendix II.

This modelling approach assumes that the growth rate is zero at two points ($N = 0$ and $N = K$). Between 0 and K the growth rate increases exponentially until K is reached, thereafter it is constant, until bat predation occurs resulting in a decrease in population size. When exploring simulations N was set equal to K to allow the moth population time to reach the steady state equilibrium (stable point). It was assumed that the environment was homogenous and that all moths had the same chance of reproducing and/or being preyed upon (Varley *et al* 1973; Pielou 1977; Edelman 1988). The closest natural biological situation to this is that of a moth in an open-air environment being preyed upon by an open-air foraging bat. For example an open air specialist such as a molossid bat hunting a moth relatively far from vegetation or other obstacles.

The population growth rate (R) was obtained from the literature (Schwerdtfeger 1941; Elkinton and Liebhold 1990; Sharov and Liebhold 1998; Selas *et al* 2001). Due to the wide range of growth rates of moth populations presented in the literature, from 0.005 to 5 percent (Schwerdtfeger 1941; Elkinton and Liebhold 1990; Sharov and Liebhold 1998; Selas *et al.* 2001), different R values were used for the simulations. Repeated simulations with different R values not only covered the range of growth rates possible within a moth population, but allowed a better understanding of how R affects the moth population under different conditions. Although it is recognised that values of R vary in a real system (due to seasons, food availability, species etc...), I considered them as an average based on the assumption that over an infinite time period and within a moth population they are normally distributed.

Caterpillars are the larvae of Lepidoptera, and in most forests of the world they consume more living leaves than all other animals combine (Janzen 1988). Therefore, carrying capacity (K) was calculated by determining the biomass of the area and estimating the number of caterpillars the areas biomass can sustain based on the average biomass requirement for a caterpillar to develop into an adult moth.

The vegetation at Algeria Forestry Station is predominantly natural mountain fynbos, which is dependent on fire to germinate and resprout. Natural fires in the fynbos biome occur within 6 - 40 year rotation periods (Kruger 1979, Kruger and Bigalke 1984) and have a major influence on the biomass of the area. Fynbos biomass increases with the increase in the fire rotation periods from as low as 220 g/m² for a 4 year old plot (Kruger 1977) to as high as 7600 g/m² for a 37 year old plot (Wilgen 1982). Another important factor for determining biomass is the species composition and diversity. To assess the age of the vegetation in the area, and determine a broad species composition, five transits on each side of the valley along the 10 km range were used. Each transit was around 750 meters long and consisted of six 3 m² quadrates every 150 meters. For each quadrate the age of the plot and the plant families present were determined. The age of the plot was determined by looking at the fire records at the Algeria Forestry Station offices. The fires only reached certain areas and only a broad knowledge of where the fires reached was available. Therefore this data was supplemented by looking at the growth patterns of specific fynbos genera. For example *Leucadendron* spp. take 3 to 4 year to produce its first cones and then produces cones once every year (Jordaan 1981). Cones leave a scar on the branch from which they have dropped and new branches grow from this scar. By following a branch tip to the base of the plant

one can count the scars/branching points and determine the age of the plant (i.e. age of the plot).

This method for obtaining carrying capacity (K) is biased toward overestimates as it assumes that only caterpillars are consuming the resource (i.e. maximum carrying capacity). To compensate for this over estimate, and to allow a better understanding of the effect of K, simulations were run under three lower K values (high, medium and low). High was set at half the value of the maximum carrying capacity; medium was set at a quarter the value of the maximum carrying capacity; and low was set at a eighth of the value of the maximum carrying capacity. These intervals showed a good range of population dynamics and were reached after running the model under various carrying capacities at 100,000,000 intervals under the default setup for each of the models (i.e. reproduction rates between 1 and 2, medium predation rate PM, learning rate of 7, habituation rate of 3 and reinforcement rate of 1 per day; see rest of methods)

Predation was assumed to be constant because bats are believed to be the main predator on nocturnal, aerial insects, and most probably the only significant nocturnal aerial threat to moths. Even though there is seasonal variation in both bat and moth numbers the results from the simulations are analysed annually as the long term stability is the main output of interest. The different moth strategies will affect the level of predation; therefore, the interaction between the predation rate (P) and the defence strategy is what defines the differences between the outcomes of the five models: Earless (i.e. non-hearing) moth model; hearing moth model; jamming moth model, aposematic moth model and startle moth model.

Earless Moths

The number of moths taken by each bat species

The earless moth model is the simplest and serves as the template for the rest of the models. Earless moths cannot hear (i.e. detect) incoming bats and therefore their chance of surviving a bat attack once detected by the bat is low and survival is mainly dependant on bat error, which is usually less than 5% (Bates and Fenton 1990, pers. obs.). This assumption implies that the moths required for a specific bat's diet is similar to the number of moths it attacks. As a bat flies in it will encounter and eat the insects it encounters, and because we are dealing with a hypothetical model in which none of the moths have hearing defences the abundance of moths in the insect population will be proportional to the number of moths in the bat's diet. I therefore, used the abundance of moths obtained from light trappings (73% moths, chapter 2) as the expected proportion of moths to be found in a bats diet if all the prey was undefended.

This estimate for the earless model assumes that all insects have the same survival in relation to bat predation (i.e. all are earless). In reality there are insects other than moths that can detect bat echolocation calls (e.g. mantids, beetles and locusts). This means that these hearing insects are less available to the bat population increasing the actual proportion of earless moths in bat diets (i.e. the 73% moths determined by the light traps is an under estimate). However, at Algeria Forestry Station the insect orders that are known to have hearing species, such as mantids, beetles and locusts, were found in low proportions. Furthermore, the main method used for insect collecting was light traps, which can be biased towards moths, causing the estimate of moths in the

insect population to be possibly higher than in reality. Taking into consideration that these two main biases affect the estimate in opposing directions, and that both are believed to be relatively weak, it is assumed that the proportion of moths obtained from light traps can be a reasonable estimate of the abundance of moths in an insect population. In summary, the earless model assumes that all moths are earless, preventing these moths from avoiding attacking bats. This suggests that bat/moth encounters would equal bat attacks on moths. Therefore, if encounter rates are determined by abundance, the proportion of moths in an insect population determines the percentage of moths in a bats diet.

By taking into account the average weight of the bat species and average absorption efficiency of bats (76.5%) (Barclay *et al.*, 1991, Mclean and Speckmen 1999) one can calculate the total energy (kilojoules) needs of the bat. From this the required moth intake in kilojoules for a particular bat species can be calculated by considering the percentage of moths in the diet, which for this model is determined by the abundance of moths in the insect population (73% based on light traps, chapter 2). Thus for each of the 11 bats species found at Algeria Forestry Station the energy contribution made by moths to the each of these bat species total energy needs can be calculated as:

$$E_m = E_b * (M_d / 100)$$

Equation 1.1

Where:

E_m — is the energy requirement in kilojoules obtained from moths for a specific bat species

E_b — is the total energy requirements in kilojoules for a specific bat species.

M_d — is the percentage of moths in a specific bat species diet based on light trap abundance of moths (all bat species will have 73% in this case).

On average a bat requires 5.23 to 5.33 kJ per gram of body weight (Barclay *et al.*, 1991, Mclean and Speckmen 1999). This gives an average of 5.28 kJ per gram of body weight. The total energy requirements in kilojoules for a specific bat species can be expressed as:

$$E_b = M_s * E_{vb}$$

Equation 1.2

Where:

M_s — is the mass of a specific bat species (grams).

E_{vb} — is the average bat energy requirement of 5.28 kJ per gram of body weight.

The number of moths required to provide the energy needs of a particular bat species can be calculated by dividing the energy requirement obtained from moths for a particular bat species (E_m , calculated in equation 1.1) with the average energy value of a moth. For Algeria Forestry Station population this can be calculated from the average energetic value of moths (obtained from the literature) and the average weight of a moth at Algeria Forestry Station. The average energetic value of moths taken from the

literature is 25.2 kJ per gram (Barclay *et al.*, 1991, Mclean and Speakmen 1999). The average weight of moths at Algeria Forestry Station was calculated from a representative sample of 200 moths.

Each moth family was represented in this sample of 200 moths in the same proportion that they made up of the total number of moths caught at Algeria Forestry Station (chapter 2). The average weight per moth for each family and the total mass of each family was also calculated (Table 2). For example Noctuidae comprised 39.7% of all moths caught, which corresponded to 79 individuals in the sample of 200. These 79 individuals were randomly selected from the total moth collection obtained from Algeria forestry Station, which had been dry for six months. The moths were weighed with a Mettler Pe 360 electronic balance (Mettler Instruments, AG – Greifense, Zürich, Switzerland) with a standard error of 0.001 and then left in a drying oven for 24 hours before being re-weighed. The before and after weights showed on average less than 0.005 grams difference, with the re-weighed sample being on average slightly heavier. This unusual result could be due to the high sensitivity of the electronic balance, which can be affected by the position of the sample on the balance plate.

Furthermore, each sample was weighed twice and the difference between the repeats was similar to the difference between the before and after samples. To correct for this variation the values were rounded off to three decimal places. The same process was followed for all families except for the families that had very low numbers. These families were all of similar size (small, < 0.7 mm in length) allowing me to group them together and the corresponding number of individuals randomly selected. The

average mass of the sample of 200 moths was used as the average weight of a moth at Algeria Forestry Station in the Cederberg Wilderness Area. The number of moths required per night per bat for each species was calculated using the following equation:

$$Ps = (Abs\ eff / ((Em / Evm) / Mw)) * 100$$

Equation 1.3

Where:

- Ps — is the number of moths eaten by a specific species of bat per night
- Evm — is the average energy value, for a moth, (25.2 kJ per gram)
- Mw — is the average weight for a moth at Algeria Forestry Station.
- Abs eff — is the average absorption efficiency of bats (76.5%)

Estimating the numbers of bats

Population sizes for the bat species were calculated from mark and recapture data for *Tadarida aegyptiaca* and supported by passively monitoring bat echolocation in a known volume of air. For the mark and recapture data a total of 124 *T. aegyptiaca* had been marked by taking 3mm diameter skin biopsy punches (for genetic analyses in a separate study) on the wing membrane nearest to the body in 2001 (March 23-28, April 20-26, July 20-26, September 21-26, 9-14 December). Bats were re-sampled in October 2002, where 49 *T. aegyptiaca* were caught of which two had scars from biopsy punches

from previous fieldtrips. These mark and recapture data were used to estimate the population size of *T. aegyptiaca* using the Peterson formula (Seber 1982):

$$Nbs = (Nmb * Nbc) / Cm$$

Equation 1.4

Where:

Nbs — is the population size of the specific bat species in question

Nmb — is the number of bats marked previously

Nbc — is the number of recaptured bats

Cm — is the number of marked bats in the re-captured sample

Due to the lack of mark and recapture data for other species the remaining bat species population sizes were estimated from their proportions relative to *T. aegyptiaca*, which constituted 51.67% of all bats captured (Table 1 in results section). This area has been sampled at least twice a year from 2001 to 2005 resulting in a large data set with relative abundances of each species. As all bats were marked any individuals caught twice would be registered, but not included in the analyses or calculations to avoid pseudoreplication. The sum of all the 11 species population estimated was used as the total population size for this method (Table 1).

The second measurement for bat population size is centred on bat densities from passive monitoring of echolocation based on activity rates from bat detectors. Estimating the density of bats is difficult (but see Pearson *et al.* 1952; Rice 1957; Speakman 1991; Speakman *et al.* 2000; Jones *et al.* 1996; Trajano 1996) and only recently has a formula been developed to calculate bat densities from bat detector activity rates (Wilson 2004, Barclay, pers. comm.). I used this formula to determine bat densities from a known detection volume of air and used these densities to calculate the total bat population. Estimating bat population size by this method has not been performed previously, primarily because it is difficult to know the volume of airspace being sampled by a bat detector, and even more difficult to know the total volume of air used by the bat community. However, it could be useful as a coarse estimate and in this case it will serve as a supplementary measurement of population size allowing the testing of its usefulness. The Wilson formula is as follows:

$$C_{25} = 25 / D * R / (L * W / FA)$$

Where:

- C_{25} — is the number of bats flying in a given time and area up to a maximum flight height of 25 m.
- D — is the maximum detection distance in metres estimated using data from Griffin (1971), Patriquin *et al.* (2003) and Wilson (2004).
- R — is the bats activity rate in passes per minute
- L — is the length of detection area estimated by multiplying bat flight speed (calculated in flight tunnel experiments) and time period of the passive

monitoring sample window (60 seconds in this case)

W — is the width of detection area in meters and is calculated using the formula

$$(D^2 - H^2)^{\frac{1}{2}} * 2$$

FA — is the area of habitat space in which a bat might be expected to fly in the time window of the passive monitoring given the bats flight speed.

H — is the average flight height (estimated as $\frac{1}{2}$ D by Wilson 2004)

To estimate bat population size from bat densities one requires the total volume of air used by the bat community. The Algeria Forestry Station is well situated for this method as it is in a long deep valley making it possible to determine the total volume of air used by the bat community in the area. During the first few trips in 2001 and 2002 various areas were sampled along the Rondegats River. In total more the ten sites were sampled covering a total range greater than 20 km. It was noticed that the highest catch rates and bat active (based on Anabat detectors) was between the Algeria Forestry Station camp site and the Nieuwoudt camp site. This allowed us to focus our trapping at three sites; the two mentioned above and one site in-between referred to as the swamps. Catch rates decreased drastically down stream from the Nieuwoudt camp site and up stream from the Algeria Forestry Station. Based on this the total foraging range of the bat community seemed to be in the range of 10 km, with the furthest sites in the 10 km range showing many molossid activity.

The majority of the bats move from their mountain roosts down to the valley to forage and drink along the Rondegat River. Therefore, by taking the average (maximum and minimum) height between the river and each of the mountain peaks, and the average

distance between the two peaks, one can calculate the main area of activity and then multiply it by the length of the foraging range, which in this case is 10 km (Figure 1). This determines the total volume of air used by the bat community. Even though some bats will use other areas it will be in very low densities and the relatively high densities of bats in the valley should compensate for the exclusion of these areas. Over all this results in an over estimate of population sizes as sampling is usually done in areas of high bat activity (i.e. lower down in the valley where bats use the river to drink and as a flight path).

The volume of air in which bat ultrasound can be detected depends on various factors, such as echolocation intensity, frequency, relative humidity and detector sensitivity (Livengood *et al.* 2001). Due to the high variation of echolocation peak frequencies of the bat assemblage in the area and the lack of literature on the call intensities and flight speeds it would be impossible to analyse the full bat assemblage. Therefore, I used the activity levels of *T. aegyptiaca* to determine the population size for this species. As with the mark and recapture method I estimated the population sizes of the other species from their proportions relative to that of *T. aegyptiaca*.

Due to the lack of information on echolocation-call intensities for *T. aegyptiaca*, and molossids in general, I assumed an echolocation-call intensity of 110 dB, which was relatively high within the range of known echolocation-calls found in the literature (Shimozawa *et al.* 1974; Schnitzler and Grinnell 1977; Kick 1982, Surlykke and Miller 1985; Troest and Mohl 1986; Faure *et al.* 1990; Miller 1991; Faure *et al.* 1993; Miller and Treat 1993; Surlykke *et al.* 1993; Waters and Jones 1995; Fenton *et al.* 1998). The

reason for this is that open air foragers have to detect prey at long ranges and need high intensity calls to generate audible echoes (Schnitzler and Kalko 2001). I used an echolocation-call frequency of 25 kHz for *T. aegyptiaca* as it falls within the range of peak frequencies obtained from the free flying recordings of *T. aegyptiaca*. This was also the frequency used by Patriquim *et al.* (2003) when measuring the minimum intensities required to detect ultrasound at a distance of 20m in different habitats. I used the same kind of bat detector and protocol used by Patriquim *et al.* (2003). An Anabat detector (Anabat II, Titley Electronics, Ballina, Australia) was placed 1m above the ground, set at a sensitivity of 8 and attached to a Pentium II computer (Intel Corp. Santa Clara, USA) running Anabat software (Titley Electronics, Ballina, Australia). The detector was set at a 45° angle in an open habitat, and we assumed that the sound transmission properties were similar to the clear-cut used by Patriquim *et al.* (2003). The known weaknesses (Barclay 1999) of the Anabat system are unlikely to have any effect on the results, as *T. aegyptiaca* has a very distinct echolocation call with no overlap with any other sympatric bat species in peak frequency (Schoeman and Jacobs 2006). During this study, only presence and absence data was obtained using Anabat detectors and no detailed analyses of *T. aegyptiaca* echolocation calls were done using recordings obtained by Anabat detectors.

To determine how far away bats could be detected I used the mean minimum sound intensity for detection at 20m calculated by Patriquin *et al.* (2003) of 73.9 dB for 25 kHz (Wilson 2004). I incorporated atmospheric attenuation and spreading loss assuming conditions of 18°C and 50% relative humidity (Griffin 1971), to estimate the additional distance that the sound could travel given the original intensity of the call. This distance

was added to the 20 m to obtain the maximum distance at which bats could be detected (i.e. total detection distance).

The passive monitoring equipment (i.e. Anabat detector and computer) was setup just after dawn at 19h00 and taken down at 23h00. This was done during October (3rd - 5th) and November (11th – 13th) 2004. In total I managed to obtain 5 nights of activity data consisting of 5 minute recordings every 10 minutes totalling 24 samples per night. The *T. aegyptiaca* calls were easy to identify as the frequency at the heel had no overlap with any other species in the area.

Due to the fact that a 5 minute sample window was used, I calculated the length of the flight path (L) by multiplying the possible distance travelled in 5 minutes with the flight speeds of *T. aegyptiaca* measured in a flight room and from hand-released bats. In the flight room I used frame-by-frame analysis of flight sequences recorded with an infrared wide-angle camera (CCIR model TBC –340w, Korea) under infrared illumination (infrared illuminator model IR 65W, Ultrak, Italy) placed 2 m above the infrared camera. Infrared illumination cannot be detected by bats and thus, has no effect on behaviour (Mistry and McCracker 1990; Arlettaz *et al.* 2001). I took care to ensure that light from the equipment did not increase light availability in the flight tunnel. I connected the camera to a RCA black and white monitor (model EN 50081-1, Risque electronic, Korea) and a VHS Panasonic time-lapse video recorder (model AG TL350, Matsushita electric, Japan) set to a 3-hour time-lapse. I counted the number of body lengths covered by the bat on film and multiplied it by actual body length obtained from the scaled digital photographs. I calculated time taken to cover the distance by counting

the number of frames and multiplying this by the speed of the film (25 frames per second). I only used flight sequences where the bat appeared to be flying at right angles to the camera.

The flight speeds showed a wide range between 4.7 ms^{-1} and 11.2 ms^{-1} with the release trials showing a significantly higher flight speed than the tunnel trials (post-hoc Tukey test, $p < 0.007$). Even though open air foragers, such as *T. aegyptiaca*, have less erratic flight paths than edge or clutter feeders they still do not have a direct linear flight pattern and often follow non-linear flight paths (e.g. rivers, roads, etc...) so their true flight speeds would be higher than the estimated flight speed based on distance between two points over time. In addition to this *T. aegyptiaca* forage while in flight, which decreases true flight speeds. Therefore, the flight speed used for this study was 5 ms^{-1} which is probably the flight speed at which this species approached its prey. The value of 5 ms^{-1} is still within the range of speeds obtained for *T. aegyptiaca*.

The use of a 5 minute sample window for passive monitoring allows a bat that is outside the detection range of the bat detectors to fly into the detection range. This means that a bats speed will determine how far a bat could be and still have time to fly from outside the detection range of the bat detectors to inside the detection range. Therefore, the possible sample area of the passive monitoring system is larger than the detection range of the bat detectors and one must consider a hypothetical bat moving through space without back tracking for one minute to approximate the area that such a bat could occupy (FA). Based on flight speeds, *T. aegyptiaca* can cover 1500 m during the

one minute sample window giving the hypothetical sample area a radius of 1500m (i.e. $FA = 1500^2 * \pi$).

The predation rate for each species was calculated (equation 1.3) using the number of bats for each species calculated from their proportions relative to *T. aegyptiaca*. The total predation rate was the sum of the predation rates of all the species known to occur in the area and was calculated as:

$$P = (Ps_1 * Nbs_1) + (Ps_2 * Nbs_2) \dots + (Ps_n * Nbs_n)$$

Equation 1.5

Where:

Ps_n — is the number of moths eaten for each of the species (S_n) occurring in the area, where n denominates the number of bat species sampled (refer to equation 1.3).

Nbs_x — is the population size for each of the eleven species occurring in the area and is based on either the mark and recapture or passive monitoring method.

Hearing Moths

The selective advantage of hearing moths can be reflected by the dominance of hearing moths over non-hearing moths (at Algeria Forestry Station about 92.7% of moths are hearing; Chapter 2). Though moths constitute 73% of the available nocturnal aerial insects, are easy to detect by bats (large wing surface to reflect echolocation-calls and can even produce ultrasound, Waters and Jones 1994) and have a high energetic

value, they constitute a very small part of the diet of bats that echolocate within moth hearing range (Schoeman and Jacobs 2003). In a study by Schoeman and Jacobs (2003) it was concluded that moth defences (hearing) was the main factor determining proportion of moths in the diet of bats found around Algeria Forestry Station, especially for bats echolocating within the hearing range of moths.

In the case of a hypothetical model in which none of the moths have any defences the abundance of moths in the insect population obtained from the light traps will equal the proportion of moths in the diet of bats. For the hearing moth model the ability to hear will allow some moths that the bats encounter to escape, decreasing the proportion of moths in bat diets. I used the proportion of moths in the diets of bats at Algeria Forestry Station determined by Schoeman and Jacobs (2003) using faecal pellets to calculate the selective advantage of moth hearing. The difference between the expected proportion of moths in bat diets based on abundance obtained from the light traps (see non-hearing model) and the actual proportion of moths in the bat's diet obtained from faecal analyses (Schoeman and Jacobs 2003) can be attributed mainly to the moth hearing (i.e. selective advantage obtained from hearing).

However, hearing is not the only thing that could influence the actual proportion of moths in a bat's diet. I estimated the influence of non-hearing factors on bat diets as the difference between the expected proportions of moths in bat diets based on light trap abundances and the actual proportion of moths in the diet of bats (faecal analyses) for bats that echolocate outside the main sensitivity range of moth hearing. The moths are deaf to these bats and cannot benefit from hearing.

From this I calculated the final percentage advantage of hearing and subtracted that from the expected 73% abundance from light trap data to obtain the percentage of moth in bat diets for each of the bat species in the area. The number of moths eaten per night per species was calculated and from that the average predation rate (taking the abundance of each species into account) was then calculated (i.e. predation rate). The difference between the predation rate of the earless model and hearing model was used as the percentage increase in the chance of an eared moth population surviving a bat attack (i.e. success rate). The selective advantage of moth hearing was included in the hearing moth model in the form of an efficiency ratio (probability of surviving a bat attack) that affected the predation rate and was calculated as:

$$DN/DT = R N (1 - N / K) - (A_h * P)$$

Equation 2.

Where:

A_h — is the hearing induced advantage to eared moths that affects the predation rate in the form of an efficiency coefficient i.e. probability of a moth being a victim of a bat attack and $A_h = S_h / 100$.

S_h — is the bats success rate (expressed as a percentage) when attacking hearing moths.

Jamming Moths

All moths that click should also be able to hear because they require hearing to time the clicking so as to maximise the jamming effect. Jamming follows the same logic as that of the hearing model, but on top of the advantages of hearing, the ability to jam bat echolocation further increases the chance of a moth surviving a bat attack. Jamming is learning independent and bats cannot habituate to this strategy, therefore it is constant and unaffected by the level of experience of the bat and should be effective 100% of the time unless the moth makes some error e.g. calling too soon or too late. To accommodate such potential moth error, four different bat attack success rates of 25%, 50%, 75% and 100% were programmed into the jamming models. The jamming model is based on the hearing moth model and can be expressed as:

$$DN/DT = R N (1 - N / K) - (A_j * (A_h * P))$$

Equation 3.

Where:

- A_j — is the jamming induced advantage to moths that affects the predation rate in the form of an efficiency coefficient i.e. probability of a moth being a victim of a bat attack and $A_j = S_j / 100$
- S_j — is the bat's percentage success rate when attacking jamming moths.

Aposematic Moths

Aposematism is only effective with experienced bats that have already formed the association between moth clicks and the moth's noxiousness. This makes the aposematic moth model density dependent. Naïve bats attacking these noxious clicking moths will start to avoid them as the bats learn to associate clicks with bad taste. This will decrease the amount of bats feeding on these moths. However, if bats do not encounter these noxious clicking moths regularly they forget or never learn of the association between the moth's noxiousness and the clicks. Thus, the densities of aposematic moths affect the ratio of naïve to experienced bats, which affects the predation rate.

To determine the ratio of naïve to experienced bats for a given density, the learning rate (i.e. the number of encounters a bat requires to form the association) and the reinforcement rate (i.e. the number of encounters required to maintain the association) are required. Big brown bats required seven trials (encounters) within the same day to form the association between moth clicks and noxiousness (Bates and Fenton 1990). The bat would forget the association if it did not encounter moth clicks for more than two days. Unlike earless moths where the number of moths taken is similar to the number of encounters, the number of encounters on hearing moths is higher than the number of moths taken by bats (P). Some moths should be able to survive encounters due to the defensive advantage of hearing. Therefore, the number of encounters can be presented as the number of moths taken (P) plus the number of moths that survived the

encounter. Based on this, the average number of encounters for an average bat in the area was calculated using the following equation:

$$E_n = ((P_{s_1} * H_a) + (P_{s_2} * H_a) \dots + (P_{s_n} * H_a)) / n$$

Equation 3.1

Where:

E_n — is the average encounter rate for an average bat in the area

$H_a = 1 + H_p/100$

H_p — is the number of times a bat misses an attack due to the defensive advantage induced by hearing. It is expressed as a percentage of the predation rate

n — is the number of bat species in the area that echolocate within moth hearing range which is 8 in the case of Algeria Forestry Station.

I used 7 aposematic encounters in one day as the required encounter rate to activate the association and then 2 days for the bat to forget (Bates and Fenton 1990). To calculate the ratio of naïve bats to experienced bats, I designed a computer program (Appendix III) which simulated a naïve bat foraging to meet its daily energy requirements and in the process randomly encountering aposematic (i.e. clicking) moths. Naïve bats that encountered the required number of aposematic moths were considered experienced bats and they remained experienced as long as they met the required reinforcement rate. The program was based on Python programming because: a) the direct nature of the programming language allows non-programmers to read the program and still understand the basic commands and actions; b) the program requires

little processing power, which permits large data analyses in relatively short time periods; and c) the program is freely available on the internet.

The program used 1000 bats each attacking moths at the calculated daily encounter rate. This was run for an equivalent of at least 356 days, which meant having a spreadsheet comprised of 1000 rows (representing the bats) and columns (representing the moth encounters). The daily encounter rate formed a set, which represented 1 day, totalling 356 sets representing the number of days that the simulation covered. For every encounter the program randomly produces either a '1' (an aposematic moth taken) or a '0' (a good tasting moth taken) for each bat. The total number of 0's and 1's were determined by the predefined proportions of aposematic moths. After each day (encounter set) each row was summed giving the number of moths encountered by each bat (row). Bats that had an encounter rate equal or higher than the required encounter rate within a day were counted as experienced (i.e. have formed the association between clicks and bad taste). However if the bat went over the predefined encounters per set without any aposematic moth being encountered, it was regarded as having forgotten the association and was reset as naïve.

The learning rate observed by Bates and Fenton (1990) for big brown bats may not necessarily be the same for other species. To better understand the effect of bat learning ability on the stability of the aposematism hypothesis the program was run under 5 different encounter rates required to activate the association between clicks and noxiousness (3, 5, 7, 9 and 11 encounters per day with noxious clicking moths) and 5 different reinforcement rates (1 encounter every 2 days, 1, 3, 5 and 7 encounters

everyday with noxious clicking moths). The reason why all the other reinforcement rates are higher than 1 encounter every 2 days is because Bates and Fenton's (1990) study did not assess the reinforcement rate, but observed that when they stopped the trials for 2 days the bats would forget the association between the sound and the bad taste. This was a fixed interval used to reset the bats memory, but the bats could have forgotten the association before this time period. The fact that daily trials occurred and the bats still went through a habituation phase supports our assumption that 1 encounter every 2 days is most likely the minimum required encounter rate to maintain the association. Furthermore, big brown bats are often used in experiments and have been shown to be easily trained and intelligent bats.

This suggests that the average bat may require more than 1 encounter every 2 days to maintain the association. As for the predefined proportions of aposematic (i.e. clicking) moths, they constitute only 2.3% (refer to chapter 2) of the total number of moths available to a foraging bat, however different environments would have different percentage of clicking moths in the total moth population. Therefore the program was run with different densities of clicking moths from 2.3 % to 50%. This allowed one to determine the minimum density required for aposematism to be viable under the different learning and reinforcement rates.

The program gave an output of the percentage of experienced bats and the percentage of naïve bats for each simulation. The experienced bats do not contribute to moth predation. Therefore, only the percentages of naïve bats were updated into the aposematic moth's predation rate to generate the change in moth population as a

function of different proportions of naïve bats. The aposematic model can be mathematically expressed as:

$$DN/DT = R N (1 - N / K) - (Aa * (Ah * P))$$

Equation 4.

Where:

Aa — is the coefficient of the density of naïve bats in the population derived (i.e. $Aa = Bn_t / 100$) from the percentage of naïve bats in the population over time (Bn_t) obtained from the program.

Startle Moths

Startle is similar to the aposematic model in the sense that it is also dependent on the ratio of naïve bats to experienced bats. However, unlike aposematism where learning is required and beneficial, learning affects the startle strategy negatively by allowing bats to habituate to the strategy and to continue preying on moths. So unlike the aposematism model, bat experience increases the predation rate because experienced bats become habituated to the clicks. The startle moth model uses the same program that was used for the aposematic moth model, but uses the percentage of experienced bats instead of the percentage of naïve bats used in the aposematic moth model. The only other difference was that the program's default encounter rate was set at three within the same day for the startle model instead of seven within the same day. Even though bats take seven encounters to form an association they only require three encounters to habituate to benign sounds (Bates and Fenton 1990).

Therefore, after every set all the bats that had a sum of more than three encounters with a moth using a startle strategy were considered experienced. If experienced bats did not encounter startle moths for more than two sets they were reclassified as naïve. As the startle strategy is only effective with naïve bats, the experienced bats are responsible for the predation rate. Therefore, the percentage of experienced bats obtained from the program was continuously fed into the startle model in a form of a coefficient. The startle model can be expressed mathematically as follows:

$$DN/DT = R N (1 - N / K) - (A_s * (A_h * P))$$

Equation 5.

Where:

A_s — is the coefficient of the density of experienced bats in the population derived (i.e. $A_s = B_{e_t} / 100$) from the percentage of experienced bats in the population over time (B_{e_t}) obtained from the program.

RESULTS

Bat population and estimates

The Algeria Forestry Station bat community is dominated by two species (*T. aegyptiaca* 51.67% and *S. petrophilus* 26.25%) of open air foraging molossids, which constitute 77.92% of the total number of bats caught (Table 1). Bat activity in the area usually started at around dusk and ended around midnight averaging 5 hours of foraging. Based on both the passive monitoring data and to a lesser extent the mist net

data *T. aegyptiaca* showed two clear periods of very high activity at around 20h00 and 22h00 (Appendix IV). The bat population estimates from the mark and recapture methods yielded a population estimate for *T. aegyptiaca* of 3038 individuals and a total bat population of 5881 individuals (Table 1).

The bat population estimate based on the passive monitoring resulted in an average activity rate of 0.6 bats per sample (i.e. 5 minute time window) for a fixed sample volume of 176,625,000 m³ (Figure 1a). Based on the total calculated foraging volume for the Algeria Forestry Station bat community of 11,086,000,000 m³ (Figure 1b) the estimate for the *T. aegyptiaca* population was 4783 individuals and a resulting total bat population size of 9259 individuals (table 1).

Table 1: This table covers three main components: 1) Bat population numbers and the abundance information for the eleven different species known to occur in the area based on actual catches. The bat populations were estimated using both the mark and recapture method (MR) and the passive monitoring method (PM) that determined bat population sizes from number of bats flying in a given volume of air based on the detection cone of bat detectors. 2) Bat's energy requirements in kilojoules per bat species based on a bat's per gram body mass energy requirement (see methods). This information was then transformed into moths consumed per day per bat species and bat population using both the abundance of moth from light-traps and percentage of moths in their diet based on faecal analyses. Note: N/A indicates not applicable and is due to the bats that echolocate outside the moth hearing range.

		<i>Cistugo lesueurii</i> (CL)	<i>Eptesicus hottentotus</i> (EH)	<i>Laephotus wintoni</i> (LW)	<i>Miniopterus natalensis</i> (MS)	<i>Myotis tricolor</i> (MT)	<i>Neoromicia capensis</i> (NC)	<i>Nycterus thebaica</i> (NT)	<i>Rhinolophus cilirostris</i> (RCL)	<i>Rhinolophus capensis</i> (RC)	<i>Sauromys petrophilus</i> (SP)	<i>Tadarida aegyptiaca</i> (TA)	Sum	Average
Bat population	Numbers of Bats	4.00	12.00	5.00	1.00	1.00	10.00	9.00	10.00	1.00	63.00	124.00	240.00	21.82
	Percentage of population	1.67	5.00	2.08	0.42	0.42	4.17	3.75	4.17	0.42	26.25	51.67	100.02	9.09
	Population est. from mark and recapture (MR est.)	98.20	293.98	122.30	24.70	24.70	245.18	220.49	245.18	24.70	1543.40	3038.00	5880.83	534.62
	Population est. from passive monitoring (PM est.)	154.59	462.84	192.54	38.88	38.88	386.01	347.13	386.01	38.88	2429.92	4783.00	9258.68	841.70
	Mass (g)	6.7 ±1.2	18.1 ±1.5	10.3 ±1.6	11.6 ±0.8	13.1 ±2.2	7.3 ±0.9	12.6 ±1.5	19 ±2.5	10.8 ±0.6	9.8 ±0.8	16 ±1.4	135.30	12.30
	Daily energy requirement (Kj) per bat	35.51	95.93	54.59	61.48	69.43	38.69	66.78	100.70	57.24	51.94	84.80	15614.83	65.19
Earless moth population	Daily Kj obtained in equal prey setup (73%)	25.92	70.03	39.85	44.88	50.68	28.24	48.75	73.51	41.79	37.92	61.90	523.48	47.59
	grams of moths eaten in equal prey setup (73%)	1.35	3.63	2.07	2.33	2.63	1.46	2.52	3.82	2.17	1.96	3.22	27.15	2.47
	# of moths eaten in equal prey setup (73%)	31.08	83.90	47.68	53.72	60.66	33.80	58.24	88.12	50.10	45.27	74.24	626.81	56.98
	# of earless moths eaten by population (MR est.)	3052.45	24663.96	5831.55	1326.84	1498.28	8287.11	12842.41	21605.69	1237.39	69866.66	225539.76	375752.10	34159.28
	# of earless moths eaten by population (PM est.)	4805.28	38830.76	9180.75	2088.56	2358.43	13047.19	20218.54	34015.88	1947.76	109997.67	355087.79	591578.59	53779.87
Hearing moth population	% of moths in diet of bats at AFS	0	0	43.5 ±48.1	0	6	0	34.9 ±27.3	34.2 ±30.4	74.7 ±27.4	0.3 ±2.2	5.4 ±13.4	199.00	18.09
	% of moths excluding other defenses	25.00	25.00	68.50	25.00	31.00	25.00	59.90	59.20	99.70	25.30	30.40	474.00	43.09
	Actual daily Kj obtained from moths per bat	8.88	23.98	37.39	15.37	21.52	9.67	40.00	59.61	57.07	13.14	25.78	312.42	28.40
	Grams of moths eaten per bat	0.46	1.24	1.94	0.80	1.12	0.50	2.07	3.09	2.96	0.68	1.34	16.21	1.47
	Number of hearing moths eaten per bat	10.63	28.72	44.78	18.41	25.78	11.58	47.90	71.39	68.34	15.74	30.87	374.15	34.01
	Encounter rate	14.88	40.21	62.69	25.77	36.09	27.80	n/a	n/a	n/a	22.03	43.22	272.70	36.10
	# of hearing moths eaten by population (MR est.)	1044.00	8443.29	5476.84	454.64	636.66	2840.03	10562.38	17503.94	1688.07	24288.50	93790.08	166728.45	15157.13
# of hearing moths eaten by population (PM est.)	1643.51	13293.06	8622.32	715.65	1002.15	4471.33	16628.96	27558.11	2657.18	38239.67	147662.26	262494.21	23863.11	

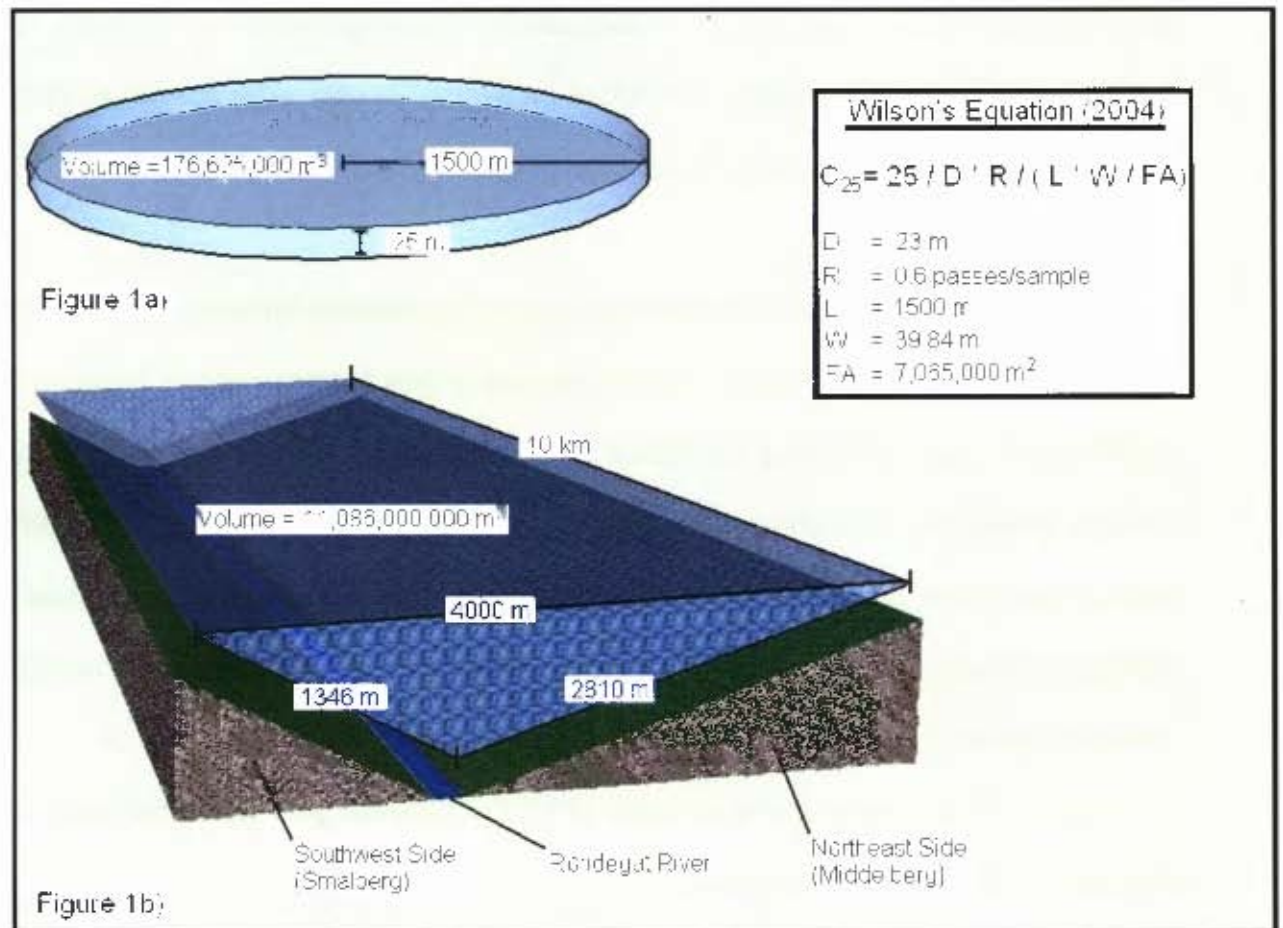


Figure 1. Graphical presentation of the detection area, sample volume of the passive monitoring and the estimated volume of air used by foraging bats in the area. Figure 1a shows the radius of the habitat space in which a bat might be expected to fly in the time window of the passive monitoring given a flight speed of 5 ms^{-1} . The flight height used by the Wilson equation (2004) is 25m, which with the sample area of the passive monitoring determines the sample volume of the passive monitoring. The Wilson equation (2004) calculated the bat density for this volume. Once the bat density is known the estimated volume of air used by foraging bats in the area shown in Figure 1b was used to calculate the total population size. Figure 1b is a rough representation of the valley around the Algeria Forestry Station. The highest points within the 10 km range, one on each side of the valley, was used as the height, while the widest cross-section of the valley with the 10km range was used as the width of the valley. Please note: for more details on the components and methods used to calculate the components in the Wilson equation (2004) please refer to the methods section in this chapter.

Moth Carrying Capacity (K)

Caterpillars consume 60% of their body weight per day resulting in a consumption rate between 40-120 mg per day depending on the species (Reichle and Crossley 1967, Despland and Noseworthy 2006). Therefore on average a caterpillar consumes 59mg per day, totalling 9 grams during the full growth period (Reichle *et al* 1973).

The vegetation in the area is predominantly natural mountain fynbos (medium to low laying shrubs and bushes). Kruger (1977) reported fynbos biomass values between 200 to 2600 g/m² in stands ranging between 2 to 17 years in age, with an average annual biomass production rate between 100 to 400 g/m². The fynbos in the study area had an average age range between 4 to 12 years. Therefore, I used an intermediate annual biomass production rate of 300 g/m², which most closely resembled the areas biomass based on age and composition. The study area had a total vegetation cover of 64,950,000 m² resulting in a total biomass of 19,377,000,000 g/m² which can sustain an estimated 2,153,000,000 caterpillars.

This method for obtaining carrying capacity (K) is biased toward over estimating as it assumes that only caterpillars are consuming the resource. Therefore, this value (2,153,000,000) was used as the “maximum” carrying capacity. To compensate for this over estimate, and to allow a better understanding of the effect of K, simulations were run under three lower K values (high, medium and low). High was half the value of the maximum carrying capacity (1,076,500,000); medium was half the value of the high carrying capacity (538,250,000); and low was half the value of the medium carrying capacity (269,125,000).

Earless Moth Model

Based on the total energy requirements in kilojoules for each specific bat species (Table 1) I calculated, assuming a 73% proportion of moths in diet (see methods), the daily kilojoules requirements obtained from moths for each bat species (table 1). This resulted in an average of 47.589 kj per bat and a total sum of 523.476 kj for all the species. The representative sub-sample of 200 moths caught at Algeria Forestry Station weighed a total of 8.664 g meaning that an average moth at Algeria Forestry Station weighs 0.0433g (table 2). This translated to an average daily consumption of 57 moths per bat.

Table 2: The sample sizes, proportions and weights of each moth family, within the total sample size of 200 moths, used to determine the average weight of a moth at Algeria Forestry Station. Due to the small size and very low weights of the species in certain moth families the samples were pooled and weighed as one mixed sample.

Earless moths	Eupterotidae	Limacodidae	Crambidae	Chrysopolimidae	Pyraustidae	Thyretidae	Pterophoridae	Tortricidae	Saturniidae
Proportion of pop. (%)	2.85	0.90	0.75	0.60	0.60	0.60	0.35	0.20	0.35
Number in sample	6	2	2	1	1	1	1	0	1
Weight of sample (g)	0.58	0.05	0.17						0.78
Hearing moths	Noctuidae	Arctiidae	Geometridae	Lymantriidae	Notodontidae	Sphingidae	Pyralidae	TOTAL	AVERAGE
Proportion of pop. (%)	38.70	20.70	14.30	9.20	3.50	3.00	2.30	8.66g	0.04g
Number in sample	79	41	29	18	7	6	5		
Weight of sample (g)	3.38	0.75	0.61	0.70	0.36	1.23	0.01		

To obtain the total predation rate it was necessary to multiply the total number of bats by the number of moths eaten per bat. However, not all bat species were found in the same proportions. Therefore, the average number of moths eaten for each species had to be first multiplied by the population size of that species and then all the species specific moth consumption added to obtain the total predation rate (Table 1). This resulted in a total daily predation rate of 375,752.103 moths based on the mark and recapture method and 591,578.591 moths for the passive monitoring method (table 1).

Table 3: Input data for the earless moth model. A total of four predation levels (based P), four carrying capacities (K) and ten reproduction rates (R 0.005, 0.01, 0.05, 0.1, 0.5, 1, 2, 3, 4, 5) were used resulting in 160 simulation variations for the earless moth model.

	Daily Predation Level	Annual Predation Level	Carrying Capacities (K)
Low (L)	187,876	68,574,758	269,125,000
Medium (M)	375,752	137,149,517	538,250,000
High (H)	591,578	215,926,185	1,076,500,000
Maximum (X)	1,183,157	431,852,371	2,153,000,000

The mathematical computer simulations outputs for the earless moth model, resulted in 160 graphs giving the moth population numbers over time for each of the different simulations. There were too many graphs to represent individually. Instead I use the stable point (value or average from a range of values that the population reaches and maintains indefinitely) from each simulation as an indicator of the stability and success of each of the 160 simulations. Each of the simulations started at a specific carrying capacity (i.e. low, medium, high or maximum) and decreased until reaching a balance between the reproduction rate (growth) and predation (death). The higher the stable point the more successful the simulation.

Based on the simulations for an earless moth population the increase in the carrying capacity increased the moth population's stable point. Also the moth population stable point increased with the increase in reproduction rate, once a high enough reproduction rate was achieved. Once the maximum stable point was reached the population stable point started decreasing with further increases in the reproduction rate until reaching zero (i.e. unstable). This pattern follows the typical nature of the negative relationship between population density and population growth rate.

In general for the moth population to be stable the reproduction rate would have to be above 0.1 and below 5 (Figure 2). At reproduction rates below 0.1 the growth of the moth population is too low to overcome the predation, even at the lowest predation rate. In simulations where the reproduction rate was too high (usually above 4 and above 5 for medium predation rates in low carrying capacity simulations) the moth population would exceed the carrying capacity very quickly, causing resource depletion and then a crash often hitting zero. In some cases the moth population would crash to low numbers then start increasing again, but after a few generations one of the moth population crashes would hit zero and end the simulation.

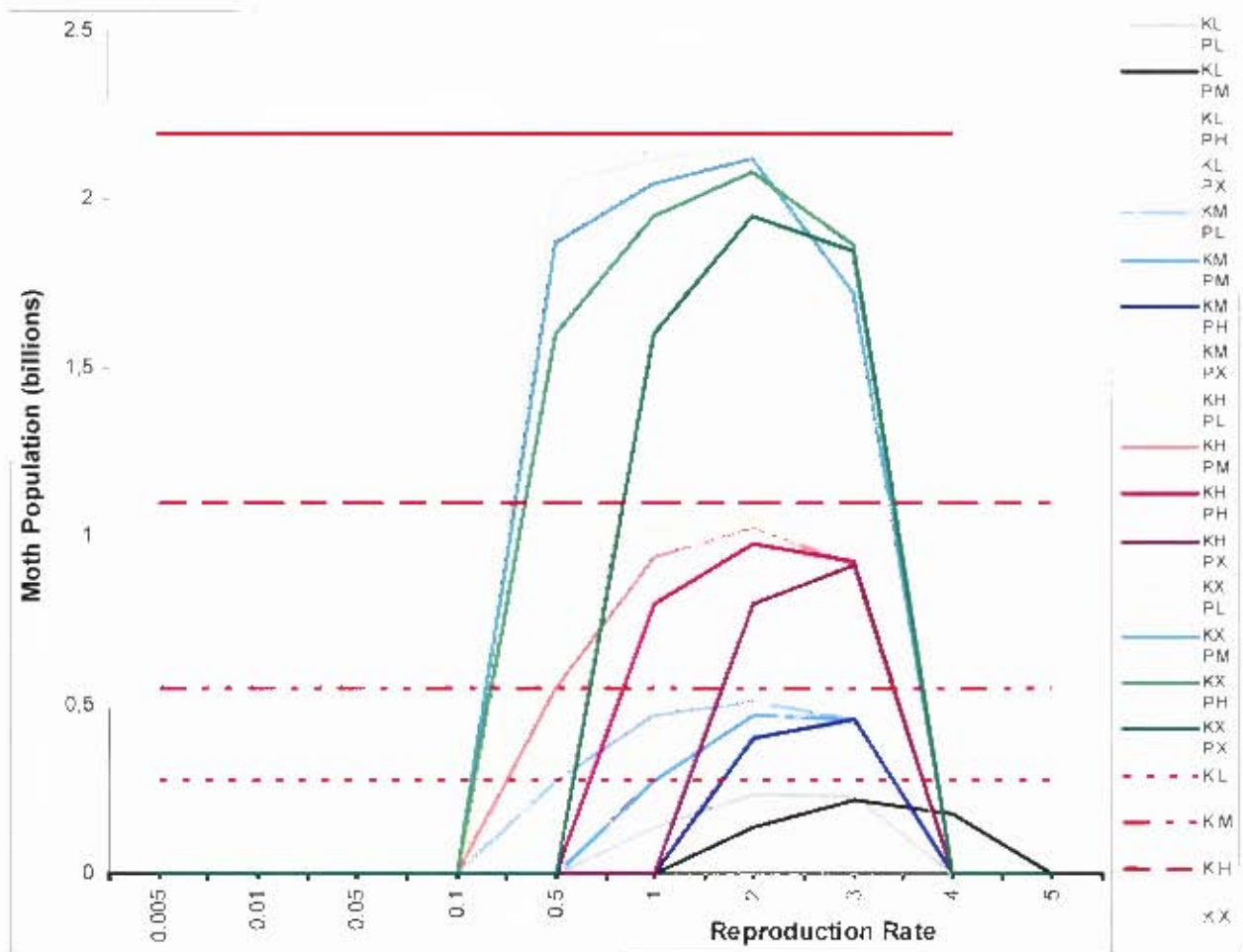


Figure 2: A summary of the 160 simulations under the earliest moth model. Each simulation was run under a specific carrying capacity, reproduction rate and predation rate, with the stable point for each simulation used as the output. Please note: Blank spaces with no coloured line in the legend represents simulations where the moth populations were not stable and crashed to zero. Red lines across the graph indicate the carrying capacity. The simulations have both a carrying capacity and predation rate indicated in the legend to help identify the input data and will have one of the following four carrying capacities KL (Low Carrying Capacity), KM (Medium Carrying Capacity), KH (High Carrying Capacity), KX (Maximum Carrying Capacity) with one of the following four predation rates PL (Low Predation Rate), PM (Medium Predation Rate), PH (High Predation Rate), PX (Maximum Predation Rate).

Low carrying capacity (KL) environments were stable under a narrower range of reproduction rates than simulations with higher carrying capacities, mainly due to the lack of stability at lower reproduction rates. The low carrying capacity simulation was stable only for the two lower predation rates and at reproduction rates above 0.5, while

all the higher carrying capacities achieved stability at reproduction rates above 0.1 for the lower predation rates. At higher reproduction rates the lower carrying capacity had some advantages, even finding stability under very high reproduction rates of 5 in simulations with medium predation (PM). The low carrying capacity limits population sizes. In smaller population sizes the same predation level removed a relatively larger proportion of the population compared to the larger populations that occur at higher carrying capacities. This allows the predation rate to have a stronger effect on the moth population, delaying the onset of resource depletion caused by excessive population growth and the consequential moth population crashes associated with the moth population exceeding the carrying capacities. This is further supported by the fact that environments with a low carrying capacity (KL) do not cope well with high predation rates, with both the high and maximum predation rates (PH and PX; Figure 2) causing the moth population to crash. As expected the lowest stable point for moth population numbers was achieved in a low carrying capacity (KL) environment, with the increase in carrying capacity corresponding to a general increase in the moth population stable point (Figure 2).

The medium carrying capacity (KM) environment was not stable under the maximum predation rate (PX, Figure 2), while high predation rate (PH) was only stable between reproduction rates of 1 to 4. The two lower predation rates (PL and PM) showed a gradual widening of the viable reproduction rates towards the lower end, with the medium predation rate being stable above 0.5 and the low predation rate being stable as low as 0,1 (Figure 2). As for the two environments with the highest carrying capacities (KH and KX), both coped with all four levels of predation as long as the

reproduction rate was high enough. As with the medium carrying capacity the high carrying capacity shows the widening of the viable reproduction rates towards the lower end as predation rate decreases (1 for PX, 0,5 for PH and 0,1 for PM and PL). The maximum carrying capacity does not show the gradual widening of the viable reproduction rates towards the lower end as predation rate decreases. Instead, all predation rates within the maximum carrying capacity environment show wide viable reproduction rates ranging between 0.1 and 4, except for the highest predation rate (PX) where the viable reproduction rates range between 0.5 and 4 (Figure 2).

The main factor that allows moth populations to cope with high predation rates in simulations with high carrying capacities is large moth population sizes. Each simulation starts with a moth population size set at the carrying capacity. As each day passes the predation reduces the population size. However, by the time the spring/summer reproductive season starts (i.e. annual reproduction phase of the simulation) the moth population size is still large enough to allow the moth population to recover to a level that can handle the non-reproductive phase of the moth population. In general if one looks at the differences in the predation rates between the different reproduction rates one notices that the higher the reproduction rates the smaller the differences between the predation rates (Figure 2) indicating the increased resilience of healthier environments and larger populations. This is due to both the higher reproduction rate which allows the growth rate to compensate for predation weakening the effect of predation, and factors that benefit from high predation rates such as lower resource depletion caused by slower growth as a result of high predation rates.

As expected the hearing model showed higher stable points than the earless moth model under the same parameters (Figure 3, 4, 5, 6). A higher stable point implies a more successful simulation that would out-compete a setup with a lower stable point. Therefore, under the same conditions a hearing moth would out-compete earless moths in most scenarios, especially under low reproduction rates. Not only are the stable points higher for the hearing moth model (Figure 3), but in the low carrying capacity setups with high predation (PH) the hearing model still manages to find stable points whereas the earless moth model crashes to zero. In fact the high predation rate (PH) from the hearing model out-competes the medium predation rate of the earless moth model.

The one area that the earless moth model may have an advantage is under medium predation rate (PM) at high reproduction rates of above 3 where the hearing models lower predation causes higher growth rates which cause resource depletion making the hearing model unstable at reproduction rates above 3. The earless moth model's higher predation level keeps resource depletion low enough to allow the population to stabilize.

Hearing Moth Model

Bats at Algeria Forestry Station echolocating outside the frequency range of moth hearing (allotonic bats) had diets comprised of an average of 48% moths (Schoeman and Jacobs 2003), which is 25% below the predicted value (73%) obtained by the light trap abundances. Hearing moths are deaf to these allotonic bats. Thus, the 25% difference between the light trap abundances and actual moths in the diet obtained by faecal analyses was used as a rough indicator of non-hearing factors influencing bat diet. The 25% was included into the percentage of moths in the diet of bats echolocating within moth hearing. This resulted in an average of 31.9% (Table 1) for the adjusted percentage of moths in the diet (i.e. excluding non-hearing factors) of bats that echolocate within moth hearing. The selective advantage resulting from the moths' ability to hear incoming bats is 41.1% (73 – 31.9%). This is similar to the 40% found by other studies (Roeder 1967, Rydell 1992, Acharya and Fenton 1999) and close to the 46% - 50% found by Hickey (1992).

Table 4: Predation rates and carrying capacity for the hearing moth model. A total of four predation level (based on P), four carrying capacities (K) and ten reproduction rates (R 0.005, 0.01, 0.05, 0.1, 0.5, 1, 2, 3, 4, 5) were used, resulting in 160 simulations for the hearing moth model.

	Annual Predation Level	Carrying Capacities (K)
Low (L)	40,390,533	269,125,000
Medium (M)	80,781,066	538,250,000
High (H)	127,180,523	1,076,500,000
Maximum (X)	254,361,047	2,153,000,000

As expected the hearing model showed higher stable points than the earless moth model under the same parameters (Figure 3, 4, 5, 6). A higher stable point implies a more successful simulation that would out-compete a setup with a lower stable point. Therefore, under the same conditions a hearing moth would out-compete earless moths in most scenarios, especially under low reproduction rates. Not only are the stable points higher for the hearing moth model (Figure 3), but in the low carrying capacity setups with high predation (PH) the hearing model still manages to find stable points whereas the earless moth model crashes to zero. In fact the high predation rate (PH) from the hearing model out-competes the medium predation rate of the earless moth model.

The one area that the earless moth model may have an advantage is under medium predation rate (PM) at high reproduction rates of above 3 where the hearing models lower predation causes higher growth rates which cause resource depletion making the hearing model unstable at reproduction rates above 3. The earless moth model's higher predation level keeps resource depletion low enough to allow the population to stabilize.

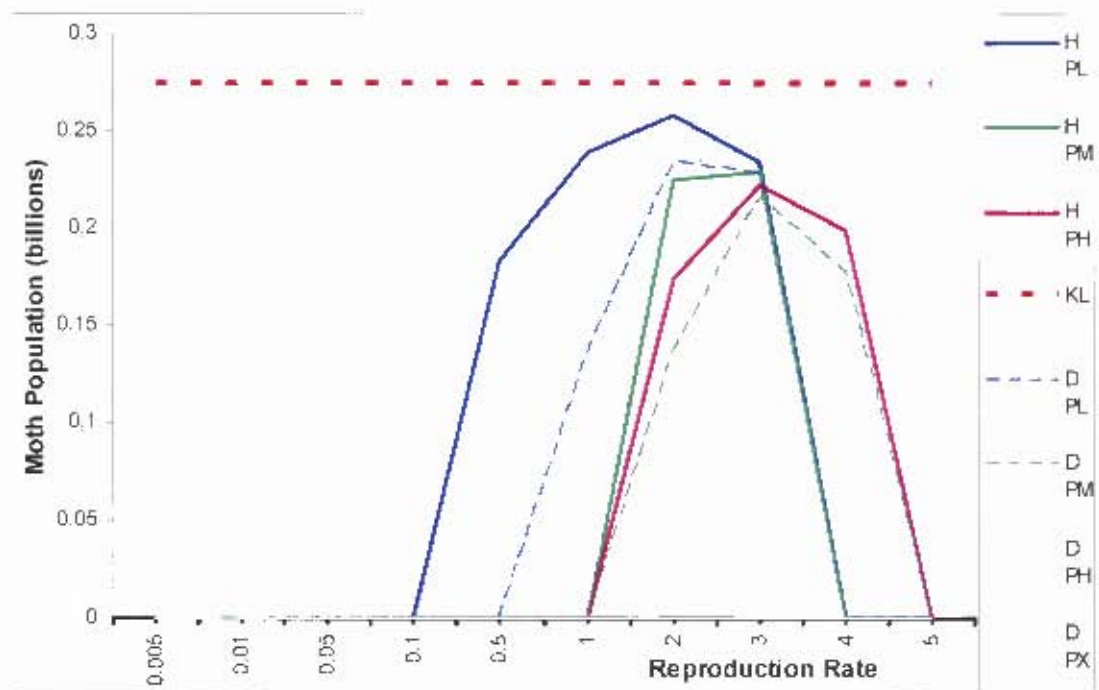


Figure 3: The Hearing versus the earless moth model within a low carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with the stable point for each simulation used as the output. The solid lines represent the hearing model (indicated by H in the legend) and the dotted line represents the earless moth model (indicated by D in the legend). Blank spaces with no coloured line in the legend represent simulations where the moth population were not stable and crashed to zero. The red line across the graph indicates the carrying capacity (KL). The simulations have a predation rate indicated in the legend to help identify the input data and will have one of the following four predation rates PL (Low Predation Rate), PM (Medium Predation Rate), PH (High Predation Rate), PX (Maximum Predation Rate).

The simulations under medium carrying capacity follow a similar trend to that of low carrying capacity, with the hearing model showing higher stable points (Figure 4). One of the differences between the low and medium carrying capacities is in the rare simulations in which the earless moth model out-competes the hearing model. With low carrying capacity the earless moth model out-competes the hearing model under

reproduction rates around 4 and medium predation rates). At medium carrying capacity the earless moth model out-competes the hearing model (higher stable point) at high reproduction rates (around 3) when the predation rate is low (PL).

This trend becomes clearer and more frequent at higher carrying capacities (Figure 5 and 6) due to the interaction between reproduction rates and predation rates within specific carrying capacities. It is noticeable that at lower stable reproduction rates the difference in the effect of predation is larger than at higher stable reproduction rates, and at around the reproduction rate of 3 there is very little difference between the effect of predation rates, with some higher predation rates resulting in higher stable points than lower predation rates.

The increased reproduction rate compensates for the effects of predation, decreasing the competitive advantage of hearing. The higher predation levels also benefit the moth population by decreasing the population growth which decreases the onset and level of resource depletion. These factors cause the decrease in the differences observed between the different predation rates and models (i.e. earless vs. hearing) at high reproduction rates.

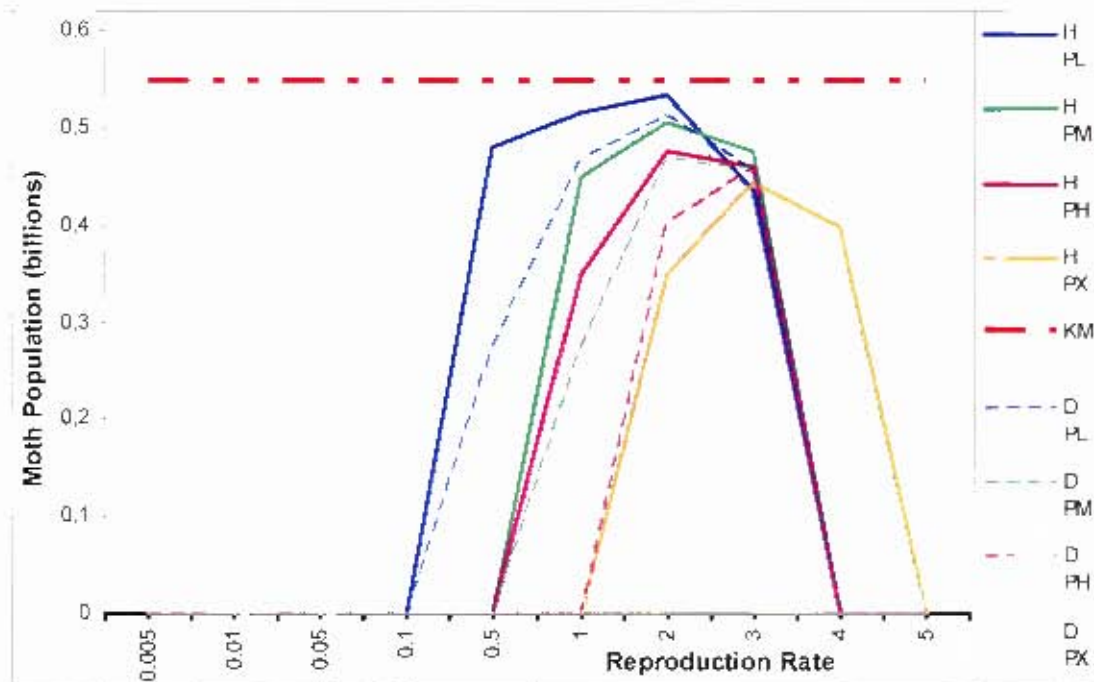


Figure 4: The hearing model versus the earless moth model within a medium carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with the stable point for each simulation used as the output. The solid lines represent the hearing model (indicated by H in the legend) and the dotted line represents the earless moth model (indicated by D in the legend). A blank space with no coloured line in the legend represents simulations where the moth population were not stable and crashed to zero. The red line across the graph indicates the carrying capacity (KM). The simulations have a predation rate indicated in the legend to help identify the input data and have one of the following four predation rates PL (Low Predation Rate), PM (Medium Predation Rate) PH (High Predation Rate), PX (Maximum Predation Rate).

When reproduction rates are low (i.e. below 3) the stable points have a very narrow range often stabilizing at a specific value. At higher reproduction rates the stable point is actually an average from a fluctuation range. The moth population usually increases at a rapid rate due to the high reproduction rate causing resource depletion, followed by a population crash. At very high reproduction rates (i.e. usually 4 or above) the resource depletion is high and the consequent population decline is large. At a reproduction rate

around 3 the resource depletion is less severe (i.e. smaller population decline) allowing the moth population to recover, grow and enter a fluctuation between growth and population crashes.

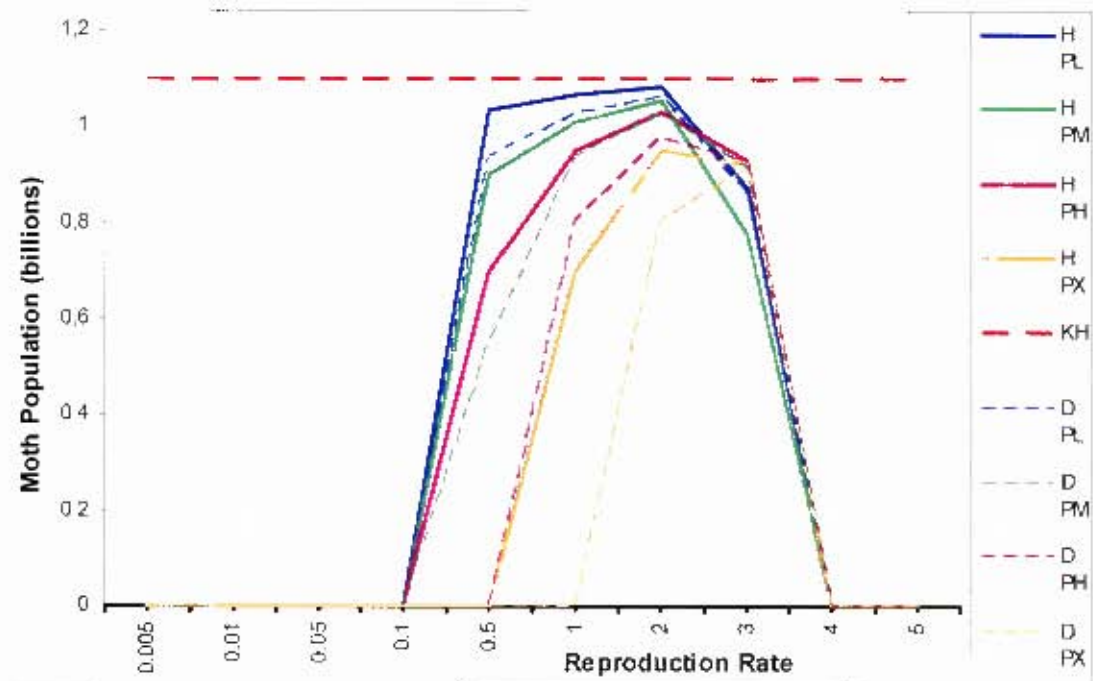


Figure 5: The hearing model versus the earless moth model within a high carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with the stable point for each simulation used as the output. The solid lines represent the hearing model (indicated by H in the legend) and the dotted line represents the earless moth model (indicated by D in the legend). The red line across the graph indicates the carrying capacity (KH). The simulations have a predation rate indicated in the legend to help identify the input data and have one of the following four predation rates PL (Low Predation Rate), PM (Medium Predation Rate), PH (High Predation Rate), PX (Maximum Predation Rate).

This implies that species that suffer from high predation rates (e.g. due to the lack of defence mechanisms) can still have high stable points and out-compete species with lower predation rates if they have high reproduction rates. However, if both species use

Jamming Moth Model

Jamming follows the same logic as that of the hearing model, but on top of the advantages of hearing, the ability to jam bat echolocation further increases the chance of a moth surviving a bat attack. Jamming is learning independent and bats are not known to habituate to this strategy, and therefore it is constant and unaffected by the level of experience of the bat and should be effective 100% of the time unless the moth makes some error e.g. calling too soon or too late. To accommodate such potential moth error, four different bat attack efficiency rates of 25%, 50%, 75% and 99.9% was programmed into the jamming models (the use of 99.9% instead of a 100% was for computational ease). Furthermore, every strategy has some error rate. The use of different efficiency rates creates four different variations for each of the four predation rate and increases the total number of possible setups (i.e. simulations) to 640 for the jamming model. The basic trend of the effect of jamming efficiencies within a specific predation rate, as it decreases from 100% to 25%, is very similar for all four of the predation rates. Therefore the medium default predation rate (PM) was used to illustrate these trends (Table 5).

the same resource the resource depletion of the species with a lower predation rate would affect the species with the high predation rate, eliminating the benefits from the lower resource depletion due to high predation rates. Therefore, the two species would have to use different resources (e.g. different host plant species) for the species with weaker defences (i.e. higher predation rates) to benefit from the lower resource depletion due to higher predation rate.

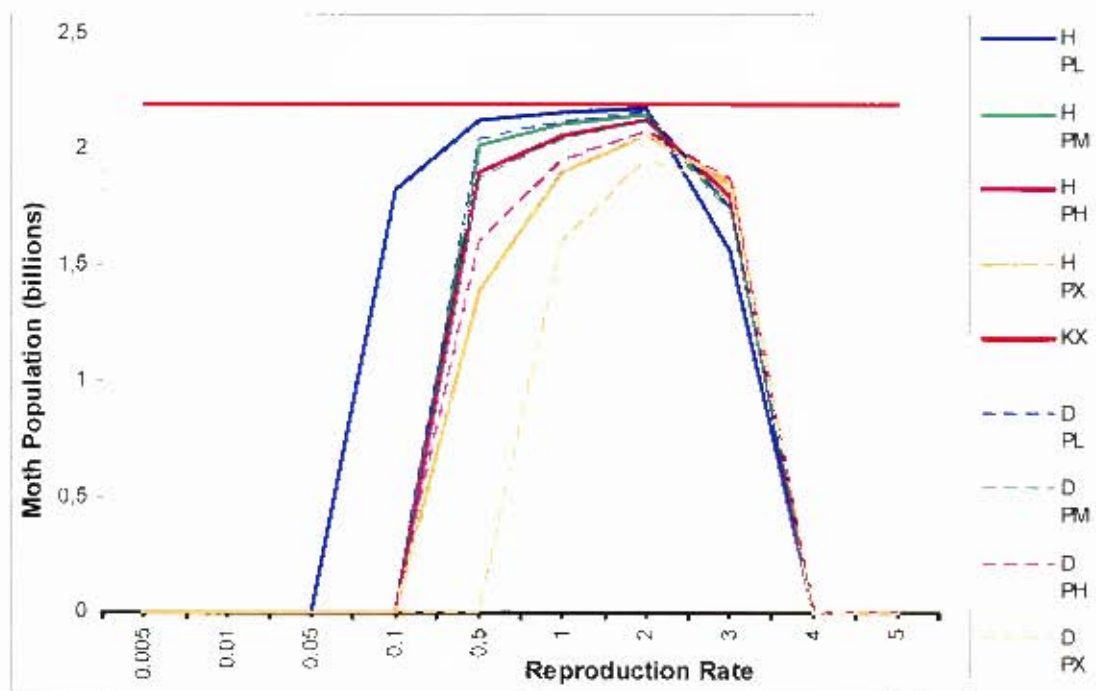


Figure 6: The hearing model versus the earless moth model within a maximum carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with the stable point for each simulation used as the output. The solid lines represent the hearing model (indicated by H in the legend) and the dotted line represents the earless moth model (indicated by D in the legend). The red lines across the graph indicate the carrying capacity (KX). The simulations will have a predation rate indicated in the legend to help identify the input data and have one of the following four predation rates PL (Low Predation Rate), PM (Medium Predation Rate), PH (High Predation Rate), PX (Maximum Predation Rate).

Table 5: Carrying capacities for the jamming model and the four different predation levels based on the four jamming efficiencies (25%, 50%, 75%, 99%) for the medium predation level (PM) for the jamming moth model. Please note: In total, for all simulation, four different efficiency rates for each of the four predation rates (P), four carrying capacities (KL, KM, KH and KX) and ten reproduction rates (R 0.005, 0.01, 0.05, 0.1, 0.5, 1, 2, 3, 4, 5) were used, resulting in 640 simulation variations for the jamming moth model.

	Jamming Efficiency	Annual Predation Level	Carrying Capacities (K)
Low (L)	99%	80,781	269,125,000
Medium (M)	75%	20,195,267	538,250,000
High (H)	50%	40,390,533	1,076,500,000
Maximum (X)	25%	60,585,799	2,153,000,000

All the simulations run with the jamming efficiency set at 99.9% were technically devoid of bat predation, allowing the moth population to be stable under very low reproduction rates, well below the ranges of reproduction rates tested. At reproduction rates below 2 the simulations stabilized close to carrying capacity. Above the reproduction rate of 2 the excessive growth rate (due to low predation and high reproduction) caused resource depletion, which caused population crashes and lowered the stable point at reproduction rates around 3 and becoming completely unstable at reproduction rates above 4. As the efficiency rate decreases so does the stable point when the reproduction rate is below 3 (Figures 7, 8, 9 and 10). When compared to the hearing model under the same medium predation rate the jamming model has higher stable points because jamming moths benefit from hearing in addition to jamming.

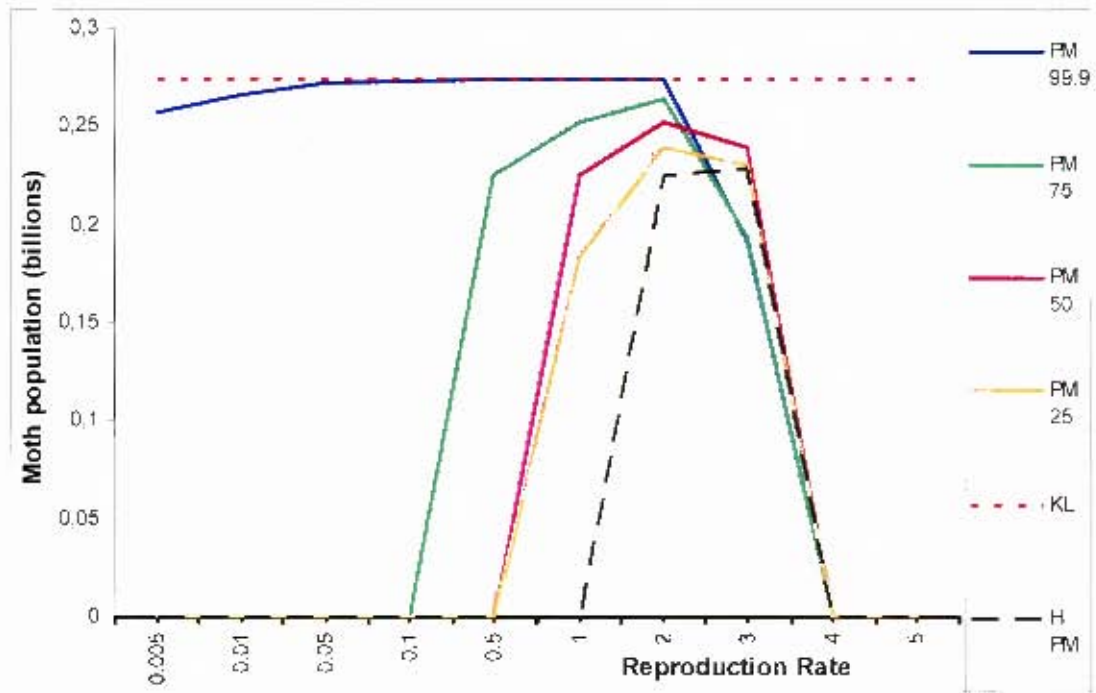


Figure 7: The jamming model versus the hearing model within a low carrying capacity environment.

Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (99.9%, 75%, 50% and 25% jamming efficiencies). This graph shows the simulation results only for medium predation (PM). The solid lines represent the jamming model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KL). The four jamming efficiencies are indicated in the legend as follows PM 99.9 (Medium Predation Rate at 99.9% jamming efficiency), PM 75 (Medium Predation Rate at 75% jamming efficiency), PM 50 (Medium Predation Rate at 50% jamming efficiency), PM 25 (Medium Predation Rate at 25% jamming efficiency).

As with the other models differences in the effect of different predation rates (in this case the jamming efficiency levels) decreases with an increase in reproduction rate. This caused the convergence of the stable points between the different simulations at high reproduction rates (i.e. around 3). At reproduction rates of around 3 the dominance of simulations with lower predation fades away, and the higher stable points are

determined by other factors such as resource depletion. For example in the medium and maximum carrying capacity simulations under reproduction rates around 3 the highest stable points were attained by the hearing model.

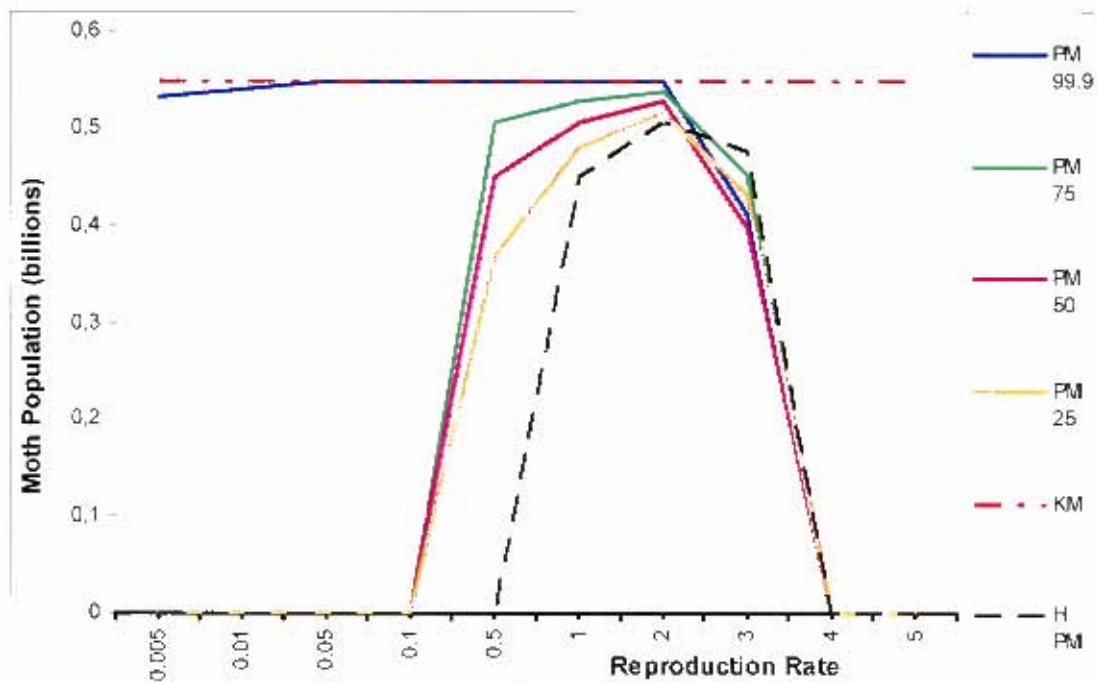


Figure 8: The jamming model versus the hearing model within a medium carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (99.9%, 75%, 50% and 25% jamming efficiencies). This graph shows the simulation results only for medium predation (PM). The solid lines represent the jamming model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red lines across the graph indicate the carrying capacity (KM). The four jamming efficiencies are indicated in the legend as follows PM 99.9 (Medium Predation Rate at 99.9% jamming efficiency), PM 75 (Medium Predation Rate at 75% jamming efficiency), PM 50 (Medium Predation Rate at 50% jamming efficiency), PM 25 (Medium Predation Rate at 25% jamming efficiency),

In general the jamming model is comparable to the hearing model in the same way that the hearing model compares with the earless moth model. However, even though the simulations between the models show similar patterns, the data collected from the field only supports the hearing model. Hearing moths constitute 92.7% of all the moths caught supporting the hearing model. On the other hand, clicking moths only constitute a small percentage of the moths caught (2.3%, chapter 2) in the field, which does not support the jamming model simulations, which yielded higher population stable points than the hearing model, especially at lower reproduction rates.

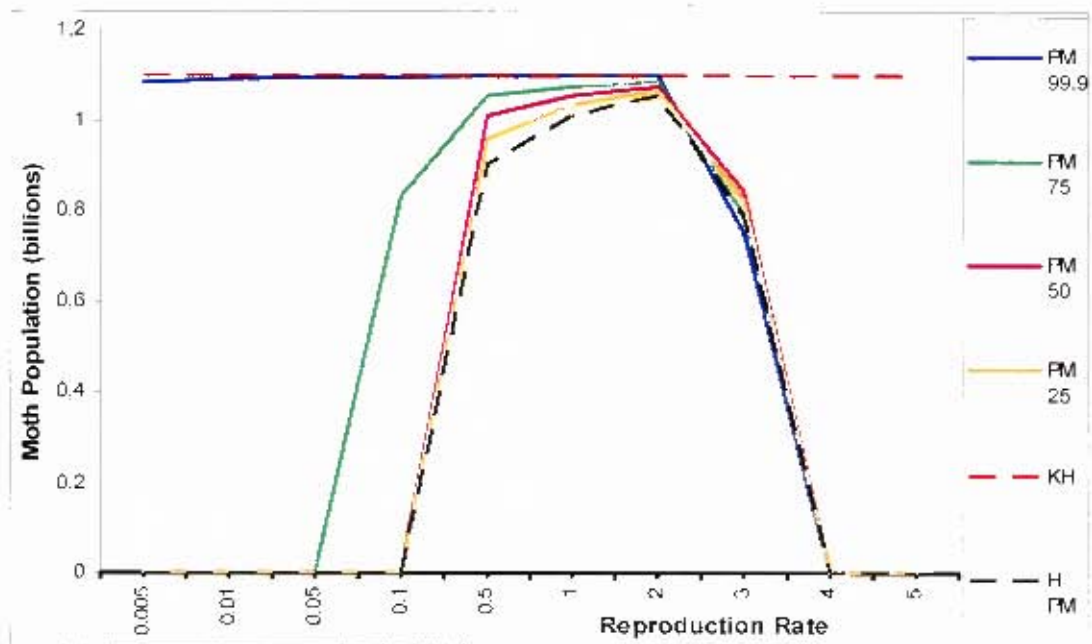


Figure 9: The jamming model versus the hearing model within a high carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (99.9%, 75%, 50% and 25% jamming efficiencies). This graph shows the simulation results only for medium predation (PM). The solid lines represent the jamming model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red lines across the graph indicate the carrying capacity (KH). The four jamming efficiencies are indicated in the legend as follows PM 99.9 (Medium Predation Rate at 99.9% jamming efficiency), PM 75 (Medium Predation Rate at 75% jamming efficiency), PM 50 (Medium Predation Rate at 50% jamming efficiency), PM 25 (Medium Predation Rate at 25% jamming efficiency),

The hearing model only out-competes (higher population stable points) the jamming model in simulations where both models have high reproduction rates (i.e. around 3). The main reason for this higher success is the lower resource depletion caused by the

higher predation level. These simulations were run independently, which implies independent resource utilisation. Under the same resource utilisation the jamming model would still out-compete the hearing model. If one considers that the majority of the moths at Algeria Forestry Station are hearing moths, which would cause major resource depletion, there would be very few scenarios where hearing models would out-compete the jamming model.

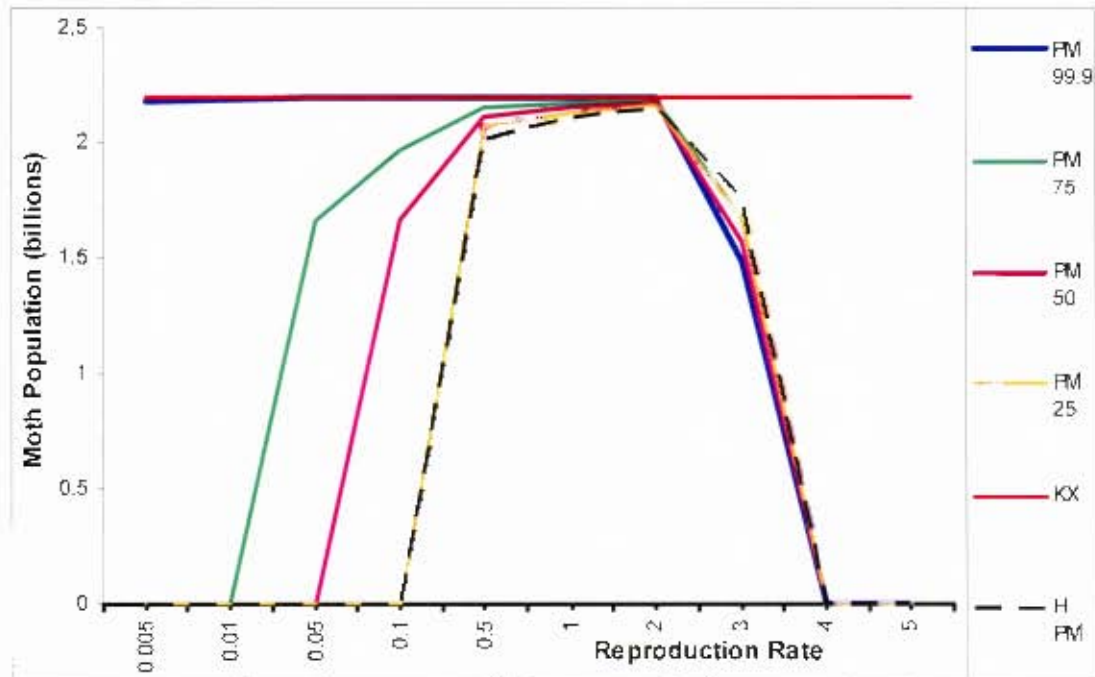


Figure 10: The jamming model versus the hearing model within a maximum carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (99.9%, 75%, 50% and 25% jamming efficiencies). This graph shows the simulation results only for medium predation (PM). The solid lines represent the jamming model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red lines across the graph indicate the carrying capacity (KX). The four jamming efficiencies are indicated in the legend as follows PM 99.9 (Medium Predation Rate at 99.9% jamming efficiency), PM 75 (Medium Predation Rate at 75% jamming efficiency), PM 50 (Medium Predation Rate at 50% jamming efficiency), PM 25 (Medium Predation Rate at 25% jamming efficiency),

Aposematic Moth Model

The aposematic model is a density dependent strategy that requires naïve bats to encounter clicking moths to form the association between the moth clicks and the moth's noxious properties. The three main components used to define the dynamics of how naïve bats form the association and gain/maintain the experience were the number of encounters a bat requires to form the association (learning rate), the number of

encounters required to maintain the association (reinforcement rate) and the proportion of clicking moths in the total moth population (percentage of clicking moths). Before any simulation could be run a good understanding of the effect of these three components had to be determined using the learning program developed specifically to calculate the influence of these components on bat experiences.

I used the results from Bates and Fenton (1990) as the default starting point for the learning rate (i.e. 7 encounters with noxious clicking moths per day). The study did not assess the reinforcement rate, but did mention that the bats lost their association after two days of not exposed to the clicks. I therefore took two days as the upper limit and one encounter per day as the default setting. The first component assessed was the influence of the proportion of clicking moths in a population. The higher the proportion of moths in the population the more encounters occur increasing the speed and number of bats that form the association between the moth clicks and the moth's noxiousness.

The results from the program simulation showed the importance of the proportion of clicking moths in a population (Figure 11). A proportion of 6% of noxious clicking moths in a moth population was enough to maintain the proportion of experienced bats (i.e. bats associating moth clicks with noxiousness) at around 5% of the bat population. At 8% clicking moths the percentage of experienced bats jumps up to just over 30% and at 10% clicking moths the percentage of experienced bats stabilizes at around 70%. When the percentage of clicking moths reached 12% the percentage of experienced bats rose to over 90% and close to 100% when the percentage of noxious clicking moths in a moth population reached 14%. Thus, a small percentage (12% to 14%) of noxious

clicking moths can form and maintain the association between moth clicks and noxiousness within a bat population.

Of further interest is the rate at which the association forms in the bat population. At percentages of noxious clicking moths of around or above 20% less than a week (sometimes 2 to 3 days) is needed to make all bats experienced (Figure 11). Even with low percentages (between 8% and 12%) the final stable percentages of experienced bats took only about a month to reach (Figure 11). Not only do these results show the importance of the proportion of noxious clicking moths, but also how little is required for the aposematic strategy to work.

However, despite the low percentage of noxious clicking moths required and the speed at which learning spreads in the bat population (Figure 11), there does seem to be a minimum percentage of clicking moths within a moth population that would allow bats to become experienced. This value seems to be around 6% (Figure 11). My field data indicated that clicking moths only constituted 2.3% of the moth population which according the model for aposematism is not high enough to produce experienced bats.

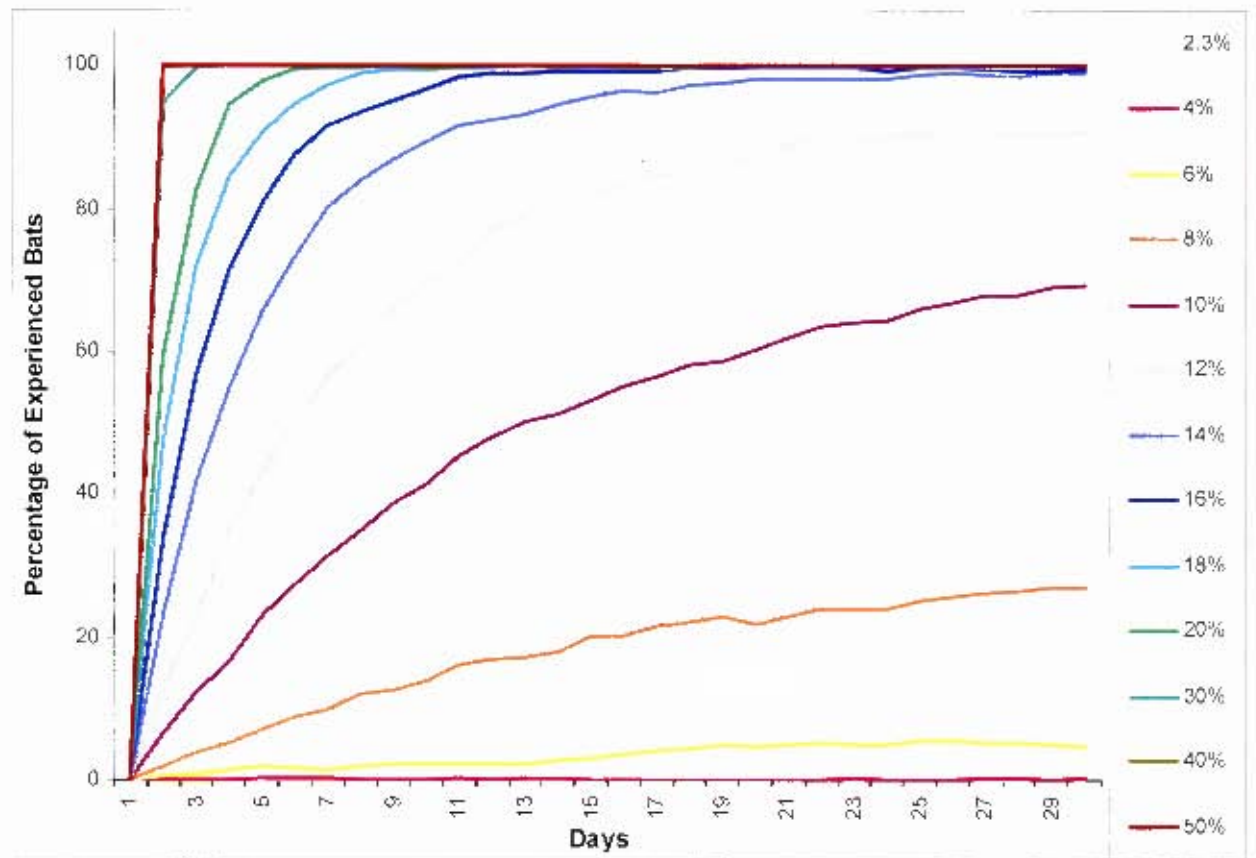


Figure 11: Effect of clicking moth percentages on bat experience over 30 days. The learning program simulations were run with a learning rate of 7 encounters per day and a reinforcement rate of 1 moth per day. Only the percentages of noxious clicking moths were changed and is indicated in the legend. Note: Due to the random generation of the placement of noxious clicking moths within the simulation by the learning program repeated simulations under the same settings showed small variations in the results. Blank spaces with no coloured line in the legend represent simulations where no bats developed the association between clicking and noxiousness.

I also assessed the influence of different learning rates on bat experience (Figure 12). At higher percentages (>20%) of noxious clicking moths the effect of learning is not as relevant to the percentage of experienced bats because the high percentage of clicking moths allows a high number of encounters between naïve bats and clicking moths. Even with the slowest learning rate (i.e. 11 encounters per day with noxious

clicking moths) over 90% of the bats became experienced (i.e. formed the association between moth clicks and noxiousness). However, learning rate does affect the time a bat population takes to reach these levels of experience. For example at a learning rate of 11 encounters per day it took about 30 days for over 90% of the bat population to become experienced. With faster learning rates (i.e. fewer than 9 encounters per day) at the same proportions of noxious clicking moths it took less than 6 days. On the other hand when the percentage of noxious clicking moths is low (2.3%) not even fast learning rates (3 encounters per day with noxious clicking moths) result in an appreciable proportion of the bat population becoming experienced even after 30 days (Figure 12), These results illustrate the importance of learning rate on the time it takes for a bat population to gain experience.

Rate of learning not only affects the time it takes for a bat population to gain experience, but also affects the proportion of bats that become experienced. The proportion of experienced bats increases dramatically when the proportion of noxious clicking moths is between 6% and 20% due to the influence of learning. At extreme noxious clicking moth percentages (i.e. below 4% and above 20%) the influence of learning on the percentage of experienced bats is limited. For example, at a noxious clicking moth percentage of 20% the percentage of experienced bats were all close to 100%, while at a noxious clicking moth percentage of 2.3% the percentage of experienced bats was equal to or below 10%.

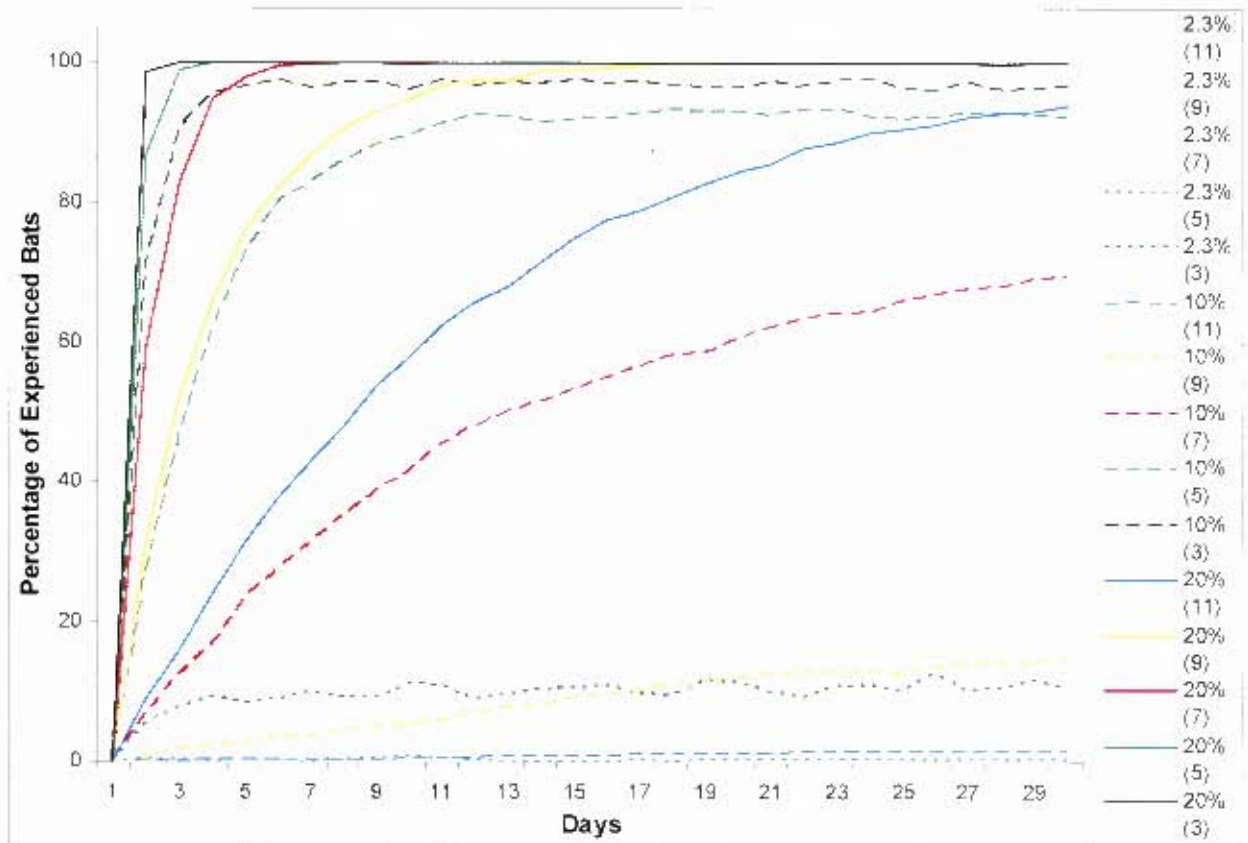


Figure 12. Effect of learning rate on bat experience under three different clicking moth percentages over 30 days. In total five learning rates (3, 5, 7, 9 and 11 encounters per day with noxious clicking moths) and three percentages of noxious clicking moths (2.3%, 10% and 20%) were run in the simulations. The legend indicates the percentage of clicking moths with the learning rate in brackets below. The simulations were all run with a reinforcement rate of 1 encounter per day with a noxious clicking moth. **Note:** Due to the random generation of the placement of noxious clicking moths within the simulation by the learning program repeated simulations under the same setup showed small variations in the results. Blank spaces with no coloured line in the legend represent simulations where no bats developed the association between clicking and noxiousness.

The reinforcement rate had a clear effect on the proportion of experienced bats. At a percentage of 20% noxious clicking moths the decrease in the reinforcement rate (i.e. more encounters are required to reinforce the association) caused a clear decrease in

the percentage of experienced bats (Figure 13). For example at the default reinforcement rate (i.e. 1 encounter per day) the percentage of experienced bats was close to 100%, but at the highest reinforcement rate the percentage of experienced bats was only 60% and it took longer to reach this level. This effect was even more pronounced at intermediate proportions of noxious clicking moths (i.e. 10%) where there was a decrease from 75% to about 7% in the proportion of experienced bats when the reinforcement rate decreased from 1 to 7 encounters need for reinforcement. At a proportion of 2.3% of noxious clicking moths the reinforcement rate had no influence because learning has to occur before reinforcement can occur.

In summary all three components influenced the percentage of experienced bats and the time it took for an appreciable proportion of the bat population to become experienced. However, both learning and reinforcement were strongly influenced by the proportion of noxious clicking moths in the moth population, with learning having a more noticeable effect on the time a bat population takes to gain experience; while reinforcement rate has a noticeable effect on the actual final percentage of experienced bats in the bat population.

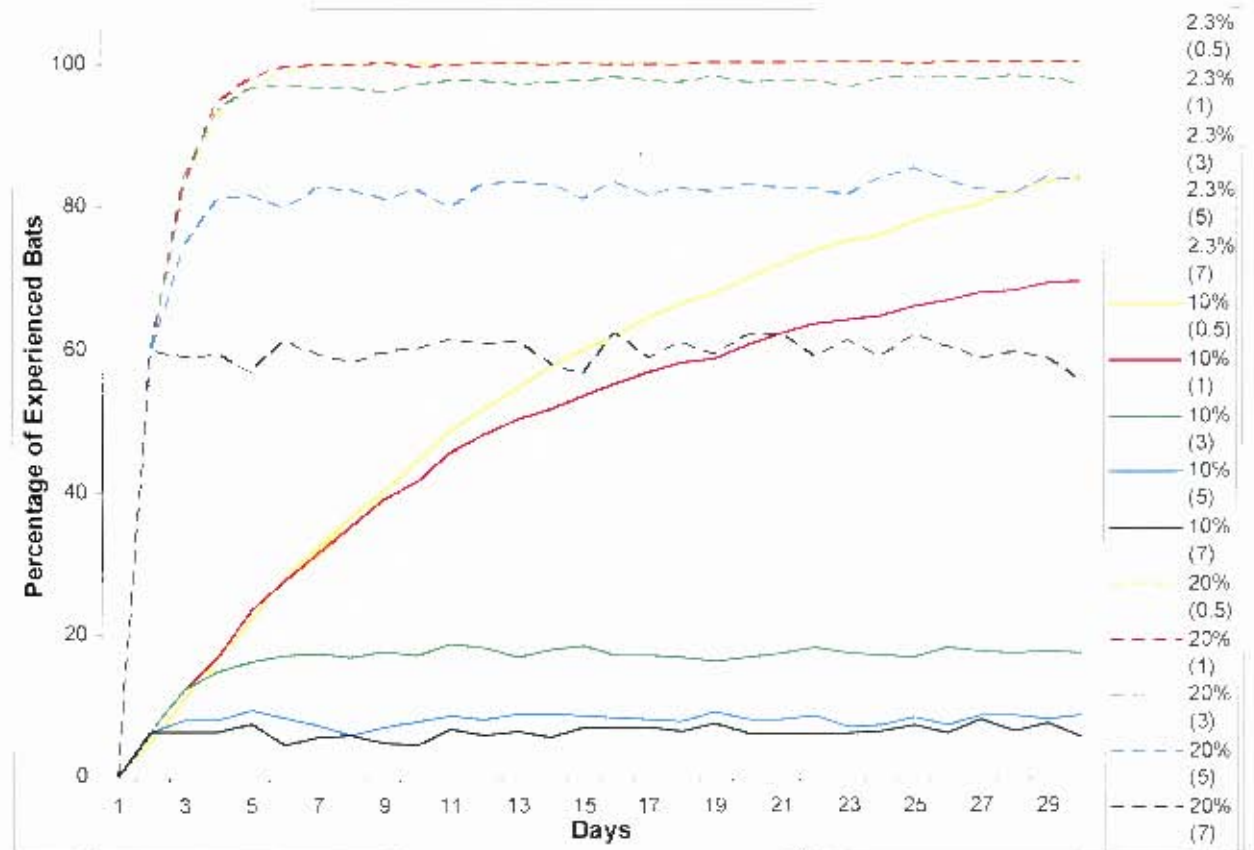


Figure 13: Effect of reinforcement rate on bat experience under three different clicking moth percentages, over 30 days. In total five reinforcement rates (0.5, 1, 3, 5, and 7 encounters with a noxious clicking moth per day) and three percentages of clicking moths (2.3%, 10% and 20%) were run in the simulations. The legend indicates the percentage of clicking moths with the reinforcement rate in brackets below. The learning program simulations were all run with a learning rate of 7 moths. Note: Due to the random generation of the placement of clicking moths within the simulation by the learning program repeated simulations under the same setup showed small variations in the results. Blank spaces with no coloured line in the legend represent simulations where no bats developed the association between clicking and noxiousness.

Based on the results from the learning program each predation rate was run under four different noxious clicking moth percentages (2.3%, 8%, 14%, and 20%). The clicking moth percentages chosen covered the actual percentages found in the field to

the proportion of noxious clicking moths (i.e. 20%), at which almost all bats (99.9%) were experienced (Figure 11, 12 and 13). The trend between the different clicking moth percentages and the predation rates was similar between all four rates of predation, so the default medium predation rate was used to illustrate these trends and the corresponding predation values are given in Table 6.

At 2.3% the proportion of clicking moths is too low to allow the aposematic strategy to function. This would imply that a clicking moth would depend solely on its hearing to avoid bat predation. This would result in the simulations under 2.3% noxious clicking moths to have exactly the same output as the hearing model. However, there is evidence that some clicking species do not perform evasive manoeuvres when under bat predation as they are relying solely on the success of the clicks (Evans 1983; Dunning and Kruger 1995). This implies that if for some reason clicks do not deter bats the defences of the moth would be below that of hearing and more similar to that of the earless moth model. Therefore, simulations were run both under the assumption that clicking moths perform evasive manoeuvres (i.e. similar to hearing moths) and that they do not perform evasive manoeuvres (i.e. similar to earless moths). Due to the dominance (i.e. most common moth type in field data) of hearing moths all the simulations from other models were compared to the results from the hearing model. I have not presented the results from the simulations that used the assumption that clicking moths behaved like hearing moths, when the clicks did not function, because they were the same as that from the hearing model. When the percentage of clicking moths becomes high enough to allow bats to gain experience, the aposematic function of the clicks becomes the determining defensive strategy.

Table 6: The different predation levels for the medium predation rate based on the four different percentages of aposematic (i.e. clicking) moths (2.3%, 8%, 14% and 20%) and the corresponding percentage of experienced bats each of the four percentages of clicking moths can sustain (0, 34%, 98% and 99% respectively). Please note: In total, for all simulation, four different efficiency rates for each of the four predation rates (P), four carrying capacities (KL, KM, KH and KX) and ten reproduction rates (R 0.005, 0.01, 0.05, 0.1, 0.5, 1, 2, 3, 4, 5) were used, resulting in 640 simulation variations for the jamming moth model. The maximum predation rate (XD) is derived from the earless moth model (i.e. assumption that moths do not perform evasive manoeuvres).

	Aposematic Ratio	Annual Predation Level	Annual Predation Level
Low (L)	20%	99%	80,781
Medium (M)	14%	98%	1,615,621
High (H)	8%	34%	28,273,373
Maximum (X)	2%	0	137,149,518

The general trend for the aposematic model when compared to the hearing model is similar to that of jamming. At a proportion of 8% of noxious clicking moths aposematism decreased predation by about 34%, allowing the aposematic model to obtain higher stable points than the hearing model at reproduction rates around 2 or below (Figures 14, 15, 16 and 17). The biggest advantage of the aposematic model over the hearing model is at lower reproduction rates where the aposematic model finds stability at lower reproduction rates just above 0.1, while the hearing model requires reproduction rates above 1. The advantage of the aposematic model at lower reproduction rates increases as the proportion of clicking moths increased and as the carrying capacity increased (Figures 14, 15, 16 and 17).

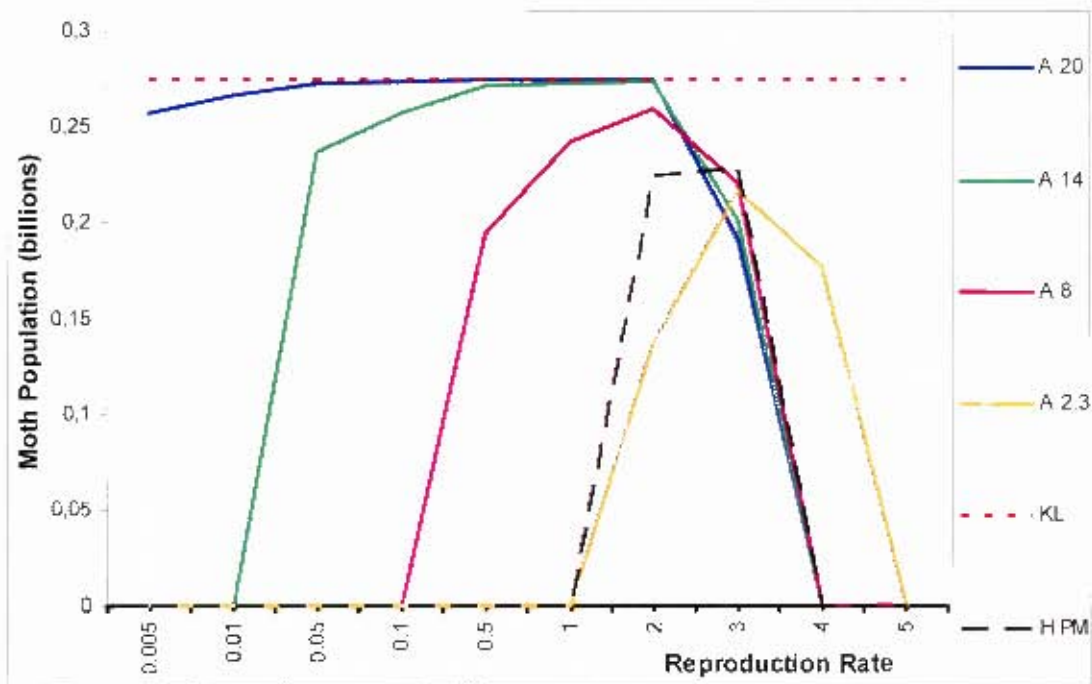


Figure 14. The aposematic model versus the hearing model within a low carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (2.3%, 8%, 14% and 20% aposematic moths). This graph shows the simulation results only for medium predation (PM). The solid lines represent the aposematic model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KL). The four percentages of aposematic moths are indicated in the legend as follows A2.3 (Medium Predation Rate at 2.3% aposematic moths), A8 (Medium Predation Rate at 8% aposematic moths), A14 (Medium Predation Rate at 14% aposematic moths), A20 (Medium Predation Rate at 20% aposematic moths).

As the reproduction rate increases the advantage of the aposematic model starts to decrease causing a general conversion around reproduction rate 3. This is the only situation that allows the hearing moth to out-compete the aposematic moth. This trend is found in most of the models due the high reproduction rate that can compensate for the effect of predation, and the lower resource depletion at higher reproduction rates.

At higher reproduction rates both the aposematic and hearing model where unstable at reproduction rates above 4.

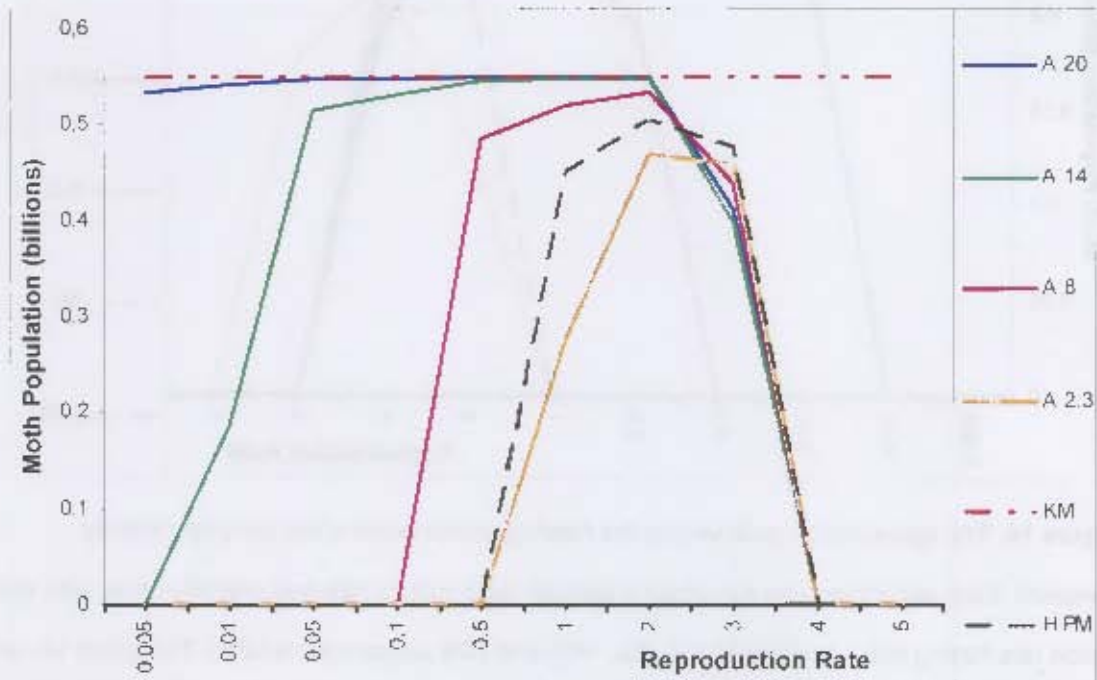


Figure 15. The aposematic model versus the hearing model within a medium carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (2.3%, 8%, 14% and 20% aposematic moths). This graph shows the simulation results only for medium predation (PM). The solid lines represent the aposematic model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KM). The four percentages of aposematic moths are indicated in the legend as follows A2.3 (Medium Predation Rate at 2.3% aposematic moths), A8 (Medium Predation Rate at 8% aposematic moths), A14 (Medium Predation Rate at 14% aposematic moths), A20 (Medium Predation Rate at 20% aposematic moths);

The uniqueness of the aposematic models is its dependence on the density of noxious clicking moths. The aposematic model requires a minimum percentage of noxious clicking moths to function and reacts strongly to increases in the percentage of

clicking moths and learning rates of bats. The field data showed that clicking moths only compose 2.3% of the moths caught. At the default setup (i.e. learning rate of 7 encounters within a day and reinforcement rate of one encounter per day the program simulations showed that at 2.3% the aposematic strategy does not have enough moths to allow bats to form the association between the moth's clicks and the moth's noxiousness. Even changing the settings did not change the outcome much, with the highest learning rates resulting in only 10% of the bats becoming experienced.

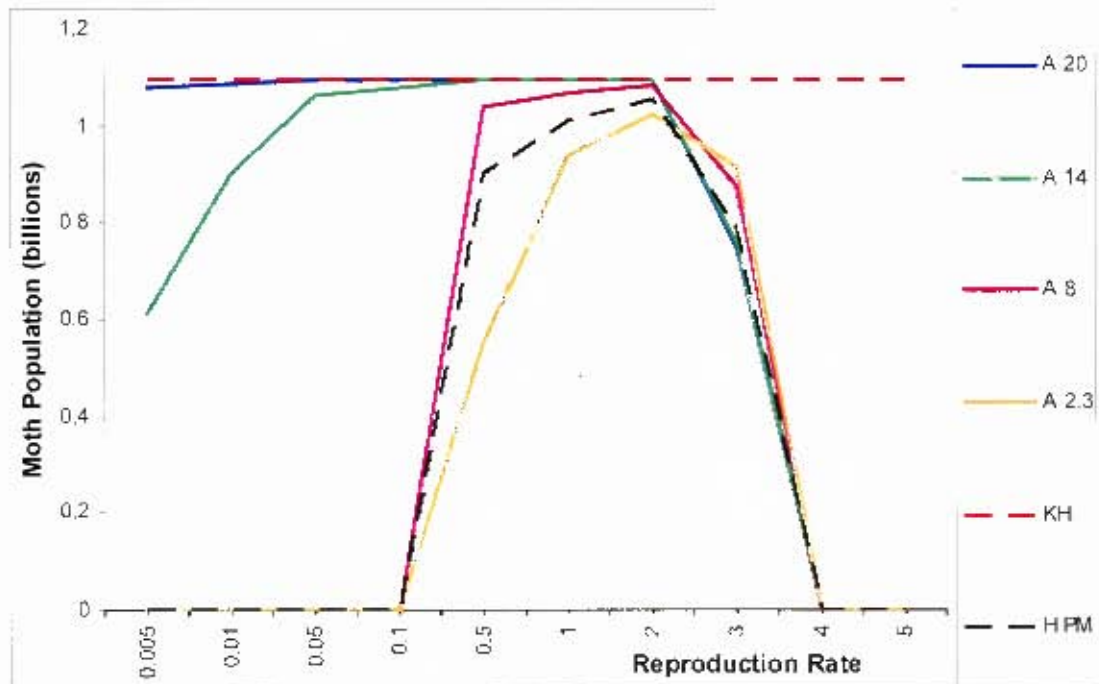


Figure 16: The aposematic model versus the hearing model within a high carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (2.3%, 8%, 14% and 20% aposematic moths). This graph shows the simulation results only for medium predation (PM). The solid lines represent the aposematic model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KH). The four percentages of aposematic moths are indicated in the legend as follows: A2.3 (Medium Predation Rate at 2.3% aposematic moths), A8 (Medium Predation Rate at 8% aposematic moths), A14 (Medium Predation Rate at 14% aposematic moths), A20 (Medium Predation Rate at 20% aposematic moths).

In general the aposematic model out-competed the hearing model (blue, green and pink line in Figures 14, 15, 16 and 17). The only simulation in which the aposematic model did not out-compete the hearing model was when the percentage of clicking moths was too low to allow bat learning (orange line in Figures 14, 15, 16 and 17). For example in the simulations with the percentage of noxious clicking moths set at 2.3%

(i.e. percentage of clicking moths found in the field) the aposematic function of the clicks is absent, leaving the clicking moth mainly dependent on startle or hearing related defences. In theory an aposematic moth is also a hearing moth and should benefit from hearing when the aposematic function of the clicks is absent.

However, some studies have shown that clicking moths do not always perform evasive manoeuvres (Dunning and Kruger 1995), which would render these clicking moths more vulnerable than hearing moths when the aposematic function of their clicks is absent. This is reflected in the simulation which shows that when the moths do not perform evasive manoeuvres they are out-competed by the hearing moths. When the moths performed evasive manoeuvres similar to hearing moths the simulations yielded the same results as the hearing model. Only 5 species of moths at Algeria Forestry Station clicked, comprising only 1.8% of the morph-species richness, but contributing 2.3% of the total moth abundances (chapter 2). The level of abundance for the two main clicking species was higher than any non-hearing moth species. This suggests the success of these species, which could be due to their hearing. This success may not necessarily be due to evasive manoeuvres, but the moths ability to move away from areas with high bat activity (i.e. moths hear bat calls from a distance and move in the opposite direction).

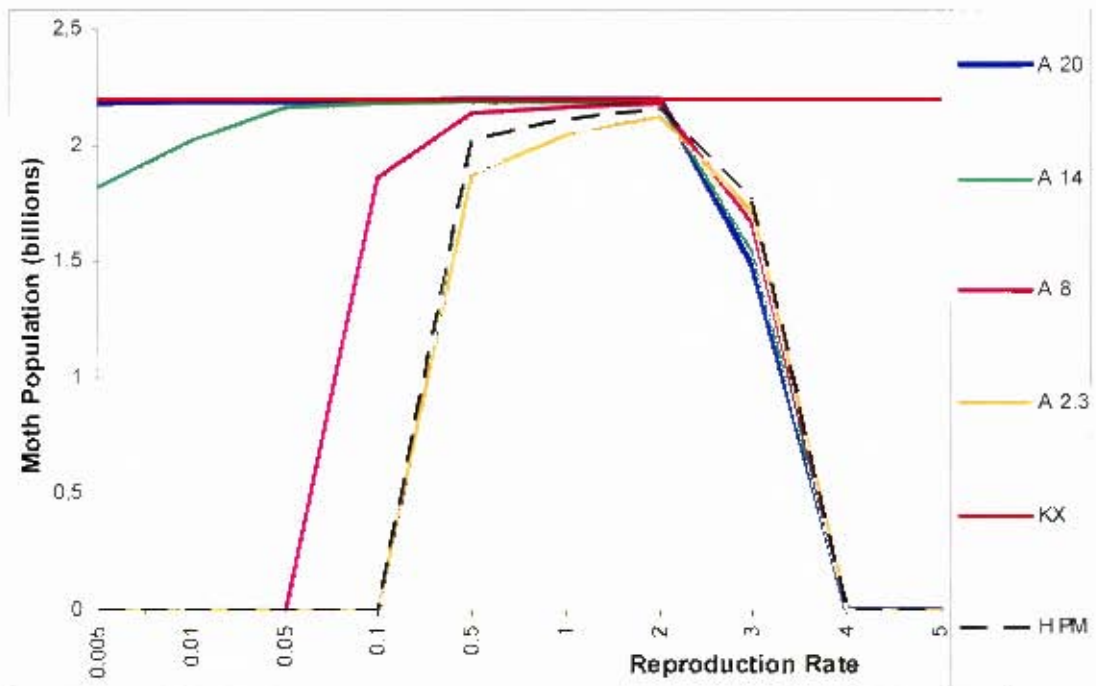


Figure 17: The aposematic model versus the hearing model within a maximum carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having four variations (2.3%, 8%, 14% and 20% aposematic moths). This graph shows the simulation results only for medium predation (PM). The solid lines represent the aposematic model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KX). The four percentages of aposematic moths are indicated in the legend as follows A2.3 (Medium Predation Rate at 2.3% aposematic moths), A8 (Medium Predation Rate at 8% aposematic moths), A14 (Medium Predation Rate at 14% aposematic moths), A20 (Medium Predation Rate at 20% aposematic moths).

Startle Moth Model

As with the aposematic model the startle model is also density dependent, but negatively affected by increases in clicking moth density. Contrary to the aposematic strategy the startle strategy is therefore most effective with naïve bats. As bats become increasingly exposed to moth clicks they start to habituate to the clicks removing the startle effect and decreasing the success of the strategy. Bats require as little as three encounters to habituate to moth clicks if no noxiousness is linked to the clicks (Bates and Fenton 1990). Habituation is a form of learning and I used the same learning program used in the aposematic model to investigate bat habituation. Low levels of clicking moths are enough to allow a high level of habituation. A percentage of 4% of clicking moths was enough to habituate about 40% of the bats. An increase in the percentage of clicking moths from 4% to 6% increased the number of habituated bats to about 75% and at a percentage of 10% of clicking moths the percentage of habituated bats was close to 100.

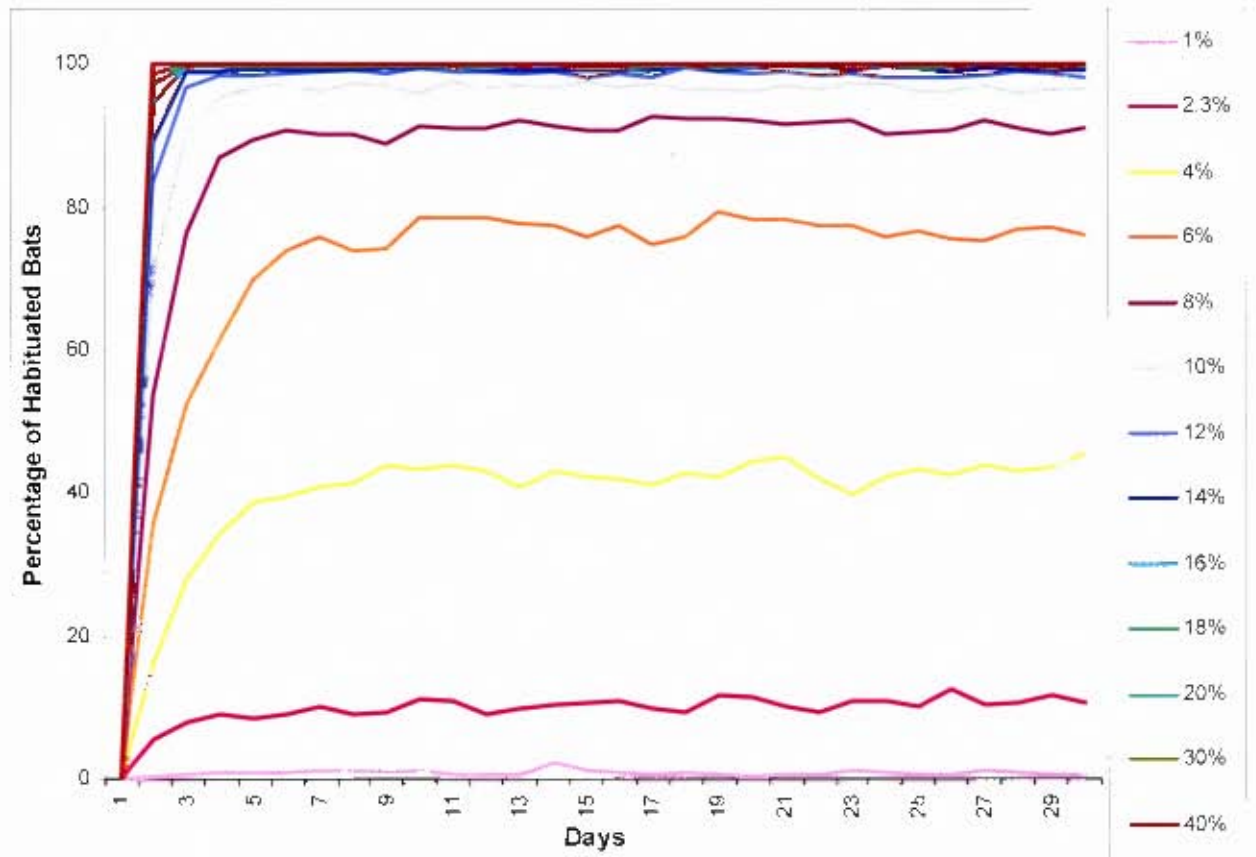


Figure 18: Effect of clicking moth percentages on bat habituation for the startle strategy over 30 days. The learning program simulations were run with a learning rate of 3 and a reinforcement rate of 1 moth a day. Only the percentage of clicking moths was changed and is indicated in the legend. Due to the random generation of the placement of clicking moths within the simulation by learning program repeated simulation under the same set-up showed small variations in the results.

The influence of learning rate on the percentage of habituated bats is the same as that found for the aposematic model in which the learning program simulated learning rates from fast (three encounters) to slow (11 encounters, Figure 12). This range covers the viable learning rates of habituation. The only simulation not covered is for learning rates below three, which showed an extremely high level of bat habituation

(more than double that of the default learning rate of three) even at very low clicking moth percentages, making the startle strategy less viable to almost impossible.

The assessment of the importance of the reinforcement rate was run at a default learning rate of three. As with the aposematic model the increase in the reinforcement rate can decrease the percentage of habituated bats. In the simulation with the clicking moth proportion set at 10% a change from a reinforcement rate of 1 to 3 encounters a day resulted in a 20% plus decrease in the percentage of habituated bats. The decrease of the reinforcement rate can also increase the viable percentage of experienced moths as can be seen in the 2.3% simulation. At the default setting the percentage of experienced bats is just below 5 %, but at a reinforcement rate of 1 encounter every 2 days the percentage of experienced moths rose to above 20% (Figure 19).

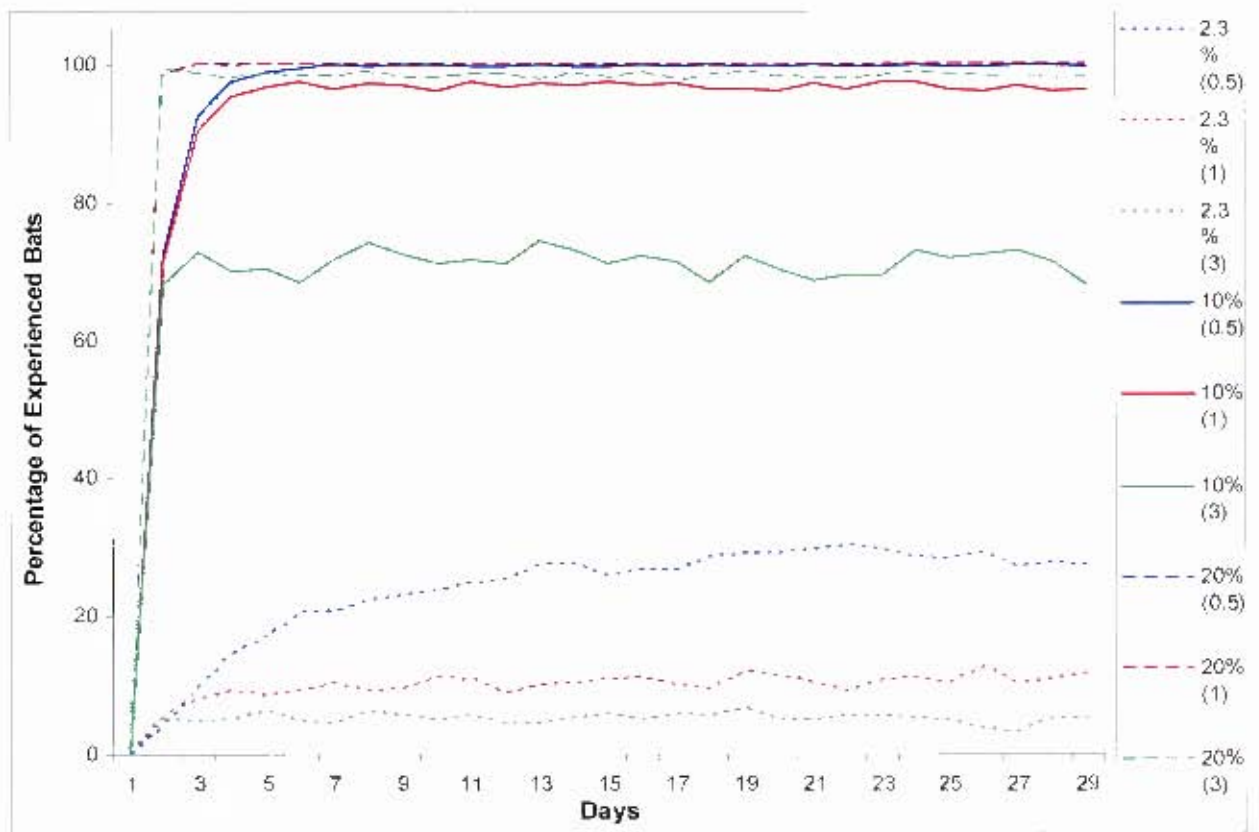


Figure 19: Effect of reinforcement rate on bat experience under three different clicking moth percentages for the startle strategy over 30 days. In total five reinforcement rates (0.5, 1, 3, 5, and 7 encounters per day with clicking moths) and three percentages of clicking moths (2.3%, 10%, and 20%) were run in the simulations. The legend indicates the percentage of clicking moths with the reinforcement rate in brackets below. The learning program simulations were all run with a learning rate of 3 moths per day. Due to the random generation of the placement of clicking moths within the simulation by the learning program repeated simulations under the same setup showed small variations in the results. Blank spaces with no coloured line in the legend represent simulations where no bats developed the association between clicking and noxiousness.

Based on the results from the learning program three clicking moth percentages were chosen to assess the competitiveness of the startle strategy (Table 7). Some studies

report that clicking moths do not take evasive manoeuvres in response to ultrasonic pulses as often as other hearing species (Dunning *et al* 1992, Dunning and Kruger 1995). This implies clicking moths rely more on clicking to escape bat predation than hearing. If this is the norm then the full advantages of hearing would not be applicable to clicking moths as usually assumed. This will effect moths employing the startle strategy most when the strategy is not working (e.g. because of habituation) as they would not be gaining advantages from hearing or clicking. Thus a fourth predation rate (XD, Table 7) was used to determine the success of the startle model when the hearing advantage was negatively impacted by the startle strategy (i.e. clicking). The predation advantages from hearing were removed and the relative predation rate calculated with the proportion of clicking moths set 10% because it is under these conditions (i.e. startle model does not function) that the impacts are most felt.

Table 7: The different predation levels for the medium predation rate based on the three different percentages of startle (i.e. clicking) moths (2.3%, 6% and 10%) and the corresponding percentage of naive bats each of the three percentages of clicking moths can sustain (98%, 25% and 2% respectively). In addition to this a four predation value was used based also on 10% startle moths, but without the advantages gained form hearing. This translates to these moths having the same success as earless moths against experienced bats that have habituated to the clicks. Please note: In total, for all simulation, four different efficiency rates for each of the four predation rates (P), four carrying capacities (KL, KM, KH and KX) and ten reproduction rates (R 0.005, 0.01, 0.05, 0.1, 0.5, 1, 2, 3, 4, 5) were used, resulting in 640 simulation variations for the jamming moth model.

	Startle Ratio	Annual Predation Level	Annual Predation Level
Low (L)	2%	98%	1,615,621
Medium (M)	6%	25%	60,585,799
High (H)	10%	2%	79,165,445
Maximum (X)	10%	2%	134,406,528

The simulations were run under two different methods. The original method had continuous adjustment of the percentage of habituated bats in relation to the percentage of clicking moths obtained from the learning program. However, the moth population always started at carrying capacity, which caused a very rapid habituation of the bat population. This habituation neutralized the advantage of startle and resulted in simulation results similar to the hearing model (similar to Figures 3, 4, 5 and 6). Even when the simulations were started at low moth numbers the relatively high stable points, even of the earless moth model, allowed for a rapid habituation by the bat population. After various simulations under numerous settings the overall conclusion was that the moth populations easily and almost always exceeded the startle model's very low number of clicking moths required to habituate a large part (if not all) of the bat population. This eliminated the startle effect of the model making it react like the hearing or earless moth model under the assumption that clicking moths do not perform evasive manoeuvres. The high stable points were due to the simulations independent resource utilization by each of the models, which eliminates competition and allows each model to react solely to the changes in reproduction, predation and the environment's carrying capacity. However, a good understanding of the model's basic dynamics is vital and the first steps for reliable deductions on the competitive nature of the model. Thus an alternative method was used to run the simulations.

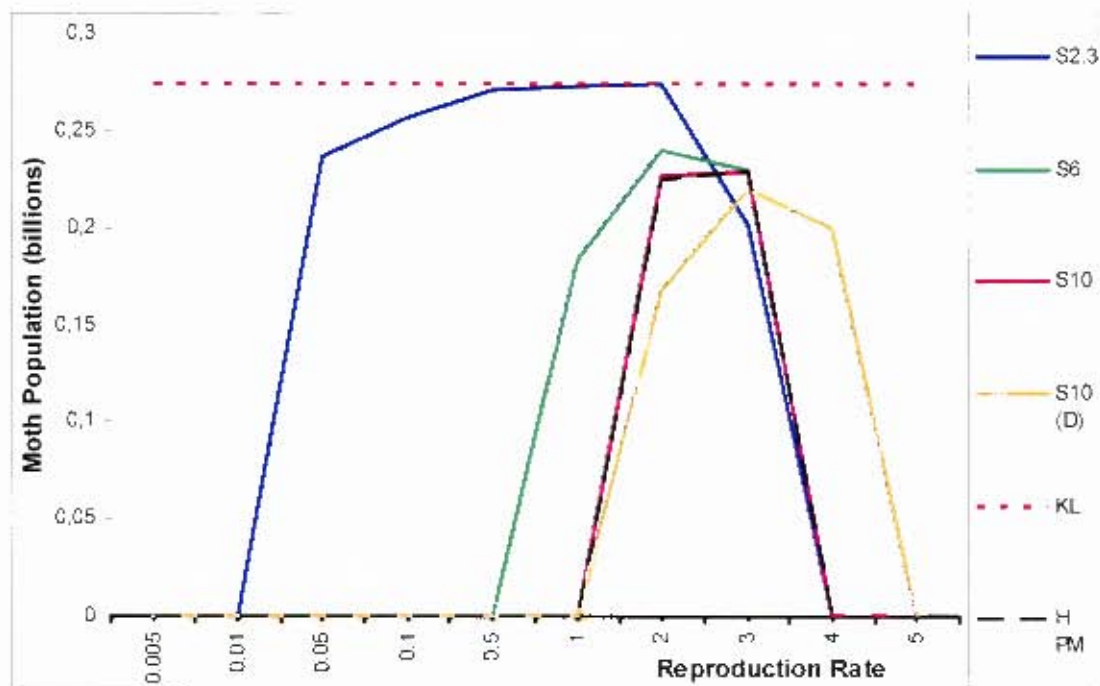


Figure 20 The startle model versus the hearing model within a low carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having three variations (2.3%, 6% and 10% startle moths). An additional setup with 10% startle moths was also included, but where the assumed advantage of hearing is removed making the startle moth react like an earless moth against experienced bats. This graph shows the simulation results only for medium predation (PM). The solid lines represent the startle model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KL). The three percentages of startle moths are indicated in the legend as follows S2.3 (Medium Predation Rate at 2.3% startle moths), S6 (Medium Predation Rate at 6% startle moths), S10 (Medium Predation Rate at 10% startle moths). The S10 (D) (Medium Predation Rate at 10% startle moths, but without the advantages of hearing).

In the second method (Figures 20, 21, 22 and 23) the predation rates at specific percentages of clicking moths were used to better understand the competitive characteristics of the startle model under different conditions. These simulations with a fixed predation rate showed a similar trend to that of other models in the sense that the

decrease in predation rates due to hearing and startle increased the stable points and the range of viable reproduction rates. However, as the reproduction rates increased the advantage decreased causing a convergence at reproduction rates between two and three. The lower resource depletion of higher predation rates creates conditions for setups with weaker defensive properties to out-compete settings and models that show a lower predation rate gained in their defensive strategies.

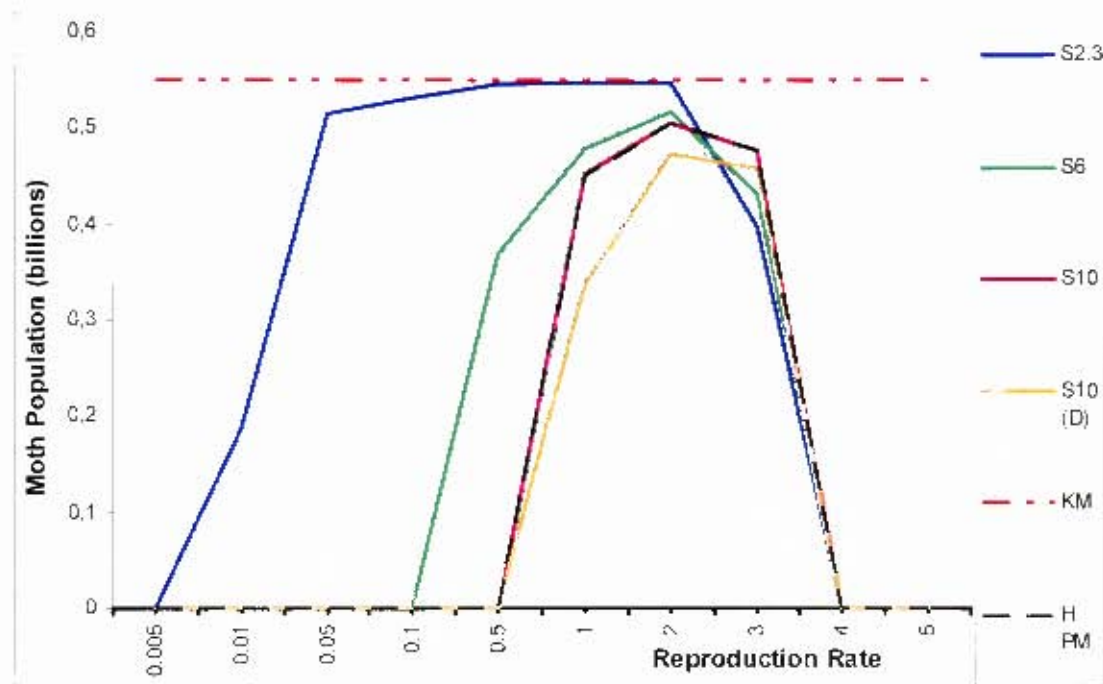


Figure 21: The startle model versus the hearing model within a medium carrying capacity

environment. Each simulation was run under a specific reproduction rate and predation rate with each predation rate having three variations (2.3%, 6% and 10% startle moths). An additional setup with 10% startle moths was also included, but where the assumed advantage of hearing is removed making the startle moth react like an earless moth against experienced bats. This graph shows the simulation results only for medium predation (PM). The solid lines represent the startle model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KM). The three percentages of startle moths are indicated in the legend as follows S2.3 (Medium Predation Rate at 2.3% startle moths), S6 (Medium Predation Rate at 6% startle moths), S10 (Medium Predation Rate at 10% startle moths). The S10 (D) (Medium Predation Rate at 10% startle moths, but without the advantages of hearing),

The highest stable point (i.e. most successful) in the startle model was found with a clicking moth percentage of 2.3% (Blue line in Figures 20, 21, 22 and 23) which is the proportion that clicking moths made up of the moth population in the field. The lower predation rate also allowed the moth population to find stability at very low reproduction

rates. As the percentage of clicking moths increased the success of the startle model decreased until reaching a level at which the majority of the bats were experienced and no longer reacted to the startle effect of the clicks. This shows the negative correlation between the percentages of clicking moths and the success of the strategy. Thus the low percentage of clicking moths caused the percentage of clicking moths to increase at a decreasing rate until the startle effect is neutralised. This means that clicking moths only have hearing as a defence and the higher predation rate starts to decrease the moth population towards the levels of the hearing moth model. This occurs in the early phases and soon after the startle model becomes like the hearing model. The big advantage of the startle strategy occurs when conditions get extremely harsh and the population decreases to very low levels. In small moth populations the strong resilience of the startle model to bat predation would allow moths using the startle strategy to survive these bad years.

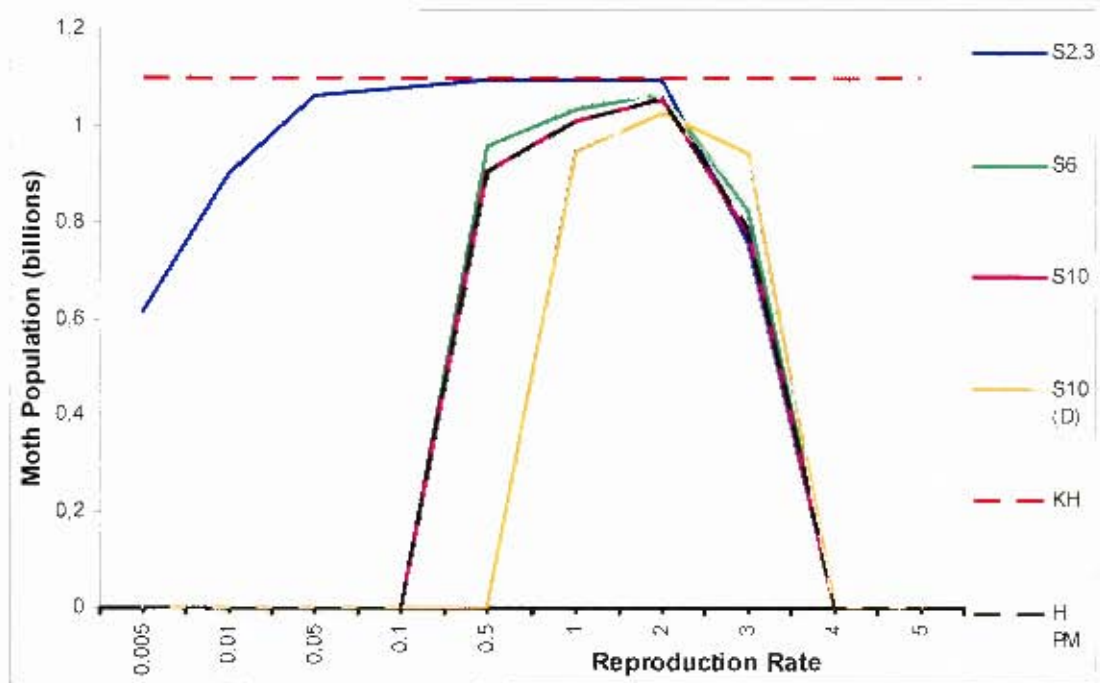


Figure 22: The startle model versus the hearing model within a high carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having three variations (2.3%, 6% and 10% startle moths). An additional setup with the proportion of clicking moths set at 10% was also included, but where the assumed advantage of hearing is removed making the startle moth react like an earless moth against experienced bats. This graph shows the simulation results only for medium predation (PM). The solid lines represent the startle model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KH). The three percentages of startle moths are indicated in the legend as follows S2.3 (Medium Predation Rate at 2.3% startle moths), S6 (Medium Predation Rate at 6% startle moths), S10 (Medium Predation Rate at 10% startle moths). The S10 (D) (Medium Predation Rate at 10% startle moths, but without the advantages of hearing).

Clicking moths would not have the advantages associated with hearing when habituation renders clicks disfunctional if moths do not take evasive action when hearing an approaching bat. At a proportion of 10% of clicking moths the majority of the bat population is already habituated to the clicks neutralizing the advantage of the startle effect of the clicks. Simulations under the assumption that clicking moths do not perform evasive manoeuvres (orange line Figures 20, 21, 22 and 23) yielded a lower stable point when compared to the hearing model. The learning program showed that at a clicking moth percentage of 6%, 75% of the bats were habituated, which makes the startle strategy less advantageous than the hearing model. At a percentage 4% of clicking moths 40% of the bats have habituated, which places the startle strategy at a similar competitive level with a hearing strategy, with both having around 40% higher success rate than an earless moth employing neither strategy. The problem with this is that below 4% bat predation on clicking moths would be very low and the advantage of the strategy would cause the population of clicking moths to grow causing a rapid habituation of the bats and the subsequent increase in predation which would not allow the startle model high enough numbers to out-compete the hearing model.

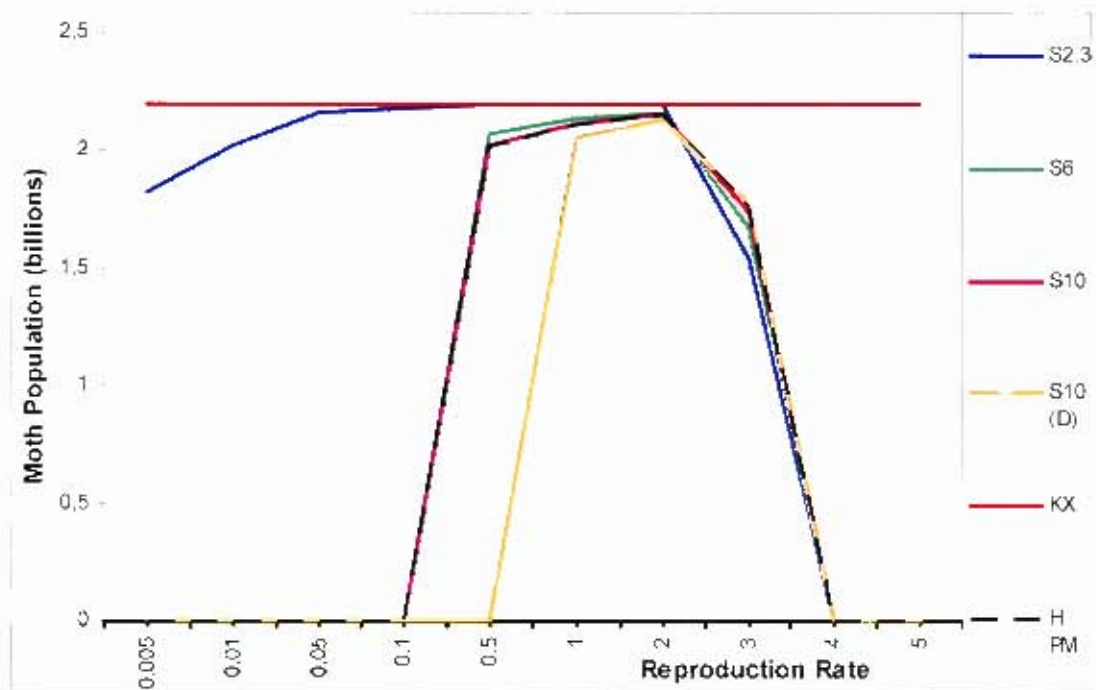


Figure 23: The startle model versus the hearing model within a maximum carrying capacity environment. Each simulation was run under a specific reproduction rate and predation rate, with each predation rate having three variations (2.3%, 6% and 10% startle moths). An additional setup with 10% startle moths was also included, but where the assumed advantage of hearing is removed making the startle moth react like an earless moth against experienced bats. This graph shows the simulation results only for medium predation (PM). The solid lines represent the startle model and the black dotted line represents the hearing model (indicated by H in the legend) under the same medium predation (PM). The red line across the graph indicates the carrying capacity (KX). The three percentages of startle moths are indicated in the legend as follows S2.3 (Medium Predation Rate at 2.3% startle moths), S6 (Medium Predation Rate at 6% startle moths), S10 (Medium Predation Rate at 10% startle moths). The S10 (D) (Medium Predation Rate at 10% startle moths, but without the advantages of hearing).

Discussion

In general the differences between models decreases with the increase in reproduction and the increase in carrying capacity. At very high reproduction rates the high growth of the moth population causes resource depletion and under certain conditions allows strategies with higher predation rates to out-compete strategies with lower predation rates. Higher carrying capacities allow for larger moth populations, which not only makes the number of moths removed by predation relatively smaller, but allows moth population to sustain high levels of predation during the low reproductive phase of the year and still have a large enough population to make a strong recovery during the high reproductive phase of the year.

Hearing vs. Earless

The simulations support the results from the field data in chapter two, with a clear dominance of hearing moths over earless moths throughout most of the simulations. This dominance decreased with an increase in both reproduction and carrying capacity. The three higher carrying capacities (KM, KH and KX) show a clear conversion of stable points in the high reproduction rates around 3 (Figures 4, 5, 6), with even slightly higher stable points found for earless moths than hearing moths in certain simulations (e.g. KM PL, KH PM, KX PL, KX PH). These higher stable points for the earless moth model are mainly due to lower resource depletion, Independent resource utilization for moths using the two strategies would thus be required for the earless moth model to out-compete the hearing model. This apparently does not occur in the field because earless moths comprised only 7.3% of the moth population at Algeria Forestry Station (chapter 2). If some of the earless moth species make sole use of a resource and have high

reproduction rates, the resource may become limited resulting in a much lower carrying capacity. Such a scenario could be possible with specialist feeders feeding on a unique resource, which would prevent hearing moths completely out-competing earless moths and allowing the existence of a low proportion of earless moths. This and other non-hearing defences (Rydell 1998, Soutar and Fullard 2004) could explain the continued existence of moths employing an apparently less competitive strategy at Algeria Forestry Station (. However, this is purely speculative and the persistence of earless moths could just as likely be due to alternative defence mechanisms against predation such as behavioural (e.g. decreased flight or flight at different times), anatomical (e.g. hairs and spines) or morphological (e.g. too big or too small) mechanisms.

Jamming

Based on the simulations jamming should be a very successful strategy allowing jamming moths to out-compete hearing moths, resulting in higher proportions of clicking moths than hearing moths. However, this is not supported by the field data in which hearing moths made up by far the largest proportion of the moth population. A possible scenario in which the hearing strategy could be more advantageous than the jamming strategy is if moths using the jamming strategy have significantly lower reproduction rates. The significantly lower reproduction rates of jamming moths would cause a slower growth of the population and the equilibrium between predation rate and reproduction may result in a lower stable point than that of hearing moths. Lower reproductive rates could arise if moths using the jamming strategy have higher physiological costs of development (e.g. because they have to develop tymbals) which could also increase the development phase (e.g. increase in the time it takes from

caterpillar to moth) or directly decrease the reproductive output as a result of allocating resources away from reproduction. If jamming moths use a different resource that is nutrient weak resulting in lower carrying capacities, this could also prolong development and decrease reproduction output. For example in a low carrying capacity setup a hearing moth can out-compete a jamming moth with a 25% efficiency if the hearing reproduction rates is around 2 and the jamming reproduction is around 1. In medium and high carrying capacity environments the hearing model can out-compete the jamming model with a jamming efficiency of 50% if the hearing reproduction rate varies between 2 to 3 and the jamming is below 1. The hearing model can even out-compete the jamming model set at a high 75% efficiency as long as the reproduction rate is at 2 and the jamming models reproduction rate is below 0.5. At jamming efficiencies above 75% the hearing model doesn't out-compete the jamming model even if the reproduction rates of jamming are very low. Furthermore, if the carrying capacity of moths using jamming was lower than that of moths using hearing as a result of the use of different resources, it implies that the two strategies are not competing and are reacting to predation independently with other factors influencing their success. This is not the case at Algeria Forestry Station where the all the clicking moths belonged to the same sub-family as a non-clicking moth, the *Lithosiinaea*. Although this sub-family is known to feed on lichens which could be regarded as a limited resource resulting in low carrying capacities and the dominance of the clicking moths, at least in this subfamily. However, the non-clicking form was the more dominant (Chapter 2). In general only very narrow and specific conditions allow for hearing moths to out-compete jamming moths, with most of these conditions representing extreme and unlikely differences in reproduction.

Aposematism

Like the jamming model, the aposematic model also out-competes the hearing model. However, the aposematic model is density dependent and only shows a high level of success when the percentage of clicking moths is high enough to allow for a significant number of bats to form the association between the clicks and the moths noxiousness. However, the field data shows that only 2.3% of the moths at Algeria Forestry Station clicked. Based on the results from the learning program this proportion is too low to allow the bat population to form the association between clicks and the moth's noxiousness. The simulations at this low proportion of clicking moths (2.3%) illustrates the weak competitive ability of the aposematic model at low percentages of clicking moths and allows for a higher dominance of hearing moths as seen in the field data. (orange line in Figures 14, 15, 16 and 17). Thus the function of the clicks produced by moths at Algeria forestry station is presently not aposematic. However, the clicks still have the potential to gain an aposematic function if the moths that click and also have noxious properties increase in numbers to a level that would allow the bat population to gain experience.

It is possible that the habitat plays a role in the success of a particular strategy reducing the prevalence of a superior strategy. Moths using the aposematic strategy must be unpalatable and need to obtain noxious chemicals from their food, making these moths dependent on specific plant species. If these plants are in low abundance as they may be in the fynbos biome where plants rich in toxins such as pyrrolizidine alkaloids are rare, they may only support a limited number of species using the

aposematic strategy. Alternatively the history of the area could be the reason why so few clicking moth species exist. The Western Cape fynbos biome has a high level of endemism and is considered a glacial refuge with a unique Mediterranean climate that differentiate it from the surrounding biomes. During the glacial period that occupied more than 90% of the last 1.5 million years many primitive species persisted due to freedom from glaciations resulting in a high level of diversity (Cowling and Richardson 1995). If clicking is a more derived character these moth species would have a harder time establishing due to a high level of competition, especially considering that any species invading from the surrounding biomes, which have a different climate to that of the fynbos, would not be as well adapted to the unique fynbos biome as the species already existing there.

Startle

Simulations suggest that the startle strategy only works at very low proportions because even low numbers of clicking moths are enough to allow the habituation of a large number of bats which neutralizes the effect of the clicks. For example a small increase from 2.3% to 6% in the proportion of clicking moths takes the percentage of habituated bats from below 10% to almost 80%. The clicking moth population would increase until reaching around 8% then start to decrease until it reaches low proportions again. This would cause the clicking moth population to fluctuate at around 8% abundance. This strategy also places selective pressure against too many species developing this strategy as it decreases the sustainability, which could explain the low number of species found clicking. At present the clicking population are just within sustainable numbers and any increase would affect the success of the startle strategy.

One can assume that the startle moths do have a strong probability of surviving harsh conditions if one considers that they can avoid the pressures of predation when the population reaches critically low numbers. The startle strategy could also give the moth a small window of a day or two before the bat population habituate, which could have a significant effect in mating or even decrease the cost of early emergence of individuals that belong to a species that relies on mass emergence.

The dynamics of the startle strategy could allow it to function in conjunction with the aposematic strategy. At low proportions the clicks could function as startle allowing clicking moths to increase to high enough numbers so that the aposematic function of the clicks become viable. This could be facilitated by the variability of clicks found in chapter two which could decrease the habituation rate and allow a higher percentage of clicking moths using clicks as startle.

In summary, mathematical modelling combined with field data from Algeria Forestry Station seems to suggest that the clicks produced by moths, at least at Algeria Forestry Station, have a startle function.

CHAPTER 4

Jamming, Aposematism or Startle?

Jamming

Neither the field data nor the modelling simulations supported a jamming function for moth clicks, at least at Algeria Forestry Station. If clicks functioned by jamming bat echolocation they should resemble bat echolocation calls in the approach to terminal phase of the echolocation sequence. Selection pressure would thus have reduced variability of the clicks as the clicks were increasingly selected to resemble bat echolocation calls. However, there was extreme variation in clicks within the same moth, between moths of the same species and between species, suggesting an alternative function for moth clicks (Chapter 2).

Furthermore, four of the five clicking moth species at Algeria Forestry Station had maximum clicking duty cycles well below the minimum duty cycle of 10%, which is the suggested duty cycle required for the clicks to have a disruptive effect on the perception of echoes by the bat's auditory system (Barber and Conner 2006). Only two individuals of the fifth species, *Marcopoliiana natalensis* (Sphingidae), showed a maximum duty cycle above 10% (i.e. 11.29%). However, I only caught males of this species and it is

unknown if females also click. If females do not click, then it is possible that the clicks produced by this species do not function in the context of bat predation but rather in the context of mate attraction.

Mathematical models based on the assumptions of the jamming hypothesis predicted higher proportions of clicking moths than non-clicking eared moths. However, the field data showed the opposite with eared moths being the most common. Even when one considers the possibility of higher reproduction rates for hearing moths, the simulations show that only in very specific and extreme setups would higher reproduction allow for hearing moths to out-compete jamming moths. The mathematical simulation did show that the use of a limited resource by jamming moths, resulting in a low carrying capacity, could allow hearing moths to out-compete jamming moths. However, within the group of four moth species at Algeria Forestry Station belonging to the sub-family *Lithosiinaea* that used a limited resource (i.e. lichens), it was the single hearing species rather than the three clicking species that dominated.

Aposematism

The unpalatability of clicking moths is a fundamental requirement for the functioning of aposematism (Rowe 1999). In general, moths obtain their noxious properties from specific host plants containing mainly pyrrolizidine alkaloids and polyphenolic compounds during both the larval and/or adult phase. Pyrrolizidine alkaloids are a large group of chemicals (usually N-oxides) with diverse structures (Boppré 1986, 1990, 1995; Hartman and Witte 1995; Roque-Albelo *et al.* 2002) and are commonly found in

plant genera such as *Heliotropium*, *Tournefortia*, *Eupatorium*, *Crotalaria*, *Senecio* (Boppré 1986) and *Asclepias* (Mabberley 2002). The latter three genera occur in the Cederberg area (Hutchinson 1946) and are known to confer their noxious properties to their lepidopteran herbivores (Mabberley 2002). Polyphenolic compounds are characterized by the presence of more than one phenol group per molecule and are commonly found in lichen (Weller *et. al* 1999). Three of the four clicking moths in this study belong to a sub-family that are known to feed on lichens (Scoble 2002).

Chemical analyses of the clicking moths were beyond the scope of a Masters thesis, so I did taste tests using human subjects as an alternative indicator of the noxiousness of the clicking moths at Algeria Forestry Station (see Dawson 1951 for methodology used and Manson and Koch 1953 for theoretical details). In total, 4 Arctiidae morphospecies, 3 Geometridae morphospecies, 3 Noctuidae morphospecies, 3 Sphingidae morphospecies and 2 controls, resulting in 15 samples, were tested by 4 human subjects in experimental trials. The 4 Arctiidae morphospecies included two of the most abundant clicking species (*S. montana* and *P. tephinata*) and the most common Arctiidae morphospecies, which is a closely related non-clicking moth from the same sub-family as the former Arctiidae clicking morphospecies. The other moth family with a clicking morphospecies was Sphingidae (*M. natalensis*), resulting in a total of three clicking species tested. The remaining non-clicking morphospecies were randomly selected among the morphospecies that had a large enough sample size. Crushed mealworms made up the initial control, with the second control being crushed mealworms with dry plant matter from a host plant known to have PA's (*Asclepias cancellata*, Mabberley 2002). Moths are known to obtain PA's from dry plant matter

(Boppré 1995; Brown *et al.* 1991), so the use of this second control was to determine if the human subjects could detect PAs.

The results from the taste tests showed that all four of the Arctiidea morphospecies were considered bad-tasting. Interestingly, the only Sphingidae morphospecies that was considered bad-tasting was not the clicking species (*M. natalensis*). This may be a further indication that perhaps ultrasound is not used in the context of predation in these moths, but rather in the context of mating. All the remaining moths were considered not to be bad-tasting, with the exception of one subject that classified a Noctuidae as bad-tasting. This moth was not included into the list of bad tasting moths, as the remaining three testers did not support the results. The control sample with the plant matter containing PAs was considered bad-tasting, while the control sample with only mealworms was considered the best tasting sample of the 15 tested.

Humans are capable of identifying a large group of PAs (Glendinning *et al.* 2001), however, the problem lies in the lack of information around the concentration to which humans and bats are sensitive. Nevertheless, there is an indication that at least two of the clicking moths at Algeria Forestry Station were noxious.

However, these results also indicate that all the Arctiidae were noxious, but they did not all click and that noxious non-clicking moths were more common than noxious clicking moths (of the 13 species tested 3 were noxious and not clickers, 1 was a clicker and not noxious and only 2 were noxious and clickers). A possible interpretation is that noxiousness arose earlier than clicking and has a strong association with phylogeny - all

Arctiidae were considered bad-tasting by the human subjects and made up 4 of the 5 noxious moths. There are many reports in the scientific literature on the noxiousness of the Arctiidae (e.g. Rothschild *et al.* 1970, Bates and Fenton 1990; Roque-Albelo *et al.* 2002; Hristov and Conner 2005). Thus, all the arctiids tested here were noxious but did not all click, supporting the view that noxiousness arose earlier. When clicking evolves in moths that are already noxious, conditions are set for aposematism to occur. If clicking evolves against bat predation within a species that is not noxious (e.g. *M. natalensis*), clicking may have a startle function. Alternatively, it may jam the bats echolocation calls by disrupting the perception of echoes by the bats' auditory system. If so, the clicks should be under selection pressure to conform to the functional constraints of disruptive jamming. Interestingly, *M. natalensis* is the only species of the clicking moths in this study that meets the maximum duty cycle required for the clicks to function as disruptive jamming. However, my results do not exclude the possibility that this is pure coincidence and that the clicks function in the context of mating rather than bat predation.

Further support for aposematism is that the clicks produced by the moths at Algeria Forestry Station fit the requirement that aposematic warning signals should be distinguishable and conspicuous. However, the high variability of the clicks contradicts the prediction of aposematic convergence. All five species that were found to click had different mean peak frequencies and click intensities. In terms of intraspecific variation, each species had at least 3 patterns, with some individuals having as many as 5 patterns, in one recording. These differences are marked and show no indication of species sharing the local cost of predator learning. One possible explanation for the lack

of convergence could be linked to the bat's ability to distinguish between different sounds. From a bat's perspective the clicks may be reliable and unique relative to other competing sounds a bat encounters, despite the substantial variability in the clicks evident to a human observer. However, given the sophistry in bat echolocation it is likely that bats can detect small differences in acoustic parameters (Tougaard *et al.* 1998)

The learning program also showed how quickly the association between the clicks and noxious properties of a moth can spread within the bat population even at low proportions and slow learning rates. This suggests that the cost of learning may not be as high as originally thought, placing weak selective pressure for convergence. In general, mathematical modelling suggests that aposematism is a superior strategy to hearing only, but only if the proportion of clicking moths remained high enough to allow bats to learn the association between the clicks and noxiousness.

At Algeria Forestry Station the proportion of clicking moths was only 2.3%, which is too low to allow aposematism to function (Chapter 3). If the proportion of clicking moths rises to high enough levels the aposematic function of the clicks could kick in (Figure 1). The different learning rates and reinforcement rates could decrease or increase the minimal percentage required for aposematism to function, and would also effect the speed at which the bats develop the association between the clicks and the moths noxiousness (Figure 1).

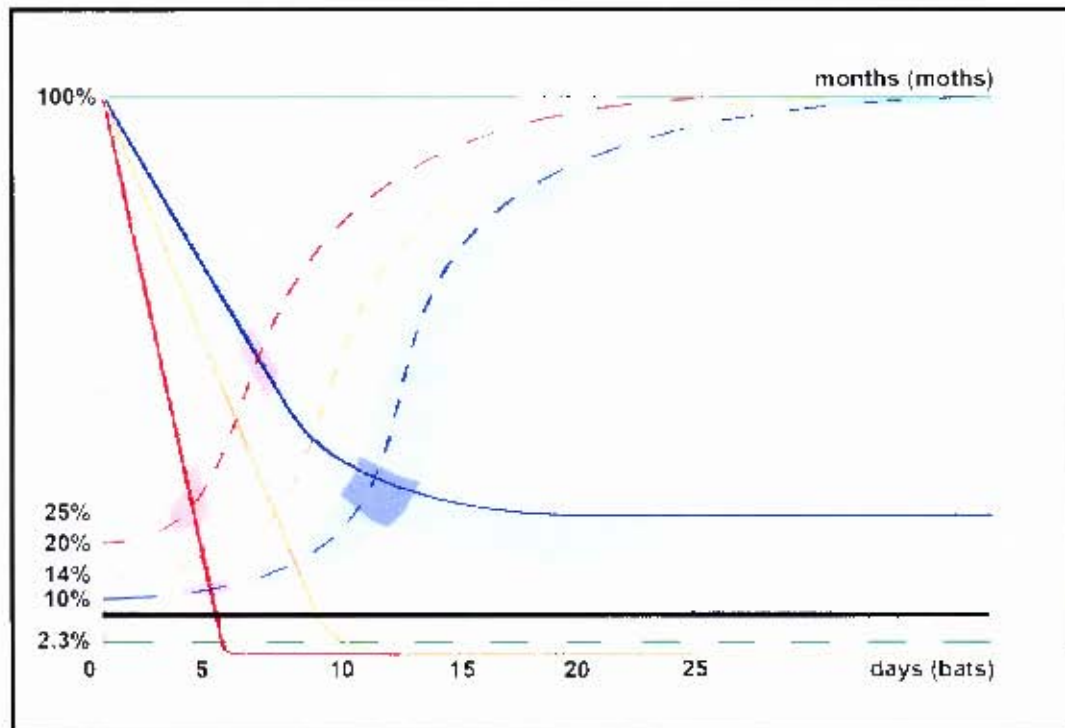


Figure 1. A graphic illustration of the aposematic model based on data from the learning program.

The dotted lines represent the clicking moth population over time in months, while the solid lines represent the percentage of naïve bats over time in days. Each colour is one scenario with the decrease in naïve bats allowing the increase in the clicking moth population over time. However, bats develop the association between the clicks and the noxiousness within days, but the benefits of the low number of naïve bats takes a while to feed into the moth population (hence the different time references). The shadows around each of the dotted lines indicate the effect of reproduction; with higher reproduction rates (shadow area to the left of line) allowing clicking moth populations to react quicker, while lower reproduction rates (shadow area to the right of line) cause the clicking moth population to react slower to the benefits of low percentages of naïve bats. The shadow area around the solid lines indicate the influence of learning and reinforcement rates, with faster learning rates and lower reinforcement rates causing a faster decrease of naïve bats (shadow area to the left of line), and slower learning and higher reinforcement rates causing a slower decrease of naïve bats (shadow area to the right of line). The thick solid black line indicates the minimal percentage of clicking moths required for the aposematic strategy to function. Faster learning rates and lower reinforcement rates can move the black line down, while slower learning rates and higher reinforcement rates moves the black line up. For example, the green simulation

is below the black line, hence the reason why the green solid line does not decrease, thereby not allowing the green dotted line to increase, which simulates the 2.3% clicking moths found in the field. The blue simulation starts at 10% clicking moths, which decreases the percentage of naïve bats down to only 25%. However, this decrease in the number of naïve bats will allow the clicking moth population to increase, which in turn will allow the remaining 25% of naïve bats to decrease to zero, but at a slower rate similar to the moth population increase (i.e. months). The larger shadow on one side of the solid blue line shows the higher sensitivity of the effect of learning rates and reinforcement rates on the decrease of naïve bats at values just above the black line.

Startle

The startle hypothesis was the only one that received support from both the field data and the mathematical simulations. Startle was the only strategy to function best at the low proportions of clicking moths found at Algeria Forestry Station.

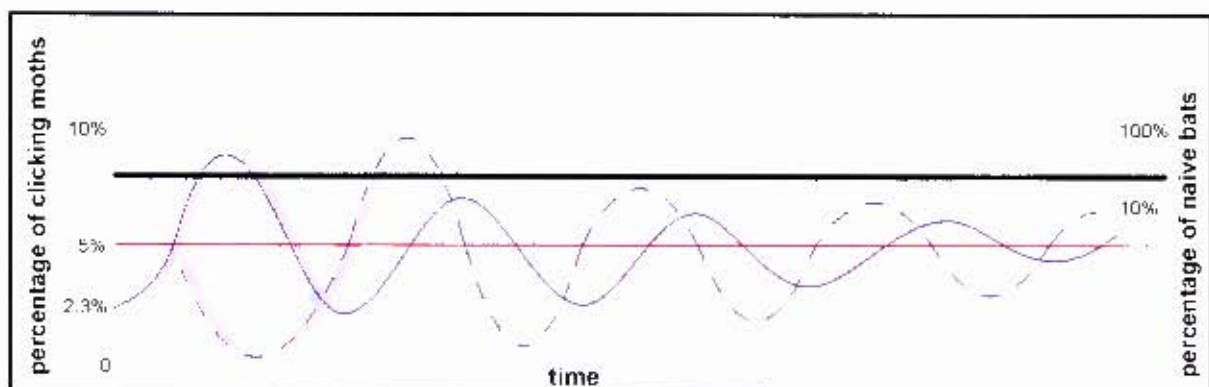


Figure 2: A conceptual graph of the change of percentage in clicking moths and the corresponding effect on the percentage of naïve bats. The solid line indicates the percentage of clicking moths and its corresponding values are on the left y axis. The dotted line indicates the percentage of naïve bats and its corresponding values are on the right y axis. The red line indicates the point at which the percentage of moths is high enough to cause habituation within the bat population, while the black line indicates the minimal percentage of clicking moths required for the aposematic strategy to function. Faster learning rates and lower reinforcement rates can move the red and black line down, while slower learning rates and higher reinforcement rates moves the red and black line up. However, the level of sensitivity of the

black and red line towards learning and reinforcement rate is different. Whenever the percentage of clicking moths goes above the red line, the percentage of naïve bats decreases, causing the percentage of clicking moths to start decreasing and pass below the red line. This causes an increase in the proportion of naïve bats and restarts the increase of the percentage of clicking moths. This pattern decreases slowly and tends towards a stable point, but can be taken out of stability by changes in the environment such as decreased reproduction from a bad year. A good reproduction year can also increase the amplitude allowing clicking moths to pass the black line and change the function of the clicks to aposematism if the moth has noxious properties. Reproduction can also change the frequency of oscillation. For example, the blue shadow of the solid line shows the effect of increased reproduction and the pink shadow shows the effect of decreased reproduction. The learning rate and reinforcement rate can also have a similar effect on the percentage of naïve bats with the blue shadow of the dotted line showing the effect of increased learning and/or lower reinforcement and the pink shadow showing the effect of decreased learning and/or higher reinforcement.

Furthermore, startle may play an interesting role in the evolution of the utility of moth clicks when assessed with one or the other of the two remaining hypotheses. For example, with the jamming hypothesis, if clicking evolves within a specific species the startle effect could sustain the species existence and allow selective pressure to divert the population variation towards the functional requirements of jamming, increasing the likelihood of jamming occurring, especially if the moth is not noxious. If the clicking moth is noxious, the startle effect of the clicking could allow the population to grow to high enough numbers to make the aposematic function of the clicks viable. For example, in Figure 2 the solid black line represents the minimal percentage of clicking moths to allow aposematism to function. When the startle strategy progresses above the solid black line the aposematic function of the clicks becomes more viable.

As was predicted under the startle hypothesis, moth clicks showed a high level of variation, with each species having specific peak frequencies and click intensities. Each individual also has at least three patterns and showed variation even within different

clicks of the same modulation cycle. In theory, the high level of variation should hinder habituation. If bats take only 3 trials to habituate, positive selective pressure is placed on clicking moths that have unique signalling characteristics, which the bats are not expecting and have not habituated to. This would imply that different species would remain with their specific characteristics and any variation within a population would be maintained. Character (i.e. clicking patterns) fluctuation could also occur as different rare phenotypes gain stronger startle effects and increase in numbers. The character would increase to levels where bat habituation would occur and cause it to decrease and become rare again. I tested this on a more complex version of the learning program with a setup of 3 to 5 patterns, where bats had to habituate to fluctuations from one pattern to another. As a pattern became rare, its startle effect became more effective, selecting for this pattern so that the population growth of moths with this pattern increased. Bats became habituated to common patterns and thus these moths are selected against, leading to their relative demise until they became rare. This see-saw dominance effect, common in game theory, could prolong habituation and even ultimately prevent complete habituation within the bat population.

Conclusions

Jamming is the most unlikely function for the clicks produced by the moths at Algeria Forestry Station. The evolution of clicks is not enough for jamming, but the evolution of clicks with specific functional parameters has to occur. This narrow set of parameters may place limits on the number of species that follow this evolutionary path and may explain the low proportion of clicking species that fit the jamming requirements. The

startle effect of moth clicks could aid the evolution of jamming but jamming will most likely not be a ubiquitous function of moth clicks.

Aposematism on the other hand takes advantage of noxiousness, which seems to be a common characteristic in certain moth families such as the Arctiidae. In this case moth clicks do not have to evolve within limiting constraints other than being distinguishable. All of the clicking arctiid moths at Algeria Forestry Station appear to be noxious and the clicks show clear conspicuous characteristics, which suggests clicks have a possible aposematic function. However, not all noxious arctiids clicked, and mathematical models based on the aposematic hypothesis suggest that aposematism cannot function at the low proportions of clicking moths existing at Algeria Forestry Station. On the other hand, the aposematic and startle models do suggest that the existence of both noxiousness and clicking create the initial conditions for the evolution of an aposematic function for moth clicks.

Based on the high level of variation and the low proportion of clicking moths at Algeria Forestry Station, startle is the most likely function of the clicks produced by the moths in this area. The startle strategy would not allow moths using this strategy to become dominant. In general, startle moths would fluctuate between the baseline defence (e.g. the evasive manoeuvres performed by hearing moths) and the maximum percentage of clicking moths tolerable before habituation occurs. However, the startle model works well in conjunction with other strategies, especially aposematism. Clicking moths most likely react the same way to experienced and naïve bats, but the same cannot be said for the bats. For a naïve bat the clicks would have a startle effect while

for an experienced bat the same clicks when associated with noxiousness would have an aposematic effect. The proportion of naïve and experienced bats are dependent on the bat learning/habituation rate and the required reinforcement rate, coupled with the proportion of clicking moths. The universality of the startle and aposematic hypotheses is thus dependent on the proportions of clicking moths at other sites and in other habitats. These proportions provide a mutually exclusive set of predictions that would allow a distinction to be made between the startle and aposematic hypotheses, the two most likely hypotheses for why moths click.

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Appendix I:

The list in this Appendix contains the definition of all variables used throughout the thesis.

- DN/DT — is the (instantaneous) change in moth population size over time.
- R — is defined as the “maximum rate per capita of growth” i.e. growth or net reproductive rate which is assumed constant.
- N — is the moth population size at time t.
- K — is the carrying capacity and is defined as the maximum number of moths that a specific environment can sustain if left undisturbed.
- P — is the fixed number of moths removed from the population by bat predation. This predation rate is calculated using a moth population that does not have any defence strategies.
- Em — is the energy requirement in kilojoules obtained from moths for a specific bat species
- Eb — is the total energy requirements in kilojoules for a specific bat species.
- Md — is the percentage of moths in a specific bat species diet based on light trap abundance of moths (all bat species will have 73% in this case).
- Ms — is the mass of a specific bat species (grams).
- Evb — is the average bat energy requirement of 5.28 kJ per gram of body weight.
- Ps — is the number of moths eaten by a specific species of bat per night
- Evm — is the average energy value, for a moth, (25.2 kJ per gram)
- Mw — is the average weight for a moth at Algeria Forestry Station.
- Abs eff — is the average absorption efficiency of bats (76.5%)
- Nbs — is the population size of the specific bat species in question

- Nmb — is the number of bats marked previously
- Nbc — is the number of recaptured bats
- Cm — is the number of marked bats in the re-captured sample
- Ps_n — is the number of moths eaten for each of the species (S_n) occurring in the area, where n denominates the number of bat species sampled (refer to equation 1.3) (in equation 1.5 eleven species, in equation 3.1 eight species).
- Nbs_x — is the population size for each of the eleven species occurring in the area and is based on either the mark and recapture or passive monitoring method.
- Ah — is the hearing induced advantage to eared moths that affects the predation rate in the form of an efficiency coefficient i.e. probability of a moth being a victim of a bat attack and $Ah = Sh / 100$.
- Sh — is the bats success rate (expressed as a percentage) when attacking hearing moths.
- Aj — is the jamming induced advantage to moths that affects the predation rate in the form of an efficiency coefficient i.e. probability of a moth being a victim of a bat attack and $Aj = Sj / 100$
- Sj — is the bat's percentage success rate when attacking jamming moths.
- En — is the average encounter rate for an average bat in the area
- Ha = $1 + Hp/100$
- Hp — is the number of times a bat misses an attack due to the defensive advantage induced by hearing. It is expressed as a percentage of the predation rate
- n — is the number of bat species in the area that echolocate within moth hearing range which is 8 in the case of Algeria Forestry Station.
- Aa — is the coefficient of the density of naive bats in the population derived (i.e. $Aa = Bn_t / 100$) from the percentage of naïve bats in the population over

time (Bn_t) obtained from the program.

- A_s — is the coefficient of the density of experienced bats in the population derived (i.e. $A_s = B_{e_t} / 100$) from the percentage of experienced bats in the population over time (B_{e_t}) obtained from the program.

Wilson Equation:

- C_{25} — is the number of bats flying in a given time and area up to a maximum flight height of 25 m.
- D — is the maximum detection distance in metres estimated using data from Griffin (1971), Patriquin *et al.* (2003) and Wilson (2004).
- R — is the bats activity rate in passes per minute
- L — is the length of detection area estimated by multiplying bat flight speed (calculated in flight tunnel experiments) and time period of the passive monitoring sample window (60 seconds in this case)
- W — is the width of detection area in meters and is calculated using the formula $(D^2 - H^2)^{1/2} * 2$
- FA — is the area of habitat space in which a bat might be expected to fly in the time window of the passive monitoring given the bats flight speed.
- H — is the average flight height (estimated as $1/2 D$ by Wilson 2004)

Appendix II:

This Appendix contains all the equations used throughout the thesis.

Equation 1.0

$$DN/DT = R N (1 - N / K) - P$$

Equation 1.1.

$$E_m = E_b * (M_d / 100)$$

Equation 1.2

$$E_b = M_s * E_{vb}$$

Equation 1.3

$$P_s = (A_{bs\ eff} / ((E_m / E_{vm}) / M_w)) * 100$$

Equation 1.4

$$N_{bs} = (N_{mb} * N_{bc}) / C_m$$

Equation 1.5

$$P = (P_{s_1} * N_{bs_1}) + (P_{s_2} * N_{bs_2}) \dots + (P_{s_n} * N_{bs_n})$$

Equation 2.

$$DN/DT = R N (1 - N / K) - (A_h * P)$$

Equation 3.

$$DN/DT = R N (1 - N / K) - (A_j * (A_h * P))$$

Equation 3.1

$$E_n = ((P_{s_1} * H_a) + (P_{s_2} * H_a) \dots + (P_{s_n} * H_a)) / n$$

Equation 4.

$$DN/DT = R N (1 - N / K) - (A_a * (A_h * P))$$

Equation 5.

$$DN/DT = R N (1 - N / K) - (A_s * (A_h * P))$$

Wilson Equation

$$C_{25} = 25 / D * R / (L * W / FA)$$

Appendix III

This script simulates the feeding experience of bats that encounter clicking moths. For example aposematic moths are noxious and bats need to eat a certain number of them before they have the experience (i.e. learning rate) to recognise them. Once this experience is gained, the bat needs to feed on a drastically reduced number of moths to maintain its experience (i.e. reinforcement rate), otherwise the bat will lose its ability to distinguish between normal and aposematic moths. The program is manipulated directly on the script and basic changes in parameters allow one to use the same program for startle moths.

```
# Bat Learning Program (Feeding Simulator)
#
# Daniel Ribeiro
# Simon Perkins
# 12 April 2006
#
# This script requires the NumPy library to run

from Numeric import *
from RandomArray import *

# Variables defining the simulation

# Variables defining the characteristics of the bat feeding matrices
nr_of_bats = 1000          # Number of bats to evaluate
encounter_rate = 36       # How many moths the bats encounters each day
aposematic_ratio = 0.023  # Ratio of aposematic moths to normal moths
nr_of_days = 356         # The number of days to simulate

# Variables used for evaluating the bat feeding matrices
nr_of_ap_moths_for_exp = 7 # The number of moths that a bat must consume
                           # in one day to achieve experienced status
nr_of_ap_moths_to_keep_exp = 1 # The number of moths that an experienced
                                # bat must consume to maintain its
                                # experienced status
nr_of_days_to_keep_exp = 1  # The number of days over which
                             # nr_of_ap_moths_to_keep_exp moths must be
                             # consumed to maintain its experienced status

# When randomly creating the feeding matrices
# we will check that the randomly generated
# numbers are close to the aposematic_ratio
# This is the tolerance percentage that we
# will accept
aposematic_ratio_tolerance = 0.95

# The actual difference from the aposematic
# ratio that we will accept
```

```

aposematic_tolerance_diff = \
    aposematic_ratio - \
    (aposematic_ratio * aposematic_ratio_tolerance)

# The main function for running the simulation

def simulate():
    feeding_matrix_store = []

    for day in range(1, nr_of_days + 1):
        feeding_matrix = getFeedingMatrix()
        feeding_matrix_store.append(feeding_matrix)

    bat_experience_matrix = getBatExperienceMatrix(feeding_matrix_store)

    createOutput(feeding_matrix_store, bat_experience_matrix)

# Returns a bat feeding matrix
def getFeedingMatrix():
    # The size of the feeding matrix
    feeding_matrix_size = (nr_of_bats, encounter_rate)

    # Create a feeding matrix with the dimensions specified
    # in feeding_matrix_size filled with random integers
    # produced with a binomial distribution.
    feeding_matrix = binomial(1, aposematic_ratio, feeding_matrix_size)

    # Check the ratio of ones to zeroes. This should be very
    # close to the aposematic ratio
    one_to_zero_ratio = \
        float(sum(sum(feeding_matrix))) / \
        float(nr_of_bats * encounter_rate)

    diff_from_aposematic_ratio = abs(aposematic_ratio - one_to_zero_ratio)

    # Print a warning if we fall outside the tolerance level
    if diff_from_aposematic_ratio > aposematic_tolerance_diff:
        print \
            "WARNING: The random generated matrix has a ratio " + \
            "of " + str(one_to_zero_ratio) + " which does not fall " + \
            "within the " + str(aposematic_ratio_tolerance * 100) + \
            "% tolerance level of the actual aposematic ratio " + \
            "(" + str(aposematic_ratio) + "%)" + "."

    return feeding_matrix

# Creates the bat experience matrix of size
# nr_of_bats x (nr_of_days + 1). Uses the bat
# feeding history in feeding_matrix_store to
# record the bat's experience in the
# bat experience matrix
def getBatExperienceMatrix(feeding_matrix_store):
    # The bat experience matrix
    bat_experience_matrix = zeros((nr_of_bats, nr_of_days + 1))

    # A sliding window recording the aposematic feeding history

```

```

# for each bat
aposematic_feeding_history = \
    zeros((nr_of_bats, nr_of_days_to_keep_exp))

for day in range(0, nr_of_days):
    # Get the feeding matrix for this day
    feeding_matrix = feeding_matrix_store[day]

    for bat in range(0, nr_of_bats):
        # Calculate the number of
        # aposematic moths eaten today
        aposematic_moths_eaten_today = \
            sum(feeding_matrix[bat, :])

        # Store this in the feeding history
        # for the bat
        aposematic_feeding_history[bat, 0] = \
            aposematic_moths_eaten_today

        # Update the bats experience for this day
        updateBatExperienceMatrix(bat_experience_matrix, \
            aposematic_feeding_history, \
            day, \
            bat)

    # We're going to shift on to a new day
    # Slide the aposematic feeding history window forward
    shiftAposematicFeedingHistoryWindow(aposematic_feeding_history)

return bat_experience_matrix

# Updates the bat experience matrix based on its
# current experience and feeding history
def updateBatExperienceMatrix(bat_experience_matrix, \
    aposematic_feeding_history, day, bat):

    # Note the sneaky hack here. The bat_experience_matrix is
    # 1 column larger than it should be. This extra column is
    # zeroed. Because of Python's negative indexing, when
    # day - 1 = -1, this extra column at the end will be
    # referened and because it is zeroed, the bat will automatically
    # be treated as inexperienced.
    if not isBatExperienced(bat_experience_matrix[bat, day - 1]):
        # If the bat is not experienced, check if
        # it has consumed enough aposematic moths today in order
        # to become experienced
        if(aposematic_feeding_history[bat, 0] >= nr_of_ap_moths_for_exp):
            bat_experience_matrix[bat, day] = 1
    else:
        # The bat is experienced. Check if it has consumed
        # enough aposematic moths over the required period
        # in order to retain its experienced status. If not
        # demote it's status to inexperienced
        recently_eaten_aposematic_moths_array = \
            aposematic_feeding_history[bat, :]

        recently_eaten_aposematic_moths = \

```

```

        sum(recently_eaten_apsematic_moths_array)

    if int(recently_eaten_apsematic_moths) < int(nr_of_ap_moths_to_keep_exp):
        bat_experience_matrix[bat, day] = 0
    else:
        bat_experience_matrix[bat, day] = 1

# Shifts the sliding aposematic feeding history window forward
# one day
def shiftAposematicFeedingHistoryWindow(apsematic_feeding_history):
    aposematic_feeding_history[:, 1:] = \
        aposematic_feeding_history[:, 0:(nr_of_days_to_keep_exp - 1)]

# Returns true if the bat is experienced
def isBatExperienced(bat_value):
    if int(bat_value) == 1:
        return True
    else:
        return False

# Creates the text output, based on the feeding patterns
# and the bat experience
def createOutput(feeding_matrix_store, bat_experience_matrix):
    output_file = file("output.txt", "w")

    output_file.write("Feeding Matrices and Experience Indicators")
    output_file.write("\n")

    for bat in range(nr_of_bats):
        line = ""
        for day in range(nr_of_days):
            feeding_matrix = feeding_matrix_store[day]

            # Output the encounters on this day for the bat
            for encounter in range(0, encounter_rate):
                line = line + \
                    str(feeding_matrix[bat, encounter]) + \
                    ","

            # Output the bat's experience at the end of the day
            if isBatExperienced(bat_experience_matrix[bat, day]):
                line = line + "E"
            else:
                line = line + "I"

            if not day == nr_of_days - 1:
                line = line + ","
            else:
                line = line + "\n"

        output_file.write(line)

    output_file.write("\n")
    output_file.write("Percentage of Experienced Bats each day")
    output_file.write("\n")

    for day in range(nr_of_days):

```

```
        nr_experienced_bats = \  
            sum(bat_experience_matrix[:, day])  
  
        percentage_experienced_bats = 100.0 * float(nr_experienced_bats) / float(nr_of_bats)  
        line = str(percentage_experienced_bats) + ","  
  
        output_file.write(line)  
  
    output_file.close()  
  
# If we're in the main execution block  
# execute the main simulation function.  
if __name__ == "__main__":  
    simulate()
```