

Acoustic Signaling, Territoriality, and Mating in Whistling Moths, *Hecatesia thyridion* (Agaristidae)

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Males of the agaristid moth Hecatesia thyridion defend small patches of coastal heathland in southwestern Australia in the late afternoon. As they fly back and forth low over their territories, they produce an acoustical signal. Neighboring males commonly fly toward each other; these interactions often result in aerial duels, with the eventual departure of one of the males. Playback experiments established that males were attracted to the sounds of other males. Females were observed to fly into territories and eventually mate with the signaling occupant. Marked males sometimes returned to the same spot on consecutive days. On any given day males occupied only a fraction of the sites that were acceptable territories. The mating system of H. thyridion appears to be a dispersed lek, with males acoustically advertising territories that are used for mating and not for feeding or oviposition.

KEY WORDS: *Hecatesia*; Agaristidae; Lepidoptera; moths; territoriality; leks; sound production; scent marking.

INTRODUCTION

Knowledge of the acoustic behavior of noctuid moths is based mainly on studies of tiger moths (Arctiidae). In this group, sounds generated by thoracic tymbals (Blest *et al.*, 1963) function in defense; they are produced by both sexes and are elicited by the sounds of echolocating bats as well as by tactile stimuli (Dunning, 1968; Fullard, 1977; Fullard and Fenton, 1977). It has been known for some time that whistling moths (Agaristidae) also produce audible sounds.

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These moths rapidly move their wings, repeatedly clashing together castanets on the leading edges of the forewings while in flight (Nicholson, 1955; Bailey, 1978). In contrast to tiger moths, only male agaristids produce sounds (Common, 1970, 1974) and do so while flying back and forth over a small area of ground (Bailey, 1978). This led Common (1974) to suggest that the acoustic behavior has a reproductive function. To date, only one study of sound-producing Lepidoptera has shown that sounds function in reproduction: Spangler *et al.* (1984) discovered that the ultrasound produced by males of a pyralid, the lesser wax moth (*Achroia grisella*), attracted females.

In this paper we describe in detail the territorial behavior of the agaristid *Hecatesia thyridion* and demonstrate that (1) males produce sounds while defending territories, (2) females are attracted to territorial males, usually copulating with them, and (3) interactions between neighboring territorial males are mediated acoustically. We compare the mating system of this species with that of certain other territorial insects.

MATERIALS AND METHODS

The study was conducted at Walpole-Nornalup National Park, Western Australia, in coastal heathland around Peaceful Bay. An observational study was made at various times during summer (November to February) 1985–1986. During December 1986 playback experiments of tape-recorded male sounds were conducted.

On 24–25 November and 2–4 December 1985 focal males were selected for observation for as long as they remained at a hovering station. The goal was to secure quantitative information on the frequency and outcome of male–male and male–female interactions and to determine how long individual males occupied their territories. On 9–11 December 1985 a transect approximately 175 m long that followed a sandy track through an area of stabilized sand dunes was censused repeatedly from midafternoon to sunset, the time period during which signaling males were active. The location of any male detected from the track was recorded and as many individuals as possible were captured, marked, and immediately released. Data gathered on these 3 days determined whether marked individuals returned to the same site on consecutive days, whether particular hovering sites were occupied from day to day, and whether there was a population of nonterritorial males ready to occupy hovering stations made vacant by the departure of a resident male that either left voluntarily or did not return after being marked and released.

On 9 and 10 January and on 1 February 1986 the transect was expanded to include an additional 325 m of track. From 1600 to 1930 an observer repeatedly walked the track censusing the number of signaling moths and their location. During these 3 days, no moth was captured for marking or any other purpose,

and the resultant data show how an undisturbed population utilizes available display sites on different days.

On 8 and 9 December 1986 playback experiments were conducted in which we determined the responses of signaling males to a tape-recorded synthetic model of the male song. Parameters of the song were obtained from Bailey (1978) and from analysis of male calls previously recorded in the field. A Rockwell Aim 65 computer generated a continuous series of pulses 14 ms apart. This signal was passed through a Neurolog TM 402 to produce the pulse duration of 0.5 ms. This pulse of known width was used to modulate the carrier frequency of 18 kHz with a fixed rise time of less than 2 ms. Figure 1 shows the time-amplitude patterns of normal and synthetic songs.

The protocol for playback experiments consisted of locating signaling males within 5 m of the track through the study site and placing a speaker (Realistic)

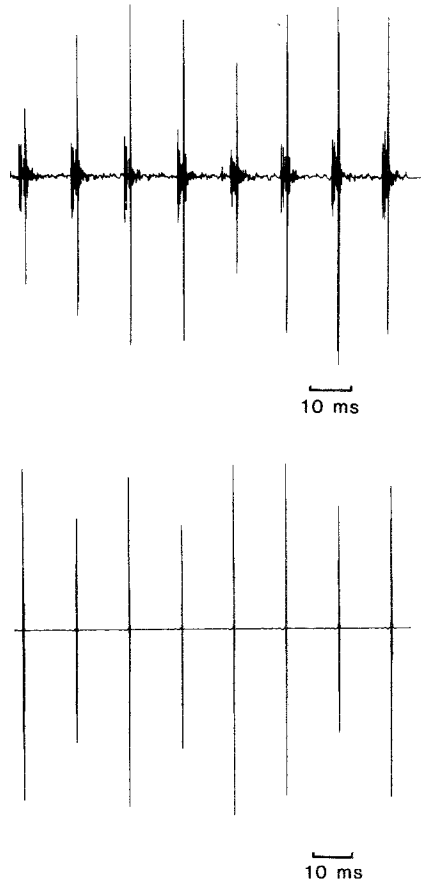


Fig. 1. Time amplitude patterns of the song of male *Hecatesia thyridion*. Top, natural song; bottom, song model used in playback experiments.

mounted on a tripod, 0.5–1 m above the ground, approximately 3–4 m distant from the center of the area in which the signaling male was flying. The song was played at 37 cm s⁻¹ from a Nagra IV SJ tape recorder and amplified through an Elta 8950 amplifier. This apparatus adequately reproduced the 18-kHz frequency of the song with minimal distortion.

Each playback trial consisted of 2 min of a control followed by 2 min of playback of experimental male call. The control differed from the experimental only in that the tape was not running. After the initial control and playback periods the speaker was repositioned on the opposite side of, or at 90° to, the approximate center of the focal male's flight area and the control and experimental periods were repeated. Sound levels of playback approximated the intensity of the natural male signal as resolved by the human ear and the intensity setting on the tape recorder was kept constant for all trials. The measured sound pressure level (SPL re: 2×10^{-5} Nm⁻²) of the playback song at 1 m was 71 dB as measured by a 0.5-in. Brüel & Kjaer 2209 condenser microphone (Type 4163) linked to a Brüel & Kjaer sound level meter (scale 1B, RMS fast; 1-Khz external filter).

RESULTS AND DISCUSSION

Daily Activity Pattern. The coastal heathland where the moth was found contained a diverse flora of small plants less than 1 m in height, with restricted pockets of taller plants including *Banksia* and peppermint trees (*Agonis flexuosa*). Males and females of *H. thyridion* were occasionally seen foraging in the heath during the early morning and late afternoon at several species of flowering shrubs (including *Parmelia rosea*, on which one female was seen making oviposition movements).

Males can fly silently or fly in such a way as to activate the acoustical mechanism (see Bailey, 1978). Foraging individuals did not produce signaling sounds; the first actively signaling males appeared as early as 1400, but more often after 1530, with the last signalers stopping at sunset (ca. 1900). As Table I indicates, the time between the first and the last sighting of signaling males varied from day to day, for reasons unknown to us. Males displayed even under windy, cool conditions, and some continued to signal during light rainfall.

Behavior of Signaling Males. Signaling males flew within 50 cm of the heath or open woodland shrubbery in their territories. A territorial male would zigzag forward, then drift back with the wind some 2–10 m before starting the flight forward once again. These males produced a continuous buzzing sound [for analysis of male sounds see Bailey (1978)]. The flight pattern was repeated over and over, with most males restricting the bulk of their signaling flight to a central 5-m² patch, with occasional forays outside this core area.

After arriving at their signaling stations, males flew to and landed on heath-

Table I. Male Activity in *Hecatesia thyridion* at Display Sites Along a 175-m Transect of Heathland Habitat Censused on Three Consecutive Afternoons in December 1985.

Date	9 Dec.	10 Dec.	11 Dec.	Total
Period of male activity	1520–1856	1730–1852	1634–1900	
Number of				
Males marked that day	8	4	7	19
Males that returned on day when marked	4	1	3	8
Occupied sites	7	11	12	17
Sites in which occupancy changed	3	2	2	6
Sites occupied on all 3 days	—	—	—	5

land vegetation within 1–10 m of the center of their territory. While on these plants males exhibited what we term vegetation rubbing behavior; the moth walked steadily up the plant material, all the while appearing to hold its head close to the substrate and vibrating its wings rapidly. This behavior is strongly reminiscent of scent-marking in certain digger wasps (*Philanthus* spp.), in which territorial males deposit volatile chemicals on vegetation (Schmidt *et al.*, 1985) and are visited by females (Alcock, 1975; Gwynne, 1978).

The frequency of vegetation rubbing by the moths was 4.54 for every 10 min of observation of a focal male (based on a total of 615 min of observations collated over 5 days at 21 locations). But the behavior occurred far more frequently than average during the early part of a male's tenure at a territory (Fig. 2). *Philanthus* wasps scent-mark most often just after arriving at a territory (Alcock, 1975; Gwynne, 1978).

Territorial Behavior. Signaling males did not respond to silent, noncalling individuals that were foraging in or passing through their territory. But occasionally another acoustically active male would fly to an area where a male had been signaling for some time. The interacting males approached one another until they were a meter or so apart, at which point a chase invariably resulted in which the competing males circled around each other in an aerial "dog fight." The interacting pair darted erratically and rapidly back and forth over the site, generally keeping low over the heath but sometimes traveling upward some 10 m or so when passing over a tree or bush. They remained within a few centimeters of each other during the chase, with both males producing sound. The frequency of such interactions was 1.5/h (based on 615 min of observation of focal males), and their duration varied from 10 s to 14 min ($\bar{X} = 3.3 \pm 4.3$ min, $N = 18$).

The end of a male–male interaction came when one male stopped calling and silently flew away, with the other male returning to the hovering site to resume its aerial display. We observed a total of six fights in which the two

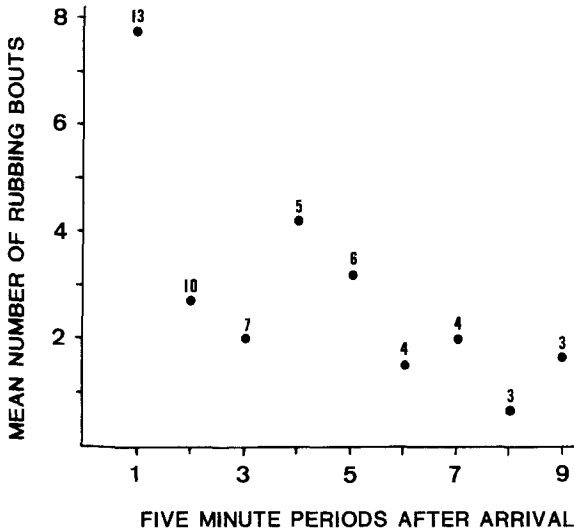


Fig. 2. The frequency of vegetation rubbing by 13 males of *H. thyridion* per 5-min period in relation to the time of arrival of these males at their display sites. Points represent means. Sample sizes (above points) vary since most males were not sampled during all 10 time periods.

participants could be identified, either because one was marked and the other was not or because of striking natural color differences between them. Residents retained control of their territories on three occasions, and newcomers ousted the previous owner on the other three. In addition, we observed two other probable takeovers in which the winner of a fight began to vegetation rub at a much higher rate than previously; we suspected that in these cases the winner was a new male because he was performing the behavior in the manner of a recently arrived individual (Fig. 2).

These observations demonstrate that (1) males are territorial, (2) some territories attract rivals that contest ownership of the sites, and (3) the moths have a ritualized system of aggression used in territorial competition.

Sound Production and Male Interactions. Observations of competitive interactions between territory owners suggested that males were attracted to each other's acoustical signals. This contention was supported in playback trials; during the 4 min of broadcast of conspecific signal, males in eight of nine trials moved away from the core area of their territory and approached to within 0.5 m of the speaker. Individuals varied in the number of approaches to the song model from one to seven ($\bar{X} = 2.4$). Most males that approached the speaker made a pass within 0.5 m before quickly returning to the core signaling area of the territory. However, two males stayed in the area of the speaker for 10 and

38 s, respectively, flying in circles around the sound source. A third male even struck the speaker. All males continued to produce sounds as they flew to the sound source. The fact that males usually make only one or two approaches toward the playback during 4 min may mean that visual cues are necessary for sustained interactions.

Only once during the nine trials was a signaling male scored as flying within 0.5 m of a control speaker. In this case the male did not fly at the speaker but flew past it on his way to a brief bout of signaling on a neighboring unoccupied territory. The number of approaches to the speaker was significantly greater during experimental periods compared to control periods (Wilcoxon paired-sample test, $P = 0.0025$).

The Defended Site. Territories were located in open areas that were bordered or surrounded by taller, denser vegetation. Signaling males were found in strips of heathland lined by peppermint trees, in a clearing along a track through an open banksia woodland, and by sandy, partly overgrown tracks lying in a depression and bordered by a dense stand of recently burnt saplings. Typically the open area selected by a signaling male contained one slightly taller bush or a prominent blackboy bush (*Xanthorrhoea preissii*) or a dark-trunked tree that seemed to serve as a focal point to which the zigzagging, erratically flying male repeatedly returned.

It appears therefore that territorial males defend locations in natural flyways through which passing females might travel more easily than in the surrounding vegetation.

Site Tenacity. Over the course of the study we secured 10 records of territorial males that displayed without interruption at one site for from 10 to 74 min on one afternoon. (Some sites were occupied continuously for longer periods, but whether by one male or two in sequence was not known, given that there was an interaction between two unidentified males in the middle of the observation period.) However, only 8 of 19 (42%) males marked on 9–11 December returned to their station after marking, and only 4 of these returned on a subsequent day as well. A single male of the eight marked on 9 December defended its hovering station on all three afternoons (for periods totaling 108, 16, and 86 min). This male was prone to display for a time and then to depart (to rest?), only to return for another bout of signaling later in the same afternoon.

The somewhat unstable nature of territorial ownership is reflected in the fact that there were a substantial number of sites occupied on some afternoons that were not occupied on other afternoons (Table I). At times when males were fighting for possession of one territory, other nearby sites were usually vacant and available. Previously popular locations were often left unclaimed for long periods or even entire afternoons. One area known to have been held on 25 November and 2–4 December was defended for 102, 26, and 13 min, respec-

tively, on 9–11 December, or only 32% of the total minutes of male activity over the 3 days.

Although capture and marking of males may have exaggerated the unstable pattern of tenure at signaling stations along the main transect, even when calling males were not netted the locations used on one day were often unoccupied on the next. A strip of heathland 0.5 km from the main transect had seven territories on 4 December, only two of which were defended on the next day when a total of six territorial moths were present.

Likewise of a total of 25 sites occupied by displaying males over 3 days (9–10 January, 1 February), only 16 were known to have been claimed on previous days of the study. On any one afternoon many apparently suitable sites were not claimed and even those that were occupied were held for only a fraction of the daily flight period of signaling males (Table II). Competition for control of a display area was observed on all days, although fights were not common; only 8% of all males were engaged in an aerial duel with a rival when approached on a census ($N = 111$ records).

Thus it would appear that there were many potential hovering stations in the study area and a large population of males that utilized these stations over a period of days, but with rapid turnover and little long-term site tenacity.

Male-Female Interactions. Four male-female encounters were observed over the course of the study. On 2 December at 1830 a female was pursued in flight by a male from a territory adjacent to the one under observation at the time. The pair flew only a few meters before landing low on a burnt sapling. Copulation ensued within a few seconds of landing, with the male facing directly away from the female. Mating lasted 135 s, after which the male returned at once to his territory, to signal again.

On 4 December at 1725 a female flew directly toward a signaling male and led him on a flight of about 2 m to a grass stem on which they both alighted. The male turned and at once achieved copulation, which lasted just 50 s. The female flew off and the male resumed calling above his territory.

Table II. Male Activity in *Hecatesia thyridion* at Display Sites Along a 500-m Transect of Heathland Habitat Censused on Three Afternoons in January and February 1986

Date	9 Jan.	10 Jan.	1 Feb.	Total
Period of male activity	1705–1915 (130 min)	1832–1924 (52 min)	1713–1912 (119 min)	
Number of sites occupied	11	9	14	25
Minutes of activity per site				
Mean (SD)	25.2 (6.3)	9.2 (2.4)	35.5 (7.7)	
Maximum	57	26	72	
Mean proportion of total daily activity period	0.19	0.18	0.30	

At 1825, 9 January a female flew to a calling male, leading him on a very short chase to the top of a plant about 1.25 m high. The male landed immediately behind the female and quickly copulated, after turning to face away from his partner. Mating lasted 98 sec. The female then left and the male returned to his territory to signal again.

On 3 December at 1730 a silent individual presumed to be a female flew into a focal male's territory, stimulating him to pursue her about 3 m. The putative female darted into a bush to land; the male appeared to lose contact with the other individual, for he did not follow but remained nearby and continued to signal as he drifted slowly about the bush. The putative female waited a short time before slipping out of the bush and flying rapidly away, undetected by the male, which subsequently returned to his territory.

GENERAL DISCUSSION

The Function of Sound Production. In whistling moths and certain other acoustic lepidopterans sounds appear to function in reproduction, as they are produced only by males and in contexts in which there is no obvious immediate threat of predation (Common, 1974; Gwynne and Edwards, 1986). Although reproduction appears to be the most likely function of stridulation in the whistling moth, *H. thyridion*, our observational data alone do not confirm this. Sounds may not be necessary for territoriality and mating; male territorial behavior that is probably associated with reproduction is also present in the nonacoustic diurnal agaristid, *Comocrus behri* (McFarland, 1976). Acoustic behavior by *H. thyridion* may have evolved as an aposematic display [one suggested explanation for the clicks of tiger moths (Dunning, 1968; Surlykke and Miller, 1985)]. The bright black and orange coloration of larval and adult agaristids may be associated with distastefulness to predators (Common, 1970), and thus the sounds emitted by diurnally active *H. thyridion* males could form part of an aposematic display of adults. The fact that only males stridulate and only while defending a mating territory may be because displaying males are more exposed to predation than females, as is true for a number of insects (Burk, 1982). Although female *H. thyridion* are attracted to displaying males, they may respond to visual or chemical signals rather than male sounds. The vegetation rubbing behavior shown by territorial males probably involves pheromone deposition.

Our experiments, however, demonstrate that sound production by males has a role in defense of the mating territory. Males fly toward neighboring territories defended by signaling males; the playback trials revealed that conspecific sound alone is sufficient to elicit this phonotactic response.

The Mating System. The diurnal pair-forming system of *H. thyridion* contrasts with that of most moths: in most species it is the females that signal by emitting a pheromone at night and attracting males. As suggested by Greenfield

(1981), both male searching and male singing probably result from intermale competition; energy expended and risks taken in singing or searching by males are probably greater than the effort expended in the corresponding female roles in pair formation, i.e., searching for singing males or pheromone production, respectively.

The fact that several male *H. thyridion* may call in an area of a few hundred square meters in the late afternoon at sites habitually used for this purpose suggests that the species can be included in the lek-forming insects, using the criteria of Bradbury (1977, 1985). Clashes between males for control of calling stations are reasonably frequent and involve the very rapid chases characteristic of a host of landmark-territorial insects (e.g., Alcock, 1987). As is true for other lekking insects, males defend places that do not appear to be visited often by foraging or ovipositing females but that, instead, seem to be along routes that may channel or guide dispersing receptive females to them. As is also typical for lekking insects, interactions between males and females are infrequent, with little, if any, courtship prior to copulation. Thus, for example, there are several convergent elements in the mating system of *H. thyridion* and that of other insects. In the nymphalid butterfly *Vanessa kershawi* (Alcock and Gwynne, 1988) and the carpenter bee *Xylocopa varipuncta* (Marshall and Alcock, 1981; Alcock and Smith, 1987), males defend territories in late afternoon. Males of both lepidopterans and the bee compete for territories by rapidly chasing intruders in back-and-forth pursuits over the waiting station. Females approach males but do not visit these areas to forage or oviposit, only to mate. Male-female encounters are very infrequent and involve a short chase with almost no courtship prior to mating, once the pair have landed.

The ecological factors that have led to convergent evolution in the mating systems of these insects have not been fully identified. But lekking in insects appears to be associated with especially abundant or evenly distributed food and oviposition resources, which cannot be readily monopolized by mate-seeking males (Thornhill and Alcock, 1983). If one host plant of *H. thyridion* is *Parmelia rosea*, then this would support the above argument, for this plant is one of the most abundant, conspicuous, and widely distributed components of the low heath at Walpole-Nornalup National Park. But in the absence of more detailed information on the ecology of females of *H. thyridion*, our understanding of male reproductive tactics in this species remains incomplete.

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