

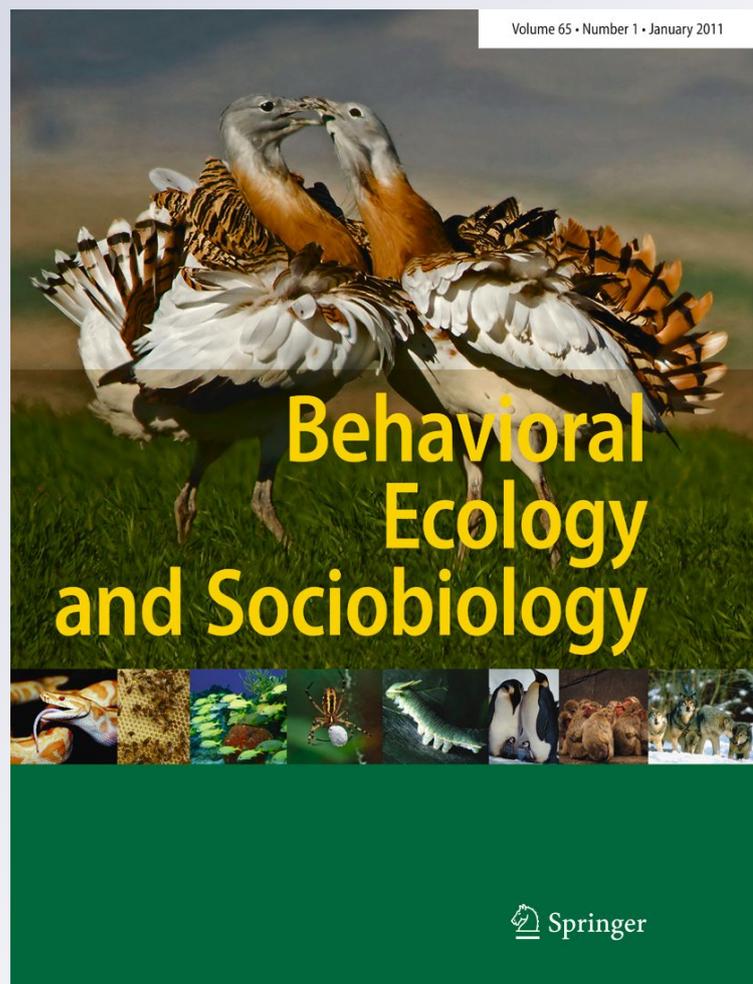
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# Bat predation and the evolution of leks in acoustic moths

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**Abstract** Theories of lek evolution generally invoke enhanced mating success experienced by males signalling in aggregations. Reduced predation has also been acknowledged as a potential factor driving lek formation, but its role is more ambiguous. Although lekking is a complex behaviour, few empirical studies have investigated the role of both claims. We studied the potential pressures imposed by mating success and predation in an acoustic moth, *Achroia grisella*, in which males gather in leks and broadcast a calling song attractive to females. We exploited the ability to manipulate the distribution of singing males in laboratory arenas to create different-sized leks and tested female preferences for these aggregations. Because *A. grisella* are vulnerable to predation by bats while in flight and on the substrate, we also tested the responses of a potential predator, *Rhinolophus ferrumequinum*, a bat species that feeds on moths, to the experimental leks. We found that the per capita attractiveness of *A. grisella* males to females rose with increasing lek size. *R. ferrumequinum* also oriented toward experimental *A. grisella* leks, but this attraction did not increase at larger leks. Thus, a male's per capita exposure to predation risk declined as more moths joined the lek. *A. grisella* males appear to benefit from advertising in larger leks in terms of both increased mate

attraction and reduced predation risk. Our results support the idea that multiple factors operating simultaneously may maintain lekking behaviour.

**Keywords** Acoustic communication · Mate choice · Sexual selection · Signal evolution · Ultrasonic signals

## Introduction

Aggregations of sexually advertising males are among the most spectacular phenomena in animal behaviour, but they have also posed some of its major problems (Darwin 1871; Magnhagen 1991; Andersson 1994). In the case of leks, aggregations at which females arrive and choose among the advertising males but do not receive direct, material benefits by virtue of mating with one male over another, it is generally proposed that a male's mating success demands his participation in a group display (Höglund and Alatalo 1995). This requirement may be driven by female choice for male aggregations per se because such groups offer the opportunity for simultaneous, as opposed to sequential, comparison of potential mates (Kokko 1997). Additionally, males may aggregate at particular points in the landscape that are frequented by numerous females (Bradbury and Gibson 1983), settle near superior signallers (Beehler and Foster 1988), or aggregate their territories to retain females who remain in estrus (Stillman et al. 1993). But male advertisement normally attracts natural enemies as well as females, and it is also proposed that the aggregation of males in leks may mitigate the per capita risk of attack (Lack 1968; Wiley 1991). That is, (1) predators encountering the elevated density of prey that a lek presents may become rapidly satiated and neglect most individuals (Kurban 1982), (2) males displaying within a lek may avail

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themselves of the enhanced vigilance of the group (Gibson et al. 2002), or (3) the group otherwise dilutes the risk of predation suffered by any one male (Turchin and Kareiva 1989). For example, if a predator perceives the signals of lekking males and then arrives and attacks a given individual, that individual's neighbours may respond to the general disturbance of the attack by temporarily ceasing sexual advertisement and other conspicuous activity. This option would not be open to solitary males.

The majority of empirical work on lek formation has concentrated on the possibility that aggregated males accrue greater mating success. However, findings are ambiguous: While many of these studies have found evidence to support this expectation (Alatalo et al. 1991; Lank and Smith 1992; Balmford 1990; cited in Höglund and Alatalo 1995), a considerable number have not (van Rhijn 1983; Bradbury et al. 1989; Deutsch 1994; Westcott and Smith 1997; Jones and Quinell 2002). Other researchers explored an alternative possibility that lekking affords safety from predation to displaying males (Koivisto 1965)—and also to visiting females (e.g. Lima and Dill 1990; Grafe 1997). Here, a smaller number of empirical studies have been conducted, but the same ambiguity has been observed: Whereas several studies support the notion that leks offer males the opportunity to evade predation while advertising to females (Ryan et al. 1981; Trail 1987), others have not found this effect (Beehler 1988; Balmford and Turyaho 1992). Such opposing data have even been found within the same species (sage grouse *Centrocercus urophasianus*, Bradbury et al. 1989; Gibson and Bachman 1992).

Empirical studies indicate that no one model is a universal explanation for lek formation. Rather, the factors involved in the lek phenomenon vary from species to species and from population to population. Moreover, lekking is a complex behaviour, and it is therefore likely that several factors act jointly in its evolution and maintenance. This latter possibility has been proposed by several researchers (e.g. Boyko et al. 2004; Jiguet and Bretagnolle 2006; Young et al. 2009) following their studies of leks in the field (but see Gibson et al. 2002). Nonetheless, very few studies have actually tested the simultaneous influence of multiple factors in lek formation in natural populations.

We addressed the potential simultaneous influences of predation and female attraction on lekking behaviour with an acoustic pyralid moth (*Achroia grisella*) in which males aggregate in small leks and broadcast an ultrasonic advertisement song that attracts females (Spangler et al. 1984) but may also draw the attention of insectivorous bats. An experimental approach was implemented wherein we created experimental leks of various sizes and tested their attractiveness and responses to bat predators. Here, we note that the behavioural interactions between moths and

insectivorous bats are textbook examples of how prey may evolve defences in response to predation pressure: In general, tympanate moths possess sensitivity to ultrasound and exhibit specialized flight manoeuvres in response to bat echolocation signals by which they may evade attack and capture (Miller and Surlykke 2001; Waters 2003). Moreover, in those moth species which use acoustic signals for sexual advertisement (Conner 1999; Nakano et al. 2009), singing males may become silent (Greenfield and Baker 2003), and females may cease orientation toward males in response to synthetic bat calls (Greenfield and Weber 2000); also see Acharya and McNeil (1998) and Jones et al. (2002). In some species of acoustic moths, advertising males are observed to gather in small groups. Thus, we asked whether the complex behaviour of lekking might afford additional protection against the risk of predation to which advertising males are exposed.

We began our study of experimental *A. grisella* leks by testing the relative attractiveness of different-sized male aggregations to females. We then proceeded to examine how males signalling in leks might experience varying levels of predation by the greater horseshoe bat, *Rhinolophus ferrumequinum*, a species that feeds on moths as well as other insects and sometimes gleanes these preys from the substrate (Griffin and Simmons 1974; Jones and Rayner 1989; Jones 1990; Pir 1994). While *R. ferrumequinum* typically prey on larger moths, they do orient toward the playback of a singing *A. grisella* and will readily feed on these insects (K. Koselj, unpublished data). Because a female adjacent to a singing male may be as vulnerable to predation as the male himself (Lima and Dill 1990; Pocklington and Dill 1995; Candolin 1997), we also tested whether females exhibit different levels of defensive behaviour in response to *R. ferrumequinum* when visiting leks of dissimilar size. Finally, we retested female defensive behaviour at leks in response to various synthetic echolocation and noise stimuli to discern the specific acoustic parameters that modulate this behaviour. Our results show that reduced per capita predation risk in addition to elevated male mating success may select for lekking behaviour in this acoustic moth species.

## Materials and methods

### Natural history of *A. grisella*

*A. grisella* are symbionts of the western honeybee (*Apis mellifera*) and are currently distributed in most regions of the world where *A. mellifera* are kept (Milum 1940). The moth larvae feed on comb and organic detritus from honeybee colonies, particularly those with low populations of worker honeybees. Mating activities of the moths

normally occur in the vicinity of their natal honeybee colony, where male moths may be observed forming small aggregations of less than ten individuals and broadcasting their advertisement songs on surrounding vegetation and other substrates during the night (Greenfield and Coffelt 1983). The song is a continuous train of high-frequency (70–130 kHz) pulses delivered at 80–100 pulse pairs  $s^{-1}$  (Fig. 1a). Individual pulses are brief ( $\approx 100 \mu s$ ) and emitted at 95-dB sound pressure level (SPL) peak amplitude (relative to 20  $\mu Pa$ ), as measured at a 1-cm distance (see Spangler et al. 1984 and Jang and Greenfield 1996 for determination of spectral and energy characters of male song). *A. grisella* song attracts receptive females up to 1 m distant, who normally run toward the males, move among them, and orient toward a given individual and immediately mate with him (Alem and Greenfield 2010). The song also attracts non-signalling solitary males who join the group and may start signalling (Greenfield and Coffelt 1983).

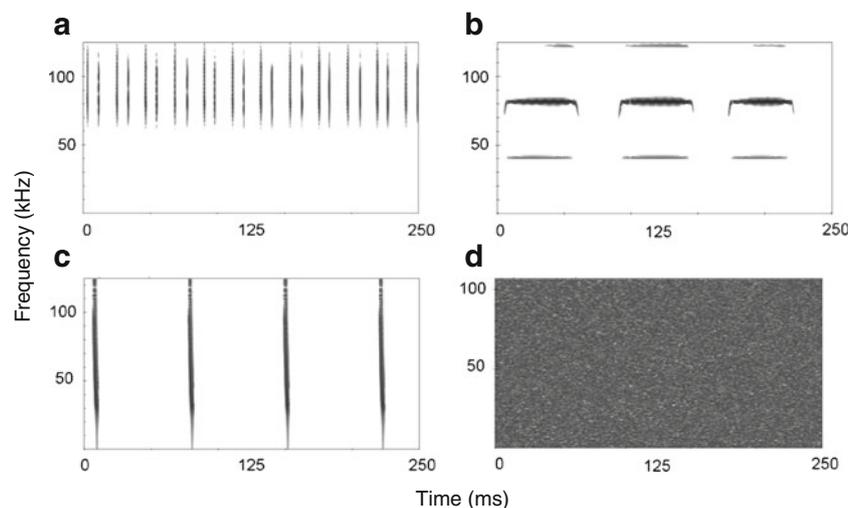
Both male and female *A. grisella* exhibit specialized behavioural responses upon hearing synthetic acoustic stimuli that resemble echolocation signals emitted by various insectivorous bats of the old world (see Greenfield and Hohendorf 2009). These behavioural responses appear to be defensive in nature (cf. Jones and Rydell 2003): flying *A. grisella* may dive to the ground (Rodriguez and Greenfield 2004), whereas singing males generally become silent (Greenfield and Baker 2003), and females running toward a singing male may arrest movement (Greig and Greenfield 2004), possibly to eliminate the production of inadvertent sounds. The latter responses may reduce vulnerability to attacks from bat species that passively

localise non-flying insect prey by detecting their locomotion sounds or movements and then gleaning them from the substrate (Faure and Barclay 1992; Arlettaz et al. 2001; Siemers and Güttinger 2006; Goerlitz et al. 2008). The finding that the dominant frequency range (30–90 kHz), repetition rate (10–25  $s^{-1}$ ), and pulse duration ( $\geq 1$  ms) of acoustic stimuli eliciting these responses match those of the search and approach phase echolocation signals of various species of bats argues that the behaviours are adaptations for avoiding attacks by these predators (Greenfield and Hohendorf 2009). This argument is bolstered further by observation of bat attacks on *A. grisella* in the field (Brandt 2003). Ours is the first study to test the reaction of *A. grisella* to echolocation calls of live bats.

Bat echolocation can roughly be classified in two major types: Bats of the first type use calls with long constant-frequency (CF) elements (Fig. 1b), and those of the second use short frequency-modulated (FM) pulses. Both groups contain species that glean prey from surfaces (Schnitzler and Kalko 2001, Schnitzler et al. 2003). The CF bats (which include *R. ferrumequinum*) echolocate at a substantially higher duty cycle than the FM bats (Vögler and Neuweiler 1983). That is why we predicted that *A. grisella* would show stronger defensive responses to the playback of CF echolocation calls than to the same amplitude playback of synthetic FM sweeps similar to the ones used by the FM bats.

#### Animals studied

We studied a laboratory population of *A. grisella* derived from moths collected at honeybee colonies in Dept.



**Fig. 1** Spectrograms of moth calling song, bat echolocation signal, and synthetic stimuli presented in experiment 4. **a** Calling song of an *A. grisella* male. **b** Echolocation signals of *R. ferrumequinum*, also used as CF echolocation stimulus in experiment 4. **c** Synthetic FM bat echolocation stimulus. See Lafaille et al. (2010) for construction of

FM stimulus and rationale for its specific parameters. **d** White noise stimulus. For playback in experiment 4, peak amplitudes of the CF, FM, and noise stimulus were adjusted to an equivalent 95 dB SPL, as recorded at the location of the test female. See Jang and Greenfield (1996) for method of calibration of SPL

Ardèche, France, in August 2008. The moths were reared on a synthetic diet (Jang and Greenfield 1996) in environmental chambers in Tours, France (Institut de la recherche sur la biologie de l'insecte, IRBI), under a 12:12 L/D photoperiod and  $23 \pm 2^\circ\text{C}$ .

We used *R. ferrumequinum* maintained in an animal facility in Seewiesen, Germany (Max Planck Institut for Ornithology, MPI), especially equipped for bat husbandry, to test interactions between adult *A. grisella* and bats. The bats had been captured in the cave Kostanjeviška jama in Slovenia in 2004 and maintained in captivity since. *R. ferrumequinum* were used because their hearing is highly sensitive to very high sound frequencies matching those broadcast by singing *A. grisella* males (Griffin and Simmons 1974; Jones and Rayner 1989). Also, *A. grisella* male song is similar in both repetition rate and carrier frequency to 'acoustic glints' that the wing movements of fluttering insect prey imprint onto the echoes of the horseshoe bats' CF calls (Kober and Schnitzler 1990). As acoustic glints are the key prey cue for horseshoe bats (von der Emde and Schnitzler 1990; Siemers and Ivanova 2004), we predicted that the song of male *A. grisella* overlapping with the echo stream might attract the horseshoe bats. Several preliminary trials showed that the bats had no aversion to feed on *A. grisella* adults and responded to playbacks of *A. grisella* calling song by turning toward the loudspeaker and increasing the repetition rate of echolocation calls, a clear indication of interest. These moths are not aposematically coloured, and there is no indication that they have any particular chemical defence. *R. ferrumequinum* have been common in natural areas in southern and central Europe (Csorba et al. 2003), regions where *A. grisella* have been present for a long time. The hunting repertoire of this bat, as well as of other European *Rhinolophus* species, includes substrate gleaning (Jones and Rayner 1989; Siemers and Ivanova 2004). Although *R. ferrumequinum* (forearm length=53–62 mm, body mass=18–24 g; Dietz et al. 2007) prefers larger prey, it also consumes a proportion of insects of the size of *A. grisella* (wingspan=2 cm, body mass=10–40 mg) and smaller (Jones 1990). These observations all indicate that *R. ferrumequinum* behaves as a potential predator of *A. grisella*, and it may indeed be one. We thus used it as an experimental model for bats that opportunistically prey on *A. grisella*.

We used six adult males from the *R. ferrumequinum* colony in our tests conducted in November 2009. The bats were fed 4 g of mealworms (*Tenebrio molitor* larvae) per day, supplied with water ad libitum, and given a food supplement of vitamins, minerals, and other essential nutrients once every 4 weeks. They were regularly allowed to fly in and explore the flight room in which testing would be conducted so that they were fully familiar with it once tests began.

## Experimental protocols

*Experiment 1 Do aggregations afford males a per capita mating advantage?* We determined the relative attractiveness of small vs. larger aggregations of singing male *A. grisella* to females by conducting a series of laboratory trials at the IRBI in Tours. For each trial, males were held individually within cylindrical screen cages (2-cm diam., 2-cm height) that were arranged in two groups – experimental leks – on opposite sides of an arena. We released a test female from the centre of the arena and observed her movement toward the male cages. Cages within a group were separated by 2 cm, and the two groups were situated 24 cm from the female release point. Males generally sang regularly within these cages, and previous studies confirmed that the screen does not modify acoustic characters of their song (Jang and Greenfield 1996).

We conducted all trials in an acoustically insulated chamber during the first half of the photoperiodic night. The chamber was kept at  $23^\circ\text{C}$  and illuminated with diffuse red light from an incandescent bulb (25 W). Test females were placed individually into a covered depression in the arena floor (diameter, 2 cm), where they usually remained on the bottom owing to a coating of Teflon® on the sides and ceiling, and allowed 3 min to adjust to their introduction. We then removed the depression cover and simultaneously raised the bottom of the depression until it was level with the arena floor. Females were allowed 5 min to leave the release point, move within the arena, and arrive within 2 cm of a male cage and remain in that zone for a minimum of 5 s, which signified her choice and the end of the trial (Alem and Greenfield 2010). We kept the females within an acoustically insulated box between their successive trials to prevent their continuous exposure to male song. Prior to starting each trial, we verified that all males were singing with an ultrasound detector (model D230; Petterson Elektronik AB; Uppsala, Sweden). Singing by all members of the group normally occurs because neighbouring males stimulate one another to display (Greenfield and Coffelt 1983).

We tested each of 36 females in three successive trials: a choice between two different two-male leks, between a two-male lek and a three-male lek, and between a two-male and a four-male lek. The specific two-male lek that a female chose in her first trial served as the two-male lek tested in her two subsequent trials. Thus, any preference observed for the three-male or four-male leks would be a conservative estimate. A minimum of 30 min elapsed between a female's successive trials. We used a pool of 72 males for the experiment, and for each trial, we effected a random selection, with replacement of the individuals that would comprise the leks except for the

two-male lek tested in a female's second and third trials. Only unmated moths 1–3 days old were used to ensure standardization of behavioural state and because female *A. grisella* seldom mate more than once.

*Experiment 2 Do aggregations afford males a per capita reduction in predation risk?* We examined the relative attractiveness of small vs. larger aggregations of singing male *A. grisella* to bats by observing the responses of *R. ferrumequinum* to caged moths in a 6×3.5×4-m (length × width × height) flight room at the MPI in Seewiesen. A cylindrical screen cage (8-cm diam., 20-cm height) was affixed on a 1.2-m vertical rod in the centre of each half (3×3.5×4 m) of the room. A specified number of males were introduced to the cages, and a bat was released in the flight room. We left each bat in the flight room for 1 h. However, we only scored a bat's behaviour with respect to the moth cages during the last 30 min, because not all moths sang reliably at the beginning of the trials (see below for the methods of real-time monitoring of songs). The moths were left in the cage at the end of the trial, the bat was returned to its housing chamber, and the observational process was then repeated for the other five bats on a given test day. The flight room was illuminated with an infrared LED lamp, to which the moths and bats were largely insensitive but which permitted video filming (see below), throughout the trials. Both moths and bats were kept under the same photoperiod.

We tested each of the six bats with a series of eight trials, one trial per test day. Days 1, 2, and 3 comprised trials of empty cages in both the left and right sectors of the flight room, days 4 and 5 comprised trials of two vs. zero males, day 6 comprised another trial of empty cages in both sectors, and days 7 and 8 comprised trials of two vs. six males. Because we observed that the bats consistently preferred the right sector on days 1–3, we placed the cage with two males in the left (non-preferred) sector on days 4 and 5. However, we switched the positions of the smaller and larger male aggregations between the left and the right sectors between days 7 and 8. Trials of two empty cages served to accustom the bats to the presence of cages in the flight room (days 1–3) and to dishabituate them to the expectation of moths within the cages (day 6). The order of testing the six bats was re-randomized each test day. A different pool of 1–3-day-old male moths was used on each of the four test days during which males were placed in the cages.

To monitor bat–moth interactions, we recorded the songs of the test males in the cages and filmed the movement of the bat during the 30-min observation period in each trial. Song recordings were made with condenser microphones (model CM16/CMPA; Avisoft Bioacoustics; Berlin, Germany; frequency response±3 dB, 20–150 kHz) suspended

above each male cage. The microphone output signals were digitized with a four-channel analogue: digital converter (model Ultrasound Gate 416H<sup>200</sup>; Avisoft Bioacoustics) coupled to a notebook computer situated outside the flight room and observed in real time via signal processing software (Recorder; Avisoft Bioacoustics). Thus, we could verify that all the males in the cages were singing. Bat movement and positions were filmed continuously with two IR cameras (WAT-902H2 ULTIMATE; Watec Co., Japan) mounted on the ceiling of the flight room. We synchronized the video camera and microphone signals (Digi-Protect; ABUS Security Group; Munich, Germany) and saved the synchronized signals from a given trial to a single computer file. Later, examination of the file, aided with a behavioural event recorder, revealed whether and when the bat flew in a particular sector of the room in each trial. We considered the relative time spent flying in the sector as a measure of bat attraction to the respective lek.

*Experiment 3 Do females modify defensive behaviour when visiting male aggregations?* Because the females visiting leks may be as vulnerable to predation as the advertising males are (Pocklington and Dill 1995), females may be expected to exhibit defensive behaviour in the presence of predators. If larger leks afford more protection, however, females might reduce such defence when visiting them. *A. grisella* females often arrest movement toward males if echolocation stimuli are broadcast, and we asked whether they tend to ignore predator cues when lek size expands. We placed an 80-cm-diam. screen arena in the flight room, allowed a bat to remain on a perch 1.2 m directly above, and examined the movement and arrestment responses of female *A. grisella* orienting toward one of either two or four males singing within the arena.

We tested 17 females in four different trials: orientation toward males singing in two- and four-male leks, in the absence and presence of a bat. Only 1-day-old females were used because anti-predator behaviour declines in older individuals (Lafaille et al. 2010). The female was released in the arena centre as in experiment 1 (except that the central depression was opened manually), and males held in individual cages were arranged on opposite sides of the arena (trials of two males) or along the four cardinal directions with respect to the centre (four males). Acoustic insulation foam placed above each male cage shielded it from echolocation calls, thus favouring continued singing. A different pool of 1–3-day-old males was used on each test day. A female's two trials in the absence of a bat were conducted first, and a minimum of 30 min elapsed between consecutive trials. We randomly selected the bat to be used on a given test day from among the six individuals.

Using the microphones and video cameras described in experiment 2, we monitored the songs of the *A. grisella*

males and the echolocation signals of the bat, and we filmed the movement of the *A. grisella* female. We only began a trial when all two or four males were singing, and the bat emitted echolocation signals (Fig. 1b) while perched, a normal foraging behaviour for *R. ferrumequinum* (Jones and Rayner 1989). Trial duration and the criteria for female orientation toward and choice for a male were as in experiment 1.

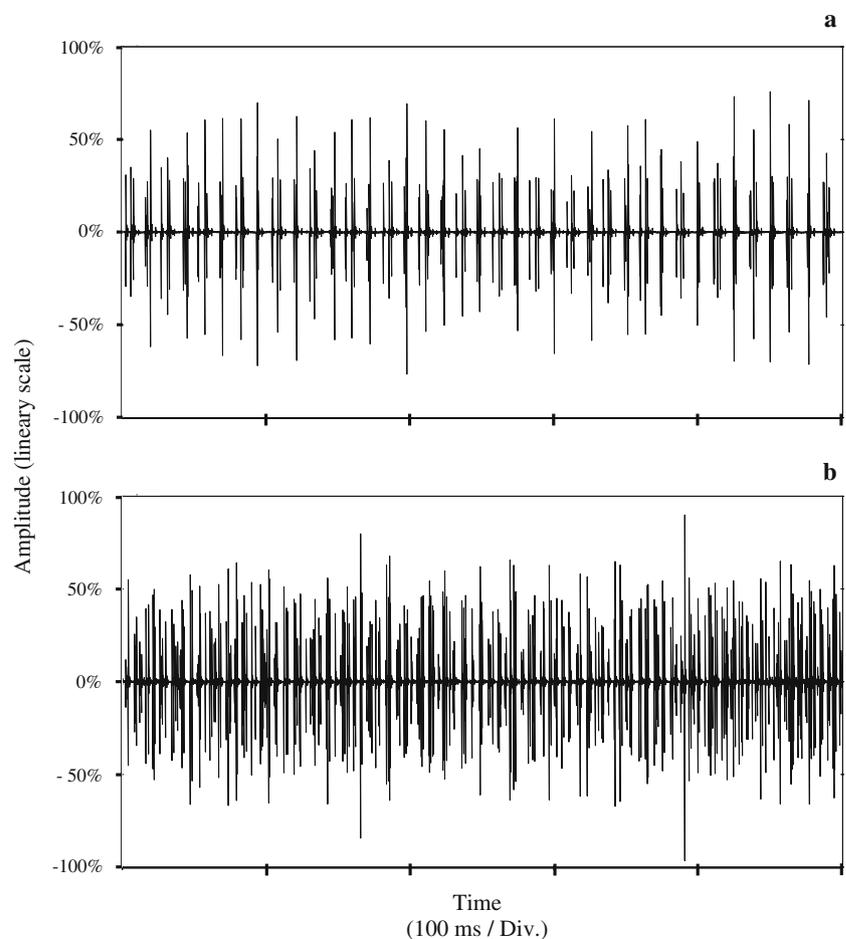
**Experiment 4 Which predator cues modulate female defensive behaviour at leks?** We repeated experiment 3 save that we replaced the live bat with acoustic stimuli broadcast from an overhead loudspeaker (model ScanSpeak, Avisoft Bioacoustics; frequency response  $\pm 2$  dB, 60–110 kHz). We examined the movement and arrestment of 22 females among two or four singing males in response to four different stimuli (silence (no broadcast), continuous white noise, a synthetic FM echolocation signal (typical for many gleaning bats that find food by detecting prey sounds), and a recording of a CF echolocation signal of *R. ferrumequinum*; see Fig. 1). Each stimulus was presented for 2 s immediately after female release and adjusted to 95 dB SPL (peak amplitude) as measured at the female release point

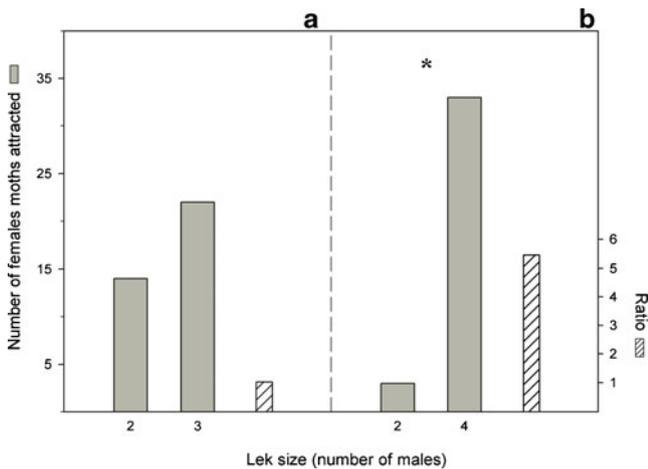
(see Jang and Greenfield 1996 for calibration by the method of peak equivalents). This would correspond to a bat roughly 2 m away or closer (Schuchmann and Siemers 2010 have measured maximum on-axis SPLs = 123 dB SPL at 10 cm from echolocating perched *R. ferrumequinum*). Experiment 4 determined whether the arrestment response represents masking of male song by the overall noise level of bat echolocation or a specialized response to these predator cues. It also determined whether the echolocation calls of some predatory bats more strongly affect the moths' behaviour than other signals do.

## Results

**Experiment 1 Do aggregations afford males a per capita mating advantage?** We recorded male calls at leks of two and four individuals and observed that the overall repetition rate increased with lek size, whereas the overall amplitude did not change (Fig. 2a and b). *A. grisella* females exhibited a significant preference for the larger experimental lek in choice trials of two vs. four males (binomial test, two tailed;  $n=36$ ;  $P<0.001$ ; Fig. 3b). Moreover, males in the four-male

**Fig. 2** Oscillograms of singing *A. grisella* males at leks in experiment 1. **a** Lek of two males. **b** Lek of four males. Both oscillograms represent examples randomly chosen among all recordings. Recordings were made at the position where females were released





**Fig. 3** Attractiveness of experimental *A. grisella* leks to females (experiment 1). For the two choice tests presented, grey bars indicate the numbers of females (total,  $n=36$ ) that oriented toward each of the two leks. The narrower, diagonally lined bars shown in **a** and **b** represent the relative per capita attractiveness of males in the larger lek to females, a proxy for relative per capita mating success. This relative attractiveness is measured by the ratio of the number of females attracted by the larger lek, divided by the number of males in that lek, to the number of females attracted by the two-male lek, divided by 2. \* $P<0.05$ , binomial test

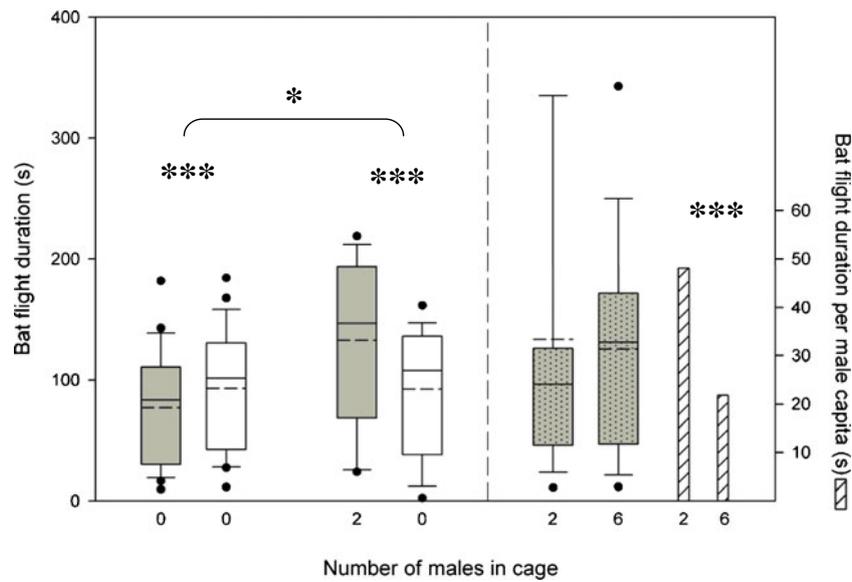
lek attracted significantly more females ( $n=33$ ) than the random expectation ( $n=24$ ) assuming that females distributed themselves commensurately with the numbers of males in the two leks (binomial test, two tailed,  $n=36$ ;  $P=0.002$ ). However, female preference for the larger lek, as well as higher per capita attractiveness of males in the large lek, was not found in the choice trials of two vs. three males (binomial test, two tailed;  $n=36$ ;  $P>0.20$ ; Fig. 3a). Because our criteria for attraction required that the female remains near a male (group) for a minimum of 5 s, we infer that the potential advantage accrued by individuals in the four-male leks would translate to a per capita mating advantage where the males are not caged but free in the arena.

**Experiment 2** Do aggregations afford males a per capita reduction in predation risk? Our test bats were clearly attracted to singing male *A. grisella*, but they did not exhibit a special preference for the larger of two experimental leks. During the first three test days, when the cages in both sectors of the flight room were empty, we found that the bats spent significantly more time flying in the right sector (non-parametric analysis of longitudinal data in factorial experiments; see Brunner et al. 2002; ANOVA-Type Statistic,  $ATS=11.22$ ,  $df=1$ ,  $P<0.001$ ; Fig. 4a). On day 6, we observed the same preference (Wilcoxon signed-rank test, two tailed;  $Z=2.201$ ,  $P=0.031$ ). In tests with moths, bats occasionally inspected in hovering flights the cages with singing males. A two-male lek was placed in the left cage on days 4 and 5, and we found that the bats then reversed how

they apportioned flight time between the two sectors (sector  $\times$  trial interaction,  $ATS=3.88$ ,  $df=1.30$ ,  $P=0.038$ ; Fig. 4a and b). Importantly, on days 4 and 5, bat flight times were longer in the sector harbouring the two-male lek than in the adjacent sector with an empty cage ( $ATS=15.63$ ,  $df=1$ ,  $P<0.001$ ; Fig. 4b). However, in choice tests of two-male vs. six-male leks on days 7 and 8, the bats did not spend more time flying in the sector containing the cage with six males (non-parametric mixed model for longitudinal data, with lek size as the first factor:  $ATS=0.63$ ,  $df=1$ ,  $P=0.43$ ; Fig. 4c). This test was performed independently of the bats' preferences for the room side, which, in contrast to the previous experimental trials, were not found on the days 7–8 (room side as the second factor:  $ATS=0.28$ ,  $df=1$ ,  $P=0.60$ ; interaction lek size  $\times$  room side:  $ATS=1.05$ ,  $df=1$ ,  $P=0.31$ ). Assuming that flight duration is a proxy for exposure to predation risk and that only one moth is successfully captured in an attack, we estimated per capita predation risk by dividing flight duration in a sector by the number of moths in the lek in that sector. We computed a longitudinal non-parametric model for these data using the same design as above, and we found that males in the larger lek enjoyed a lower per capita predation risk (lek size as the first factor:  $ATS=25.97$ ,  $df=1$ ,  $P<0.00001$ ; room side as the second factor:  $ATS=0.22$ ,  $df=1$ ,  $P=0.64$ ; lek size  $\times$  room side interaction:  $ATS=3.14$ ,  $df=1$ ,  $P=0.076$ ; Fig. 4c).

**Experiment 3** All test females moved toward males in the two trials where a bat was not present overhead, confirming the receptivity of these individuals. But in the trials with a bat echolocating on the overhead perch, 14 and 13 of the 17 test females exhibited an arrestment response en route to one of the two or four males, respectively, and never arrived at a male cage (Fig. 5). These significantly elevated proportions of arrestment (binomial tests, two tailed;  $P<0.01$ ) indicate clearly that female *A. grisella* exhibit defensive behaviour in the presence of *R. ferrumequinum*. However, the proportions of females arresting movement did not differ between the two situations (McNemar test, two tailed;  $\chi^2=0.0$ ,  $P=1.0$ , power=1.0), suggesting that females may not modify defensive behaviour substantially when visiting larger leks.

**Experiment 4** As in experiment 3, the receptivity of all 22 test females was confirmed by their movement toward males in the trial where no stimulus was presented from the overhead loudspeaker. Overall, the proportion of females arresting movement differed significantly among the eight stimulus/lek size combinations tested (Cochran's test, two tailed;  $Q=14.067$ ,  $df=7$ ,  $P<0.001$ ; Fig. 5). In post hoc comparisons of responses to echolocation stimuli and silence, we observed that significant proportions of females arrested movement when either the CF or FM stimulus was



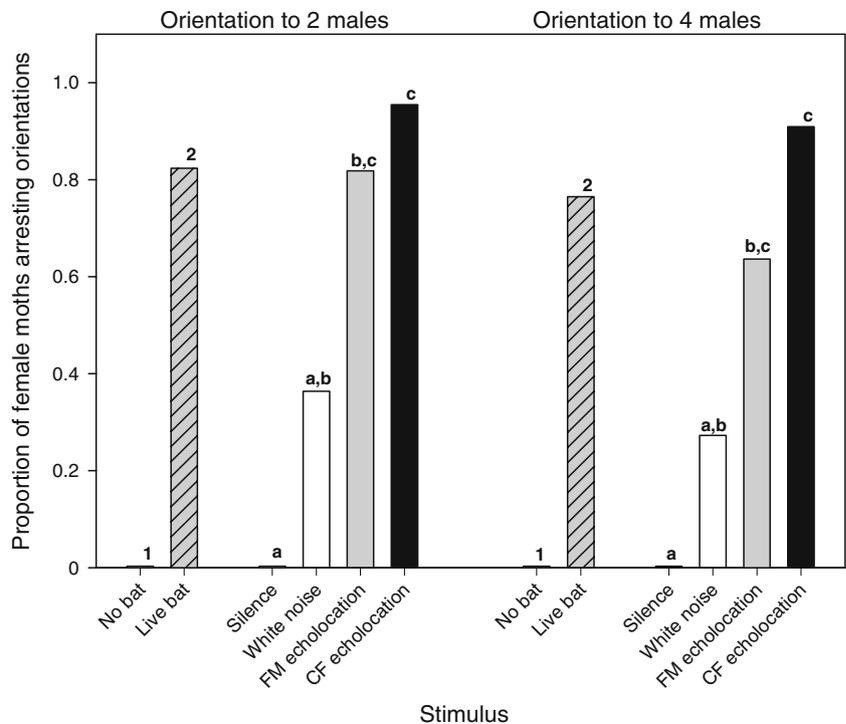
**Fig. 4** Flight of test bats adjacent to moth cages (experiment 2). **a** Tests presenting an empty cage in both the left and right sectors of the flight room (days 1–3); **b** tests of a two-male cage in the left sector vs. an empty cage in the right sector (days 4–5); **c** tests of a two-male cage vs. a six-male cage (days 7–8), with cages switched between sectors after day 7 (Outlier for the two-male cage on days 7–8, 628.120, is not depicted). *Box plots* indicate mean (*dashed line*), median (*solid line*), and 25–75% range for flight durations in a given sector by test bats; *whiskers* indicate 10th and 90th percentiles, and

*black dots* are outliers; for **a** and **b**, *grey bar* represents the left sector of the room, and *open bar* represents the right sector. The *narrower diagonally lined bars* shown in **c** represent the per capita exposures of males to test bats, a proxy for the per capita predation risk. Exposure is measured by the mean flight durations of bats in a sector divided by the number of males present in that sector. \*\*\* $P < 0.001$ , \* $P < 0.05$ , non-parametric analysis of longitudinal data in factorial experiments (Brunner et al. 2002)

presented (Fig. 5). However, in comparisons of responses to echolocation stimuli and white noise, we observed that significantly higher proportions of females arrested move-

ment only when presented with the CF stimulus. Both sets of post hoc results held whether females oriented toward leks of two or four males.

**Fig. 5** Incidence of arrestment response by *A. grisella* females. Data represent proportions of test females arresting movement toward leks of two or four singing males after being presented with a live bat (*R. ferrumequinum*) echolocating on an overhead perch (Experiment 3) or an acoustic stimulus broadcast from an overhead loudspeaker (Experiment 4). *Bars* accompanied by the same numeral (comparison of responses to live bat) or letter (comparison of responses to loudspeaker broadcasts) are not significantly different ( $\alpha = 0.05$ ; McNemar test, with sequential Holm correction for multiple comparisons, Holm 1979)



## Discussion

Our behavioural data from bats and the acoustic moth *A. grisella* suggest that moth lekking behaviour may be maintained by both the elevated mating success and the reduced predation pressure that males enjoy when singing in aggregations. We found that larger aggregations of singing males attracted more females but not more interest from predatory bats than smaller aggregations did. Whereas the attraction of females to a male aggregation outpaced an increasing number of singers joining the group, the attraction of bats lagged this increase. Thus, per capita attractiveness to females rose while per capita exposure to predation risk declined as more males joined. We note that we found no evidence for an increase of predation risk with lek size even though we had used a larger difference in lek size in the predation experiment (two versus six males) than in the female preference experiment (two versus four males), where we did find a size effect. This imbalance in lek size difference underpins the conservativeness of our findings. These findings indicate that selection pressure imposed by differential mating success and predation pressure may operate jointly and in the same, positive direction on male aggregation in *A. grisella* such that lek formation is favoured. Here, we suggest that males may continue to join *A. grisella* leks until a further increase in lek size is opposed by factors such as excessive male–male competition and demographic limitations on the number of receptive females. In nature, singing males were observed to form leks of less than ten individuals (pers. obs.).

Leks are reported in many animal classes, but most analyses of the phenomenon have focused on birds, with smaller samples on mammals, amphibians, fish, and insects (see Introduction and also Werner and Lotem 2003; Booth-Binczik et al. 2004; Loiselle et al. 2007; Weldon 2007 for several additional examples). While these studies have offered valuable information on the maintenance and evolution of leks, they have mostly tested only a single mechanism. Responding to the general ambiguity found in studies testing single mechanisms and to the complexity of lekking behaviour, we assumed that several mechanisms might act simultaneously in lek formation, and we designed our study of experimental *A. grisella* leks accordingly to encompass both male mating advantage and predation risk.

Our approach of using experimental leks indicated how lekking behaviour in *A. grisella* may be sustained, but various questions remain on the mechanisms by which groups might benefit from higher mating success and lower predation risk. At present, we do not know how females discern groups of singing males from solitary individuals, but we may infer that a slightly faster pulse rate broadcast

by individual males competing within a group (Jia et al. 2001) and a much faster rate broadcast collectively by an entire group (see Fig. 2a and b) are the likely features: Playback experiments and tests using live males have repeatedly shown in various *A. grisella* populations that females orient preferentially toward male song delivered at faster pulse rates (Jang and Greenfield 1996, 1998). Our data suggest that this increase in moth duty cycle due to larger lek size did not increase the attractiveness to bats. We also note that the SPL emitted by a group of singing males might exceed that of a solitary singer. However, such an increase would normally be small: An increase of 3 dB will result if the equivalent pulses of two males occur precisely at the same instant (summation of independent, incoherent sound sources by the standard formula from linear acoustics; Crocker 1998), but such synchrony would be unlikely given the low duty cycle ( $\approx 2\%$ ) of *A. grisella* song. Otherwise, groups and solitary individuals would broadcast at the same SPL, and females may thus not perceive any amplitude-related differences in attractiveness.

Our results showed that *R. ferrumequinum* were attracted by singing *A. grisella* males. Two cues may be involved in this attraction: the acoustical glints that the fanning wings of singing moths imprint on the echoes and the song of the moths itself. For prey detection, horseshoe bats are known to use acoustic glints (Schnitzler 1987; von der Emde and Schnitzler 1990; Siemers and Ivanova 2004). Nonetheless, the responses of *R. ferrumequinum* in preliminary playbacks indicate that they may also use ‘passive’ acoustic cues to some extent.

The lower per capita predation risk that *A. grisella* males may enjoy in larger groups poses questions at several levels. While *R. ferrumequinum* are attracted to singing *A. grisella* males, the response of the bats did not parallel that of *A. grisella* females (cf. field crickets, *Gryllus lineaticeps*, and parasitoid flies, *Ormia ochracea*; Cade 1981), and a significant preference for larger male groups over small ones was not observed (Fig. 4c). Perhaps, this relative indifference of *R. ferrumequinum* reflects their preference for larger insect prey (Jones 1990; Koselj et al. 2011) and a much broader diet than that in insect parasitoids. If correct, this inference would support a general advantage for lekking in *A. grisella*, because no bat species is known to specialize on attacking these moths. Rather, we assume that *R. ferrumequinum* and several other Palearctic bats occasionally prey on this lekking moth when opportunities arise. Given that larger *A. grisella* leks may not attract significantly more bat predators, we propose that males in larger leks could benefit from a reduced per capita risk because of a dilution effect: If a bat arrives at a lek and happens to attack one male, possibly an individual who had not already ceased singing, other males in the lek can detect the nearby

attack and escape predation by silence or flight. But as lek size diminishes, the chance that a given male is the one attacked increases greatly.

Our proposed mechanism for the dilution effect in *A. grisella* relies on a basic assumption: When a bat arrives at a lek, it attacks no more than one moth. We suggest that this assumption may generally hold owing to two factors. First, a bat engaging in substrate gleaning is unlikely to land and capture one moth without disturbing neighbouring moths sufficiently such that they become inactive and silent, or flee. We base this latter prediction on our observations of *A. grisella* in the laboratory, where disturbing a given singing male within a group normally results immediately in the silencing of his nearest neighbours. For the same reason, a second bat arriving at a lek of *A. grisella* immediately after the attack of a first bat may fail in the capture: The moths that have evaded capture by the first bat are expected to become silent within a fraction of a second (Greenfield and Baker 2003) and thus be unavailable to the second bat.

The dilution effect proposed above may also allow females to benefit when visiting larger leks, which could further strengthen selection for lek formation (but see Isvaran and St. Mary 2003). In both experiments 3 and 4, we observed a non-significant, but nonetheless consistent, reduction in defensive behaviour by females visiting larger leks (Fig. 5). This observation invites further study of hunting bats and signalling moths, as males singing in larger leks might expect more sustained movement by females when bats are hunting and echolocating in the vicinity. Moreover, and unlike females, males decrease their level of anti-predatory responses at leks (Brunel-Pons et al. 2011). The mechanisms that may play a role in this process (song masking, signal competition, and/or the dilution effect) may also act differently in both sexes. Our results also confirmed that the defensive behaviour exhibited by *A. grisella* females is a specialized response to predator cues and that the CF echolocation signal of *R. ferrumequinum* might be more effective than a generic FM signal in eliciting defensive behaviour in a noisy environment (see Jacobs et al. 2008 for differential responses to playbacks of CF and FM echolocation call sequences in two other moth species). As *R. ferrumequinum* is not known to specialize on *A. grisella*, we suggest that the heightened response to the CF signal reflects its higher duty cycle and higher concentration of energy in a frequency band of high hearing sensitivity by *A. grisella*. Tympana of *A. grisella* are broadly sensitive to sound frequencies from 40 to over 100 kHz, and they exhibit maximum sensitivity at 90 kHz (Rodríguez et al. 2005). Thus, the stronger response to 82-kHz CF echolocation calls may reflect specific hearing characteristics in *A. grisella*. The slightly higher response to the CF signal in experiment 4 than to live bats in

experiment 3 (Fig. 5) possibly resulted from differential SPL between the two stimuli.

Ultrasonic hearing and acoustic behaviour of moths are a well-established example of evolutionary responses of prey species to predation, in this case hunting by insectivorous bats (Waters 2003; Ratcliffe and Nydam 2008; Corcoran et al. 2009). Recent studies show that this acoustic behaviour includes defensive responses on the substrate as well as in flight, the former probably serving as defence against bat species that may glean their prey from vegetation and the ground, a foraging strategy abundantly represented in the majority of bat faunas around the world (Kalko and Handley 2001; Schnitzler and Kalko 2001; Schnitzler et al. 2003). These studies also show how selection pressure from bat predation has influenced the evolution of sexual communication in those moth species wherein pair formation is effected by male song that attracts females (Nakano et al. 2009). We now show for the first time that selection pressure from bat predation may yet be responsible, in part, for the maintenance of the complex lekking behaviour in acoustic moths. We demonstrate that *A. grisella* males singing in groups may expect a lower per capita predation risk as additional singers join the group, a factor that complements the higher per capita mating success in aggregations.

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