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# On Wing Sound Characteristics and Their Role in Hummingbird Communication

Todd Alexander Hunter

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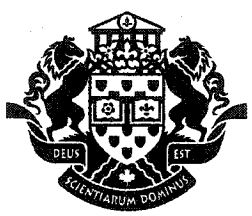


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## THESIS ABSTRACT

The limited ability of humans to decipher the signals produced by other animals has undermined our understanding of the level of communication they possess. Within the avian world, non-vocal sounds have frequently been suggested, as possible forms of communication, but to date have not been tested. Previous studies of hummingbird wing sounds and wing beat frequencies have been limited by technological capabilities and/or sampling effort and have subsequently produced incomplete results. Despite this, several studies have used these questionable results to calculate such things as the relationship between wing length and wing beat frequency. In the absence of a firm understanding of the variability of wing beat frequency within and between individuals of each sex, these studies are subject to an unknown degree of error. Chapter one comprehensively documents the wing sounds of four hummingbird species that breed in Canada. Additionally, I document wing trill characteristics, a new interaction behaviour involving an increase in wing beat frequency and the first account of a wing trill in a female hummingbird. In chapter two, supported by the findings of chapter one, I investigate the role of these non-vocal sounds in intra- and inter- species communication by using wing sounds as playback stimuli. The later chapter's positive communication findings open the door to the field of non-vocal hummingbird communication and beyond into the use of non-vocal communication signals in other avian species.

## THÈSE RÉSUMÉ

La capacité limitée qu'ont les humains de décoder les signaux émis par d'autres animaux a nuit à notre compréhension du niveau de communication dont ils jouissent entre eux. Dans le monde avien, on a souvent voulu croire que les sons non-vocaux étaient des formes possibles de communication, mais jusqu'à présent, rien n'a encore été testé. Les études antérieures sur les sons produits par les battements d'ailes des colibris, ainsi que les fréquences de battements d'ailes, avaient été limitées par la technologie et/ou le travail d'échantillonage, et n'avaient subséquemment produit que des résultats incomplets. Malgré cela, plusieurs études avaient utilisé ces résultats discutables pour effectuer des calculs tels que la relation entre la longueur d'aile et la fréquence des battements. En l'absence d'une solide compréhension de la variabilité de la fréquence des battements d'ailes chez les animaux des deux sexes, ces études sont en proie à une marge d'erreur inconnue. Le chapitre un documente en détail les bruits d'ailes de quatre espèces de colibris qui se reproduisent au Canada. De plus, je documente les caractéristiques des trilles d'ailes, un nouveau comportement d'interaction comportant une augmentation de la fréquence du battement d'aile, ainsi que le premier compte rendu d'un trille d'aile chez la femelle d'une espèce de colibri. Dans le chapitre deux, appuyé par les resultats du chapitre un, j'explore le rôle de ces sons non-vocaux dans les communications entre les individus et les espèces à l'aide d'un stimulus de bruits d'ailes. Les résultats positifs obtenus dans ce dernier chapitre en ce qui a trait à la communication ouvrent la voie au domaine de la communication non-vocale des colibris, voire même à l'utilisation de signaux non-vocaux de communication chez d'autres espèces d'oiseaux.

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Most importantly though I thank the hummingbirds themselves for inspiring this project, for allowing me into their fascinating world and for making ours more enjoyable.

## FORWARD

The following two chapters are written in Condor journal format where they are to be submitted for publication. Some formatting may not follow the typical formatting style of the University of Ottawa. As a result of the country of publication, the English is consistent with that required by publishers in the United States. I have never been sure what America has against 'U' anyway.

This work is in part dedicated to honoring the work of Dr. Calder and Dr. Ortiz-Crespo; their research and love of hummingbirds will be missed. The remainder of this work is dedicated to self-determination and the desire to investigate things in nature out of curiosity rather than direct human benefit.

**CHAPTER ONE**: The wing sounds of four hummingbird species that breed in Canada

*Abstract.* The rapidly beating wings of hummingbirds have long held a fascination to those who marvel and study their aerial abilities. Previous research into the characteristics of hummingbird wing sounds has been limited and has provided little understanding of their basis from which to formulate predictions as to the possible role of these sounds in communication. Digital recordings of the wing sounds of both sexes of four Canadian breeding hummingbird species were made and analyzed using computer based sound software. These technologies improve upon previous techniques of analysis by using finer temporal scaling, an improved low frequency response, rapid manipulation of sound files, and the ability to make high fidelity in-field recordings. The results revealed that previous recordings were not fully representative of the species or sex that was studied. In all species, male hummingbirds had higher wing beat frequencies than conspecific females. Within individual sampling showed a higher level of variation in wing beat frequency than previously documented and showed that wing beat frequency in hummingbirds is not constant during hover flight. I provide the first description of the context and sound characteristics of a behavioural interaction, that I have named the 'Cobra', in which a hummingbird dramatically increases its wing beat frequency. Analysis of wing trill sound characteristics- produced by the modified outer primary feathers- revealed a pulsed sound pattern with variable temporal onset, pulse duration and relative amplitude both within individuals and between species. I report previously undocumented wing trill components within the wing sounds of female Black-chinned hummingbirds (*Archilochus alexandri*). The ability of hummingbirds to vary these wing trill sounds, and their apparent lack of other function, strongly suggests that they play a role in communication.

*Résumé.* Le battement d'ailes rapide des colibris fascine depuis longtemps tous ceux qui étudient leurs prouesses aériennes et s'en émerveillent. Les recherches antérieures sur les sons d'ailes des colibris et leurs caractéristiques ont été limitées, de sorte qu'on a peu de connaissances de base pour formuler des hypothèses sur le rôle possible de ces sons dans la communication. Des enregistrements numériques des sons d'ailes des deux sexes de quatre espèces de colibris nichant au Canada ont été produits et analysés au moyen d'un logiciel spécial. Ces technologies constituent des améliorations par rapport aux techniques d'analyse antérieures, en permettant un échelonnage temporel plus fin, une réponse basse fréquence améliorée, la manipulation rapide de fichiers sonores et la capacité de produire des enregistrements haute fidélité de colibris *in situ*. Les résultats indiquent que les recherches antérieures n'étaient pas pleinement représentatives des espèces et des sexes en question. Dans toutes les espèces, les fréquences de battement d'ailes des colibris mâles étaient supérieures à celles des femelles de même espèce. En outre, les variations individuelles de ces fréquences étaient plus grandes que ne l'indiquaient les études antérieures, les fréquences de battement d'ailes des colibris n'étant pas constantes pendant les vols sur place. L'analyse de ces caractéristiques sonores des battements d'ailes a révélé une structure pulsée du son variable des points de vue de l'apparence temporelle, de la durée d'impulsion et de l'amplitude relative tant entre les individus qu'entre les espèces. J'ai découvert des composantes sonores non encore documentées du battement d'ailes des femelles colibris à gorge noire (*Archilochus alexandri*). En outre, j'ai établi les premières descriptions du contexte et des caractéristiques sonores d'une comportement d'interaction que j'ai nommé le « Cobra », dans lequel un colibri augmente de façon spectaculaire sa fréquence de battement d'ailes.

Cette expérience permet de mieux comprendre la variabilité des fréquences de battement d'ailes tout en révélant les caractéristiques variables des sons associés. Le contrôle de ces sons et le fait qu'ils n'aient pas d'autre fonction incitent fortement à croire qu'ils jouent un rôle dans la communication.

## INTRODUCTION

As expressed elegantly by Kroodsma and Byers (1991), "to experiment first is human, to describe first, divine." Most research in hummingbird acoustics has focused on vocalizations rather than the non-vocal sounds produced by their rapid wing beats. While planning a series of playback experiments into the role of hummingbird wing sounds in communication, it became apparent that there were anomalies and gaps in that literature and that it would be necessary to first study the variability and characteristics of these non-vocal sounds.

The terminology used to describe the types of sounds created by the wings of hummingbirds needs clear definition. A number of terms have been used in the literature to describe the two major types of wing sounds (noise, buzz, hum, trill, sound and whine) (Ortiz-Crespo 1980, Stiles 1982, Miller and Inouye 1983, Pytte and Ficken 1994, Robinson et al. 1996, Zyskowski et al. 1998, Hurly et al. 2001). This has lead to some confusion as the terms have been used interchangeably or not fully described. I use *wing hum* (WH) to describe the fundamental sound produced by the beating of the wings. The WH is present in both males and females and is generally <100Hz. The fundamental frequency of the WH is equivalent to the actual wing beat frequency (WBF) of the bird. *Wing trill* (WT) is used for the high frequency sound (>1kHz) produced by air rushing over the tips of the modified $9^{th}$ and $10^{th}$ primaries of male hummingbirds (Armstrong 1963). WT is often compared to the sound of a cicada or a metallic whine (Calder 1993). Collectively, these two types of mechanically produced sound are termed *wing sounds* (WS).

Despite the long fascination with the rapid wing beat of many hummingbird species and in the wing sounds they produce during flight, there has been little comprehensive study of their actual sound characteristics or their variability. Deficiencies in prior studies of WBF have usually included lack of comparison between the sexes, failure to compare equivalent flight types between species or examine individual variability, or lack of adequate sample size.

I could not find any information on the WBF of the Calliope hummingbird (*Stellula calliope*) during hovering or non-ritualized flight. Robinson et al. (1996) quote Greenewalt (1960) as stating that the WBF of the Ruby-throated Hummingbird (*Archilochus colubris*) is 53Hz (Beats • $sec^{-1}$) in all types of flight, with no difference between the sexes. Actually, Greenewalt (1962) had reported the WBF to be 70Hz for Ruby-throated males and 52Hz for females, but sample size was not mentioned. Calder (1993) stated that the hovering WBF of the Rufous Hummingbird (*Selasphorus rufus*) was 44Hz, but the sexes were not distinguished. The origin of his statement and the methodology by which the rate was determined was not given. For the same species, Wells (1993) obtained values from 49-54Hz under experimental conditions in which the size of the flower on which the bird was feeding varied. Again sex was not stated and only one individual was used. An inverse relationship between wing length and WBF has been documented repeatedly in hummingbirds (Lasiewski and Lasiewski 1967, Greenewalt 1975, Corben 1983). Considering this relationship and the known dimorphism in wing length in North American hummingbirds (Kodric-Brown and Brown 1978, Mulvihill et al. 1992, Pyle 1997, Waser and McRobert 1998), it is surprising to find statements in recent literature to the effect that the sexes have the same WBF.

In the most comprehensive study to date into WBF, Ortiz-Crespo (1980) used audiospectrographic measurements to examine six species of hummingbirds, although only two females were included. He recorded four types of flight (hovering, non-ritualized directional flight, dive display and shuttle dance), but unfortunately there are gaps in the data concerning non-ritualized flights, which makes comparisons between species and/or sexes impossible. The Black-chinned Hummingbird (*Archilochus alexandri*) is the only species of the four in my study that Ortiz-Crespo (1980) recorded in hover flight (WBF 63.9Hz, range 58-67Hz, $n$= 8). Lasiewski and Lasiewski (1967) reported a single recording of a Black-chinned hummingbird with an exceptionally long wing (51mm) of having a WBF of 42.5Hz, but again the sex was not stated.

Laboratory experiments during hover flight suggest that hummingbirds maintain a narrow range of WBFs even under changing external and internal conditions. Neither molt nor body mass changes were found to significantly alter WBF (Chai et al. 1996, Chai 1997, Chai et al. 1999). Chai and Dudley (1999) suggested a maximum increase of 4-6% in WBF with most changes in power originating from modulation of wing amplitude. Dropping ambient temperature from 35°C to 5°C resulted in a mean drop in WBF of 3Hz (Chai et al. 1998).

Although diverse terminology has been used to describe WT, data pertinent to its frequencies and sound characteristics are scarce, and are mostly a by-product of studies into other aspects of hummingbird sounds or displays. Pytte and Ficken (1994) showed a Black-chinned male WT in the range of 2-3kHz during agonistic encounters. A WT of 9000Hz can be extracted from the study of Rufous dive displays by Hurly et al. (2001).

A WT of 4-5kHz was noted for a male *Atthis heloisa* hummingbird hovering with a WBF of 61.3Hz (Zyskowski et al. 1998).

Stroboscopes, high-speed and commercial video have been used to determine WBF in hummingbirds (Greenewalt 1960, Lasiewski and Lasiewski 1967, Chai et al. 1996, Chai 1999). An error of up to 10% can occur with the stroboscope method, due mostly to the difficulty of bringing the instrument to equilibrium on fast moving hummingbirds (Greenewalt 1962). Extracting WBF from video methods can be time consuming and frequently results in few samples per bird. Stroboscope and video methods are generally more suited to captive studies (Lasiewski and Lasiewski 1967). Since the fundamental WH frequency is equivalent to the actual WBF, audio methods have surfaced as a powerful tool that allows concurrent investigation of both types of wing sound while collecting precise WBF data. For decades the standard for sound analysis has been sonograms produced by sonagraphic machines. Ortiz-Crespo (1980) pointed out however that this equipment was incapable of recording or analyzing sounds below 80Hz. Values below this level were estimated by counting beats within the WT. This method may be subject to error due the presence of harmonics, the relatively low resolution of sonagraphic machines and because WT may not be in a 1:1 ratio with the WBF. With the advent of digital analysis software and microphones with lower frequency response levels, computer generated sonograms and spectrums have become powerful tools for sound analysis. These methods allow the accurate and rapid collection of multiple samples from a sound file, with the additional benefit of allowing for finer temporal scaling and direct analysis of lower frequencies with finer resolution of waveforms.

The highly territorial and aggressive nature of hummingbirds, and the resultant high number of intra- and inter- specific interactions at feeding sites, led to predictions that species and sex specific wing sounds are a form of communication that signal threat, which could alter the behavior of other hummingbirds in a predictable way. The original goal of my research was to investigate if wing sounds do in fact play a role in hummingbird communication. A review of the literature revealed that the published data on wing sounds provided an inadequate framework from which to base predictions of the role of these sounds in intra- and inter- species interactions. Furthermore, Pennycuick (1990) cautioned that historical or unpublished data might contain errors because of variation in the collection of data and poorly defined methodology. It also became clear that WT sound characteristics had not been studied in detail. A greater understanding of basic wing sound characteristics is a prerequisite to discovering their source and degree of variation, and for allowing the study of their possible role in communication. The advent of new digital sound analysis technology provides the capacity to perform these studies.

I predicted that the inverse relationship between WBF and wing length would hold true in that males, with their shorter wings, would have higher WBFs than their conspecific females and that species with shorter wings would show higher WBFs. The objectives of this study were to document both the intra- and interspecific variability as well as the within individual variability of wing sounds, to analyze its specific component characteristics, and to explore the capabilities of modern digital technologies in avian acoustic recording and analysis. This study permitted subsequent evaluation of the role of these sounds in hummingbird communication (Hunter 2004).

## METHODS

Both sexes of four species that breed in Canada were chosen for study, and four letter abbreviations are used throughout this paper to indicate the respective female and male of each species; Rufous (RUFE/RUMA), Calliope (CAFE/CAMA), Ruby-throated (RTFE/RTMA), Black-chinned (BCFE/BCMA). For simplicity, I will use 'types' hereafter when referring to the collective eight, species and sex combinations.

### STUDY SITES

Recordings of Ruby-throated hummingbirds were made at three sites in and around the University of Wisconsin-Milwaukee Field Station (N43.3, W88.0) near Saukville, Wisconsin (13-20 May 2002) and at two sites in Low, Quebec, Canada (N45.8, W75.8) (25-30 August 2002). The three western species were recorded in the Okanagan Valley, British Colombia, Canada (N49.3, W119.5) on 4-28 July 2002 (six sites), and 15 April to 15 May and 7 July 2003 (eight sites). Sites were separated by a minimum distance of 3.0km to decrease the possibility of recording the same individual at two sites (Stromberg and Johnsen 1990). Private landowners provided the established artificial feeders with the only selection criteria being that the sites were quiet and undisturbed, and held large hummingbird populations.

### RECORDING EQUIPMENT AND SET-UP

The recording set-up and equipment was held constant between sites. The same four-spout saucer bottomed cylinder feeder was used throughout. This feeder had no protruding plastic corollas as these have been found to interfere with normal wing kinetics and cause an increase in WBF (Wells 1993). This was deemed especially

important in working with CAHUs- the smallest species in North America. Three of the feeding holes were covered with tape in order to force consistent orientation and position of the target bird in relation to the microphone that was mounted 20cm from the open spout. Perches were removed so as to ensure continuous flight. A concentration of 33% sucrose solution was selected as it is preferred by hummingbirds and reduces searching behavior compared to the standard 20% solution (Blem et al. 2000, Stromberg and Johnsen 1990), and because it is in common use by many site homeowners.

I made all recordings using a tripod mounted Audio Technica 3035 condenser microphone (20-20kHz frequency response) held by a shock-mount and with fine adjustment via a gooseneck adapter. Periodically, one of three other shotgun or cardioid microphones (Audio Technica 877, Sennheiser MT816, Nakamichi CM-100) was used along with the 3035 to record simultaneously on a second channel. The AT3035 provided superior signal to noise ratio and clarity, but all microphones showed less than 0.5Hz deviation from a standard 440Hz tuning fork during testing, and all dual recordings provided similar fundamental frequency values, and confirmed the accuracy of the wing sound frequencies gathered by the AT3035. Seven meters of low impedance XLR cables connected the microphone(s) to a Midiman Audiosport Duo USB audio interface pre-amp unit that provided the necessary phantom power and signal amplification while converting the signal from analogue to digital. The digital signals were then stored using Soundstudio software running on an Apple Ibook (OsX) through the USB input. This avoided the risk of sound degradation or frequency alteration inherent to portable computer soundcards. Recording levels were adjusted at the pre-amp in order to maximize signal level and minimize clipping of sounds. Once a target bird came in to

feed I identified its sex and species, and when possible, as an individual bird (through color markings or continual observation in the area). I controlled the recording equipment and made observations at a distance of 6m from the feeder. Recordings were made during all daylight hours, with the only restrictions being that wind velocity had to be low to minimize sound interference and that it not be raining because of the equipment being used.

SPECIES AND INDIVIDUAL IDENTIFICATION

Estimating the population and individual identification are two major difficulties when studying wild hummingbirds (Lyon et al. 1977, Gass 1979, Tamm et al. 1989, Powers and McKee 1994, Rusch et al. 1996). Some researchers have stated that individual hummingbirds can be identified reliably in the field by morphological markings but this claim has not been tested. Gass (1978) supports his claim to field identification of hummingbirds by referencing Bateson (1976) who used photographs of the beak of Bewick's swans to distinguish individuals. Clearly, one cannot assume such results are directly transferable to hummingbirds. Miller and Inouye (1983) showed, using marked Broad-tailed hummingbirds that only 13 of 62 males were territorial, leaving the remainder of the population to float between or through territories. Although a keen observer may be able to identify an individual bird with a distinct morphological characteristic that is holding territory in a sparsely populated area, it seems doubtful that multiple, unmarked individuals could be tracked in a relatively dense, free-ranging population.

I used a combination of methods to maximize recordings of unique individuals and to record repeat visits from known individuals, while also avoiding pseudoreplication.

Recordings of unique individuals were ensured by the use of a distinct morphological marking when available, color markings, different study sites, and the dual recording of two individuals where one bird was replaced during recording by a conspecific of the same sex. The latter tracks were immediately split and labeled accordingly. Unlike Gass (1978 and 1979) morphological markings were used to determine that individual 'A' was not individual 'B', and not to obtain a repeat recording of 'A', as it was impossible to know with certainty if a marking was truly unique in the local population. Repeat samples from known individuals were gathered by either color marking or by uninterrupted visual contact, which was used more frequently at less populated sites where fewer interactions and less competition allowed for undisturbed perching close to the feeder.

Color marking was done in accordance with the North American banding protocol (permit #23202) using non-toxic Liquitex© brand acrylic paints. A cylindrical feeder trap (60cm diameter * 1m) made of soft screening with a nylon top and bottom was used. This fully collapsible and portable trap was newly designed using the basic models found in the Hummingbird Banders' Manual (Russell and Russell 2001). The natural behaviour of the birds was used to trap them rather than having an observer triggered door closing over the opening (15x20cm). After feeding, it was found that hummingbirds rise up from the spout to fly off. By placing the bottom of the feeder a few centimeters below the top of the door, birds would become disoriented when exiting after feeding, and fly to the top of the trap from where they were retrieved for marking. The soft-walled fine mesh was found to be far less abrasive to hummingbird wings than the heavy gauge metal wire used in most freestanding designs.

The decision to use multiple methods to separate individuals was made for several reasons. Firstly, in 2002 initial color marking at two sites showed that local populations were far larger than expected. With 65 marked CAFEs in one area, only 15% of birds visiting the feeder the next day were marked individuals. More importantly, in 2002 the research did not begin until July, which is nearing the end of the breeding season for both the Calliope and Rufous hummingbirds in the Okanagan (Tamm et al. 1989). Late in the season, male hummingbirds tend to defend feeders for only a few hours (Ewald and Rohwer 1980) and many of the local males would have already begun their southward migration. My efforts to color mark revealed two important considerations: 1) the number of males was far lower than the number of females (and juveniles), 2) many of the marked males were never seen again, probably because they were migrating through from other regions. Therefore, intensive marking at a few sites would not have allowed for the collection of a sufficient number of samples of all target types. In fact no CAMA recordings were made in 2002 because none were seen after the first few days spent marking.

## RAW SOUND FILES AND FREQUENCY ANALYSIS

Where possible, multiple recordings of each species and sex present were made at each site because of the variable quality of recordings. Many recordings were not used because of a lack of individual identification or separation. Recordings were selected, prior to frequency analysis, based on the quality of the sequence in terms of its signal to noise ratio, length (preference for longer recordings) and minimal background noise or interference. I judged overall sound quality by listening to each recording and by examining the waveform within Amadeus II© software.

A total of 350 recordings were collected during 2002 and 2003, and 229 of these individual sound files were used in the analyses. The raw sound files varied in length from 7 to 150 seconds. The method of frequency analysis of the sound files depended on the type of wing sound being analyzed because of important differences in the frequency characteristics of the two types.

*Wing Hum*

The resultant waveforms were representative of normal feeding behavior, which included actual feeding (in), and feeding pauses (out) when the bird backed away from the feeder (5-15cm), and the between flight motion of moving in and out. In addition, there was often some form of '*twitchy*' flight if another bird entered the general area or if the target bird moved to search other parts of the feeder. Hovering flight was the focus of analysis, and so directional flight segments were excluded. From the digital waveform, segments of uninterrupted hovering flight, termed segments, were sectioned and marked using Soundstudio software. These sound segments varied in length (mean 1.15s, +/-0.91 SD, $n$ = 1278, min. 0.3s) due to variations in the feeding behavior of the birds. These sound segments were selected by auditory and visual inspection of the waveform prior to any frequency analysis, and the number of samples chosen from a specific file was dictated predominantly by its total usable length (mean 6.1 segments, range 3-20). Three samples were taken from each segment, one 0.1sec in from the beginning, one 0.1sec in from the end, and the third from the middle.

Each sample was then analyzed using the spectrum function of Amadeus II© software with a frame length of 32768 sample points, with the resultant fundamental frequency

recorded to two decimal places. I ran repeated tests on digitally produced sine waves of frequencies within the expected range of 40 to 100hz and found this wide frame length consistently produced frequency values accurate to two decimal places. The trade off in using a wide frame length is loss of temporal precision, but given the relative consistency of wing beats compared to vocal sounds, and because the focus of the study was on frequency, temporal accuracy was deemed less important. The Cobra maneuvers (vide infra) were analyzed using the same software settings as described but with measurements being made every 0.1 seconds in order to determine the peak frequency and the overall duration of the behaviour.

*Wing Trill*

The WT component of male hummingbirds wing sounds was analyzed using Cool Edit Pro software. Whereas WH is constantly present during flight, WT is far more sporadic in its occurrence as it is produced with greater amplitude during rapid changes in the direction of flight (personal observation). Five frequency samples were taken from each first visit male sound recording using a frame length of 128 points. The higher frequencies being analyzed allowed for the use of a narrower band length while the shorter duration of these sounds further required a narrow band that would correctly sample from a single pulse of sound. Pulse characteristics were analyzed by taking measurements of the WT pulse in relation to the wing beat on highly enlarged waveforms. Three measurements of each flight type (hovering and directional flight) were taken from different WT sections within each individual's first visit recording. Directional flight refers to any rapid movement from a hovering position and as a result could be either forwards or backwards.

The WT components of the BCFE were analyzed as per males, with the exception that only the final departing flight section was used, with three samples being taken from this section for each useable individual. Due to the reduced amplitude of the sound, lower frequencies (<1kHz) were filtered out to accent the frequencies of interest.

### STATISTICAL ANALYSIS

Species and sex differences were analyzed using a balanced mixed factor Generalized Least Squares (GLM) linear model ($\alpha$= 0.05) using the first visit data of all individuals and the first five segments of each (three replicates per segment). Attempts to run models using the entire data set were unsuccessful because it was unbalanced and because of the number of parameters involved. Mean, standard deviation, and percent change were calculated for the WBFs of each individual and then the collective individual values were averaged for each combination of species and sex. These average values were based on the middle segment values, which were believed to be the most representative of the true hovering frequency. A mixed model one-way ANOVA was used to compare the WT of those species with similar means. Means, standard deviations and 95% confidence limits were derived for WT pulse duration based on the individual means (3 samples/individual) for both types of flight.

## RESULTS

### WING HUM FREQUENCIES

*Species and sex variations*

The species and sex means, number of individuals, standard deviations and 95% confidence limits of the fundamental WH frequencies (equivalent to the WBFs) are

shown in Table 1, with the means of each species and sex represented graphically in Figure 1. The balanced GLM based on the first five chunks (three replicates each) of each individual's first visit revealed that males showed significantly higher WH (WBFs) than conspecific females ($F_{1,96}$=123.07; P<0.001). The interaction of species and sex was non-significant ($F_{3,96}$ = 2.5; P>0.05) showing that the sex difference was similar for all four species types.

Results showed that overall, species showed significant differences ($F_{3,96}$ = 68.64; P<0.001). Post hoc multiple comparisons using a Tukey's test showed that all pair-wise species combinations were significantly different (P<<0.05) with the exception of the RUHU and RTHU which were not significantly different from one another. The statistically significant inverse relationship between WBF and wing length is shown in Figure 2.

*Within individual variation*

Single Visits

The amount of variation that exists in the WBFs within individuals during a single visit to a feeder is shown in Table 2. For individuals with multiple visits, only their first visit was used in this analysis. The average percent change from mean WBF is similar amongst hummingbird types, ranging from +/-2.67 to +/-3.65%. The minimum percent change results indicate that at times, individuals are capable of maintaining extremely constant WBFs (+/- 0.18%) throughout a visit. Conversely, the maximum percent change indicates that at times this variability within an individual can be high (+/-9%).

Multiple visits

Marked or known individuals made up a small proportion of the individual recordings in this study. The number of visits by a given individual ranged from two to seven, with a median of three (Table 3). No multiple visits were collected for RUMA hummingbirds.

The results for multiple visits (Table 3) indicate that the within individual average percent change in WBF is more than twice that found for single visits (+/-7.78% multiple versus +/-3.25% single). The minimum variability substantially increases compared to the single visit minimum (+/- 4%). Similarly, the maximum percent change shows that some individuals cover a large range in WBF (+/- 15%).

## WING TRILL FREQUENCIES

### *Species frequency variation*

Average, standard deviation, and 95% confidence limits of the WT frequencies for the males of the three western species are shown in Table 4. The CAMA and RUMA wing trills are in the same frequency range (8kHz to 10kHz) and do not differ significantly from one another (Table 4). The BCMA WT ranges from 4kHz to 4.7kHz and is clearly different from either the CAMA or RUMA WT in its fundamental frequency. Despite the presence of WT pulses within the waveforms of RTMAs, distinct frequency values could not be determined, and as a result, the RTMA was dropped from further WT analysis.

### *BCFE wing trill*

WT has not been thought to exist, much less has it been knowingly recorded, in the female of any North American species. I found that BCFE hummingbirds do produce a

distinct WT when moving from hovering to forward flight. The mean, standard deviation, and range of their WT frequencies are shown in Table 4. BCFE WT was found to be of significantly lower frequency ($P<0.05$) than male conspecific WT, but is more similar to male conspecifics than to either RUMA or CAMA, whose WTs are in a frequency range twice that of BCFEs. WT was not found in the females of the other three study species.

*Pulse characteristics*

Although WT has been thought to be a pulsed sound, the visualization of this phenomenon was limited to counting the peaks from relatively low-resolution sonograms. The high resolution of waveforms in computer based sound analysis software allowed me to visualize the relative placement of the WT component within single wing beats (Fig. 3). From this, I found that the WT variation of different species was not limited to the fundamental frequency, but also included its pulse duration relative to that of the wing beat. Unlike the fundamental frequency, the duration of the pulse relative to the wing beat was substantially less during regular hovering than during directional flight for all three male western species (Figs. 3 and 4). Furthermore, Figure 4. shows that the CAMA and RUMA differ in pulse duration, even though they overlap in fundamental frequency. This experiment was not designed to properly measure amplitude and as a result only rough scales of the amplitude of the WT in relation to the WH amplitude are given (Figure 4). In general, the WT amplitude is greater during directional flight than during regular hovering.

COBRA

The previously undocumented Cobra maneuver was a rarely observed behavior, in part due to the limited context in which it is used and in part because of its subtle features. A Cobra consisted of a given individual quickly increasing its WBF (with a resultant change in pitch and amplitude of the WH), with an equally rapid decrease back to its normal hovering WBF. The behavior was only observed in birds at the feeder when another individual entered the feeding area, but prior to the intruder showing any antagonistic behavior. Generally, the source bird remained in a horizontal body position similar to that when feeding, or in a 45 degree body position similar to normal hovering. In the majority of cases the feeding individual would turn to face the direction of the intruder, but not in all cases. Occasionally the source bird would simultaneously move in to an agonistic vertical body position with flared tail and bill pointed towards the intruder. This body position however is commonly seen during interactions without the production of the Cobra sound (personal observation) and as such is likely not directly related to the change in wing sound. If both the intruder and feeding bird were females, the interaction frequently did not escalate and the two birds fed without further confrontation.

Cobra behaviors were exhibited by both sexes of all three western species, but I was only able to collect a representative number of samples for the CAFE, which appear to perform the behavior more frequently than other hummingbird types. Table 5 shows the mean base WBF, the peak WBF during the behavior and the percent increase in WBF for six CAFE individuals, as well as the approximate duration of the behavior. Overall, the mean and median percent increase in WBF was 30.36% and 32.55% respectively. This is double the maximum percent increase in WBF documented for a CAFE during normal

hovering over multiple visits. The peak frequency values (70-77.5Hz) were all well above the standard maximum hovering frequency of 64Hz recorded for any CAFE. The mean duration of these displays from initial rise in WBF, to the peak, and the return to baseline was 1.41s (median 1.23s).

*Pulse characteristics*

I made an unexpected discovery while investigating the frequency change during these Cobra behaviors. The WT pulse pattern found in male waveforms, described above, was found within the CAFE Cobra sections (Fig. 3). During these brief moments of increased WBF, in which the base WH amplitude increases, the females produce the equivalent of a low amplitude version of the WT pattern observed in male conspecifics. A distinct frequency for this WT sound could not be identified, suggesting that it may be a wider band of frequencies resulting in the lack of appearance of a distinct peak during frequency analysis.

## DISCUSSION

### WING HUM/WING BEAT FREQUENCIES

*Species and sex variations*

The prediction that male hummingbirds, with their shorter wings than their respective conspecific females, would have higher WBFs/WHs was supported by the results. The lack of a species sex interaction, thus expressing that sex differences were relatively constant across species is consistent with the relatively similar dimorphism in wing length between the sexes of these four species (Pyle 1997).

Though not available for all hummingbird types in this study, comparisons of WBFs to previous research can be made in some cases. Calder (1993) presented a value of 44Hz for the WBF of a RUHU during hover flight, without distinction of sex, the methodology used or the sample size the value was derived from, making any specific discussion impossible. In relation to my findings, this value would be at the extreme lower limit of any value recorded for a RUFE and would be well below the minimum WBF of the RUMAs. Wells (1993) put forth a WBF range of 49-54Hz for a single RUHU but again the sex of the individual was not stated. If the individual were in fact a RUFE, these values would be in range of those found in this study.

For the RTHU, my findings are comparable with the previously stated WBFs by Greenewalt (1962) of 52 Hz for females and 70 Hz for males. The reference by Robinson et al. (1996) to Greenewalt's (1960) work is misrepresentative in that it implies that the WBF is the same for both sexes and is constant in all types of flight. Sex differences are well documented in the present study and Ortiz-Crespo (1980) documented that WBF will vary with flight type.

Ortiz-Crespo presented a range in WBF for the BCMA ($n$=8) of 58-67 Hz during hover flight. These values are well above my findings with even my maximum value falling below the lower range presented. The equipment used by Ortiz-Crespo did not directly record or analyze any frequencies below 80Hz. Rather the WBFs were calculated by counting peaks in the WT component of the male's sound. The use of WT pulses to calculate WBF in Ortiz-Crespo's (1980) study had a few distinct drawbacks. Firstly, WBF values for females, which do not produce distinct WT pulses during normal hover flight, could not be calculated. Secondly, Ortiz-Crespo believed that WT pulses

occurred on a 1:1 ratio with the wing beat. I discovered however that WT pulses can be created during both strokes of a wing beat. Though generally much reduced, it is highly probable that these secondary pulses would on occasion give rise to peaks of sufficient amplitude to be counted, subsequently causing an erroneous increase in the calculated WBF. In addition, the counting of peaks on sonograms, with their lower resolution than digital software, may have resulted in further error. These later two points could explain the higher WBF values presented by Ortiz-Crespo when compared to the results of this study. In perspective of the wing length to wing beat relationship shown in Figure 2 however it appears as though his mean values are equidistant above the trend line as my mean values are below the line. Another explanation that would require further exploration that the mean wing length of BCMAs is significantly different between geographic regions seeing as Ortiz-Crespo's research was done in California and mine in British Colombia.

My findings for the BCFE and both sexes of CAHU appear to be consistent with their respective mean wing lengths and in terms of the standard deviations associated with the WBFs collected when compared to the overall range of other hummingbird types in this study.

Species mean WBFs roughly followed the inverse relationship with wing length, with the largest species (BCHU) having the lowest mean WBF and the shortest winged species (CAHU) having the highest WBF (Fig 2). The similarity in the mean WBF between the RUHU and RTHU is understandable since the mean wing lengths of these two species are similar and the degree of overlap in wing length range is high.

*Within individual variation*

It was thought previously that individual WBF was essentially constant. Comprehensive sampling within individuals during this study has shown that WBF fluctuates, even within single visits. Given the short duration of these visits at feeders (7-150s), these WBF fluctuations cannot easily be attributed to changes in external weather or internal physiological conditions. The greater variation observed over multiple visits, which in some cases spanned several days, raises the possibility that these more conspicuous changes could reflect variables that act to influence/modify individual WBF. A more detailed study will be required to ascertain which, if any, external/internal factors affect the WBF of individuals. The use of captive rather than free-ranging hummingbirds in previous studies may have masked some of the within individual variability.

Published research on the relationship between WBF and wing length may require reassessment, given the findings from this study that show that a given individual hovers with a wider range of WBF than previously thought. This may be especially important where mean species WBF values were derived from small sample sizes (Greenewalt 1960, Ortiz-Crespo 1980, Calder 1993).

WING TRILL FREQUENCIES

*Species frequency variation*

The WT results were consistent with the findings of Hurly et al. (2001) for the RUMA WT frequency. However, the BCMA results are not consistent with Pytte and Ficken (1994) who reported a WT frequency between two and three kHz. I carefully re-examined the BCMA to ensure that my values were not harmonics of a lower amplitude fundamental frequency. No evidence for this could be found and given the larger

between individual and within individual data set, I consider my findings to be accurate. The wing trill found in Pytte and Ficken (1994) however was recorded during an agonistic interaction whereas this study used only hovering or directional flight samples. Pytte (personal communication) raised the possibility that wing trill frequencies may vary with behavioural context. This hypothesis will require further investigation.

These are the first WT frequencies presented for CAMAs. To the ear, the RUMA and CAMA WT have distinct sound qualities and yet their WT frequencies are within the same range. The different pulse characteristics and relative amplitudes appear to be at least partially able to explain this difference in sound quality. Overall, within each flight type (hovering and directional), the RUMA WT is of greater pulse duration and intensity relative to the CAMA WT. In addition, the RUMA WT frequencies, based on the shape of the frequency analysis peaks, appeared to be of a more concentrated frequency bandwidth than those of the CAMA. Though requiring further study, I suggest that this concentration of frequencies is a reflection of the width of the outer primaries with the thinner feathers producing more concentrated frequency band WT sounds, which subsequently produces a sharper and more audible WT.

Although the RTMA creates WT sounds, the actual frequency range of these sounds could not be determined by frequency analysis, suggesting that they are not as concentrated and distinct as the WT of the other three study species. Given the essentially allopatric existence of the RTHU in relation to all other breeding hummingbirds, it is plausible that the lack of interspecific competition has reduced the evolutionary pressures to develop a distinct, species specific WT. In areas where hummingbird species are cohabiting, the ability of females to distinguish males of

different species may result in an inclusive fitness benefit to the development of a unique WT- a situation not applicable to the RTHU.

As first mentioned above, the use of digital software revealed that two WT pulses can appear within a given wing beat. The less distinct WT pulse generally appears when the primary WT pulse is of high amplitude and long duration. These lower amplitude pulses must vary the overall sound quality of the WT sound by decreasing the spacing between pulses, which would effectively increase the temporal intensity of the sound. Further study will be required to determine when these sounds are produced, their frequency characteristics and the overall affect they have on the sound quality of the WT. Differences in their production between species will require further study, but at this time I can state that they do appear in the males of the three western species and somewhat surprisingly, quite strongly (relative to the primary pulse), within both the BCFE and BCMA.

*BCFE wing trill*

WT has previously only been associated with male hummingbirds and I have not come across any literature that even suggests it can be produced by female hummingbirds. WT in the BCFE is most audible during the change from hover to forward directional flight. If WT is in fact a communication signal, the presence of the sound during this sudden change to forward flight would suggest that the sound plays a role in signaling threat, as this change to forward flight would occur when a bird is beginning an attack. It could also play a role during exits from areas by reducing chase behaviour as a result of the threat it signals to a would be chaser. The lower amplitude and temporal frequency of the

WT in the BCFE is likely attributed to the more rounded tips of the outer primaries of the females when compared to the more reduced and narrowed tips of the BCMA.

## COBRA

This is the first time that the Cobra maneuver has been documented. The Cobra examples documented in the CAFE represent a behaviour that has large energetic costs similar to the ritualized 'buzz' display performed by conspecific males which can similarly show increases in WBF of 30-40% (unpublished data). The extremely short duration of these behaviors (1-3s) further attests to the high energy demands of such behaviors. Given the limited interaction context in which this behavior has been observed, I believe that it is a defensive response behavior rather than an offensive type display.

The sudden appearance of WT components within the wing sounds, not present during normal hovering, suggests that these higher frequency pulses may be a communication signal in whole or in part. The lower amplitude and less distinct frequency band of the CAFE Cobra WT compared to the CAMA is likely a result of the greatly rounded tips of the outer primary feathers in the females compared to the narrowed feather tips of the males. Ortiz-Crespo (1980) suggested that WT might be a result of the WBF increasing above a certain threshold. This behavior lends support to this statement but further study will be required before this can be verified.

## FUTURE STUDY

With the foundation of information on wing sounds gathered from this study, work on the role of these wing sounds in communication can be investigated. WT and the Cobra

display would benefit from further study of their sound characteristics with focus on the body positions or mechanisms controlling their production and on the amplitude fluctuations. The relationship between WT characteristics and the width and length of the outer primaries could reveal why WT varies in amplitude and peak frequency bandwidth between species. Further study of feather shape in both sexes may lead to a better understanding of the evolution of these sounds. The presence of a weaker WT pulse on the opposing stroke (two pulses per beat) requires further exploration to determine the species and conditions in which this sound is produced and its overall affect on the WT sound quality of individuals. Finally, focused study of within individual WBF between visits may lead to a better understanding of whether external weather changes or internal physiological variables are responsible for the sizeable individual variability in WBF.

Figure 1. Estimated marginal means of wing hum (wing beat) frequencies (Hz) for each species and sex type derived from a balanced mixed Generalized Least Squares model (GLM) of the first five segments (three replicates each) of the first visit of all individuals. For all species, the male means are significantly higher than conspecific female means ($P<0.05$).

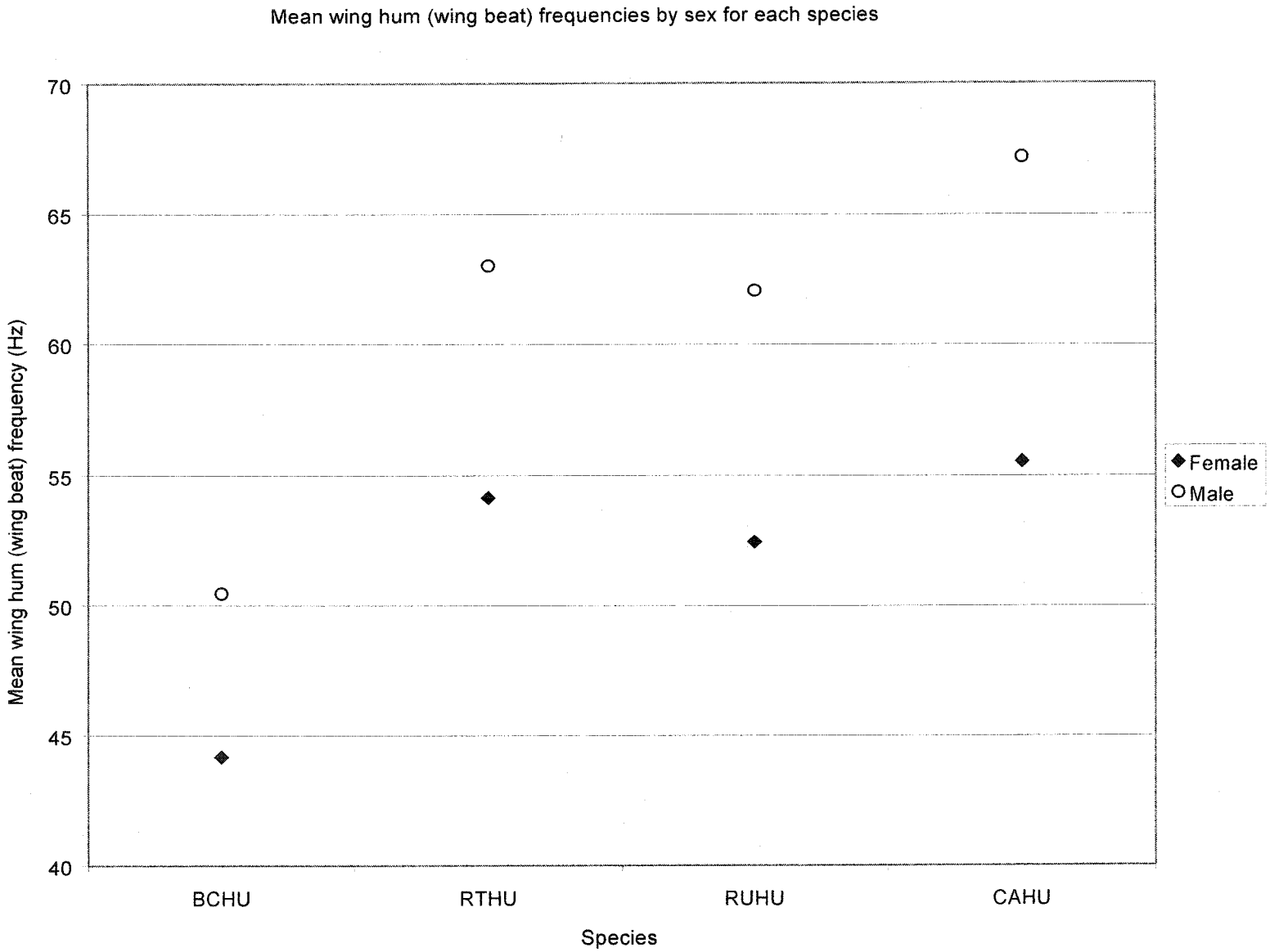

Mean wing hum (wing beat) frequencies by sex for each species
Mean wing hum (wing beat) frequency (Hz)
70
65
60
55
50
45
40
BCHU
RTHU
RUHU
CAHU
Species
Female
Male

Figure 2. The mean wing beat frequency (WBF) versus wing length with upper and lower 95% confidence limits for the eight hummingbird types based on the averages of all individual means. Individuals with multiple visits were averaged over visit means in order to balance for unequal sampling within visits. Wing lengths are from Pyle (1997) and represent the 95% confidence limits of measurements on no fewer than 20 individuals per species and sex type. Note that wing beat frequency values and wing length data are not from the same individuals. The r-values of the three Pearson's correlation linear trendlines are all statistically significant with $P<0.02$ ($df=6$).

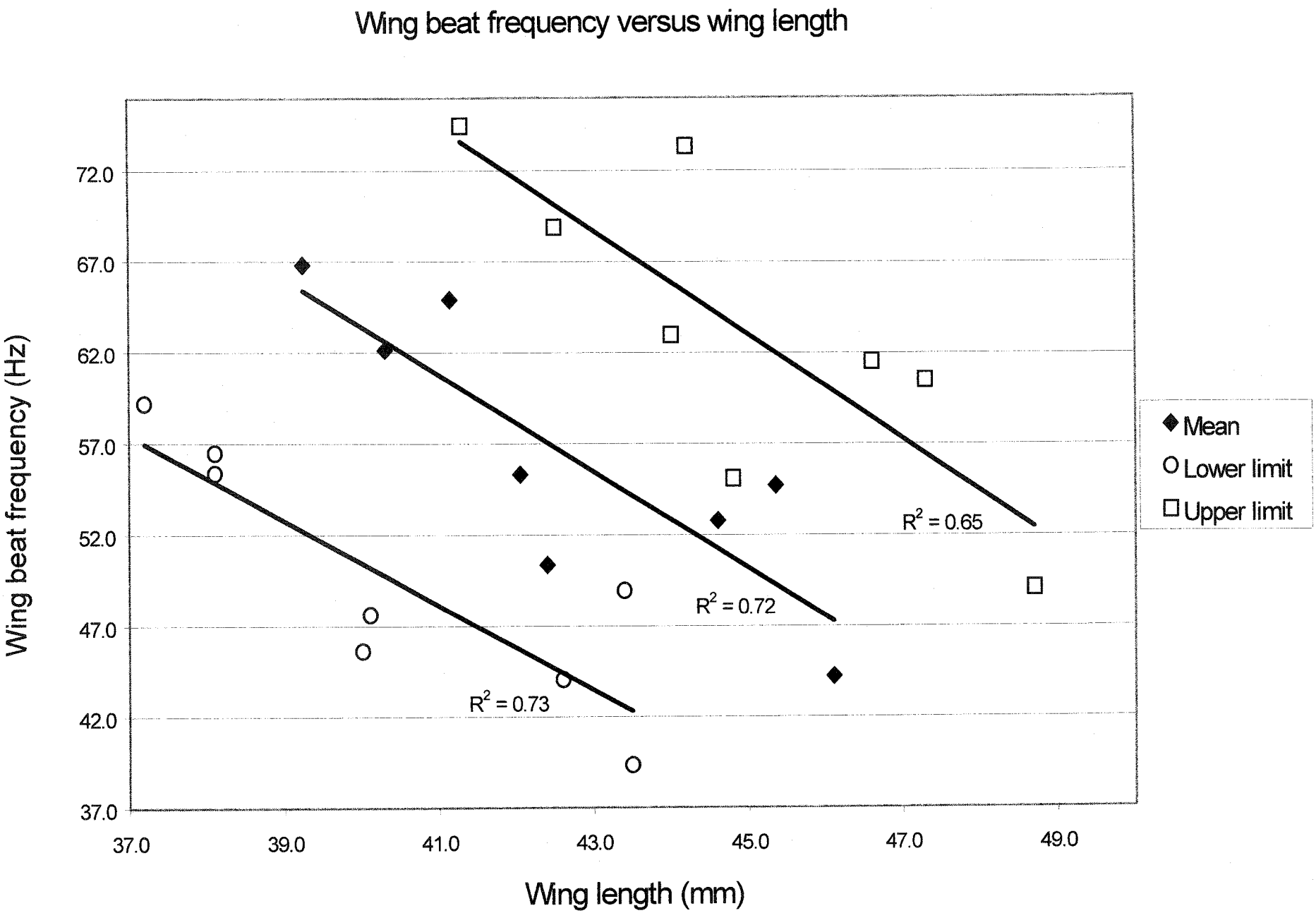
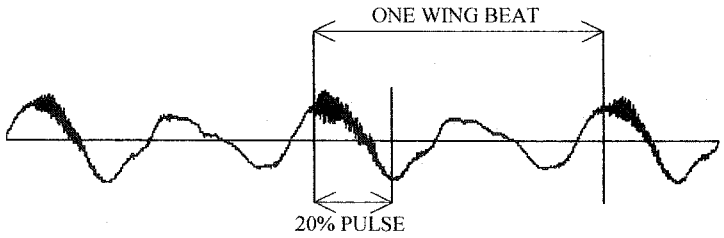
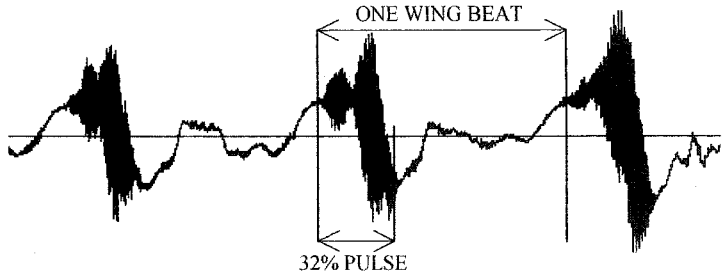

Wing beat frequency versus wing length
Wing beat frequency (Hz)
72.0
67.0
62.0
57.0
52.0
47.0
42.0
37.0
37.0
39.0
41.0
43.0
45.0
47.0
49.0
Wing length (mm)
R2 = 0.65
R2 = 0.72
R2 = 0.73
Mean
Lower limit
Upper limit

Figure 3. Appearance of wing trill pulses on wing hum waveforms of various species during various types of flight. The percent pulse represents the duration of the pulse in relation to the duration of one full wing beat. Waveforms may appear as more than one wing beat due to the first harmonic being of greater amplitude than the fundamental wing beat frequency. Measurements were made within the analysis software with graphical lines here for visual representation of the pulse ratio concept only.

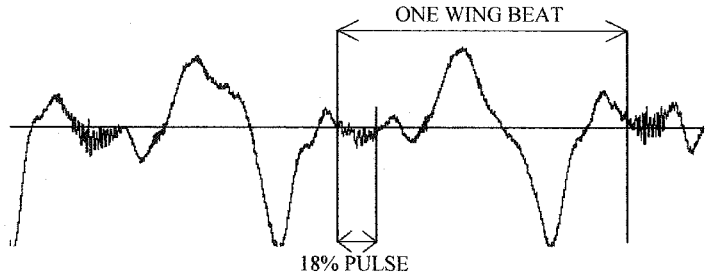
RUMA hover pulse ratio



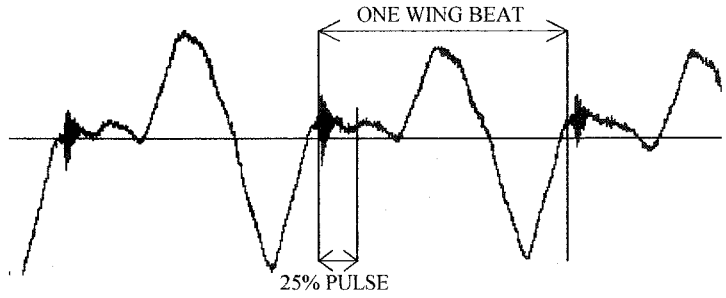

RUMA directional pulse ratio



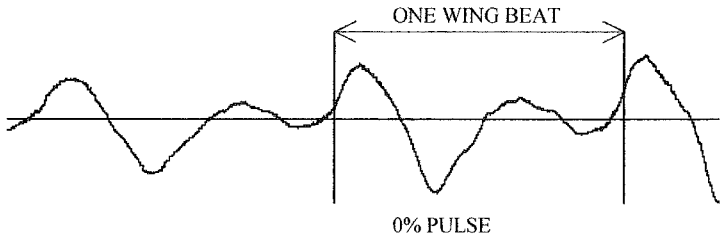

BCFE directional flight pulse ratio




CAMA directional flight pulse ratio




CAFE hovering – no wing trill pulse




CAFE Cobra – hovering pulse ratio

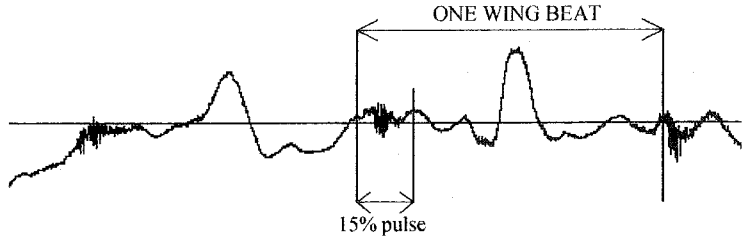


Figure 4. The mean percent duration of the wing trill (WT) pulse in relation to the wingbeat for the males of the three western species during hover and directional flight as well as for BCFE during directional flight. Each data point represents the mean of five individuals with three measurements taken from each individual for each type of flight. Error bars represent 95% confidence limits based on the individual means. The relative amplitude of the WT compared to the WH is provided for each point but represents only a rough estimate of the amplitude.

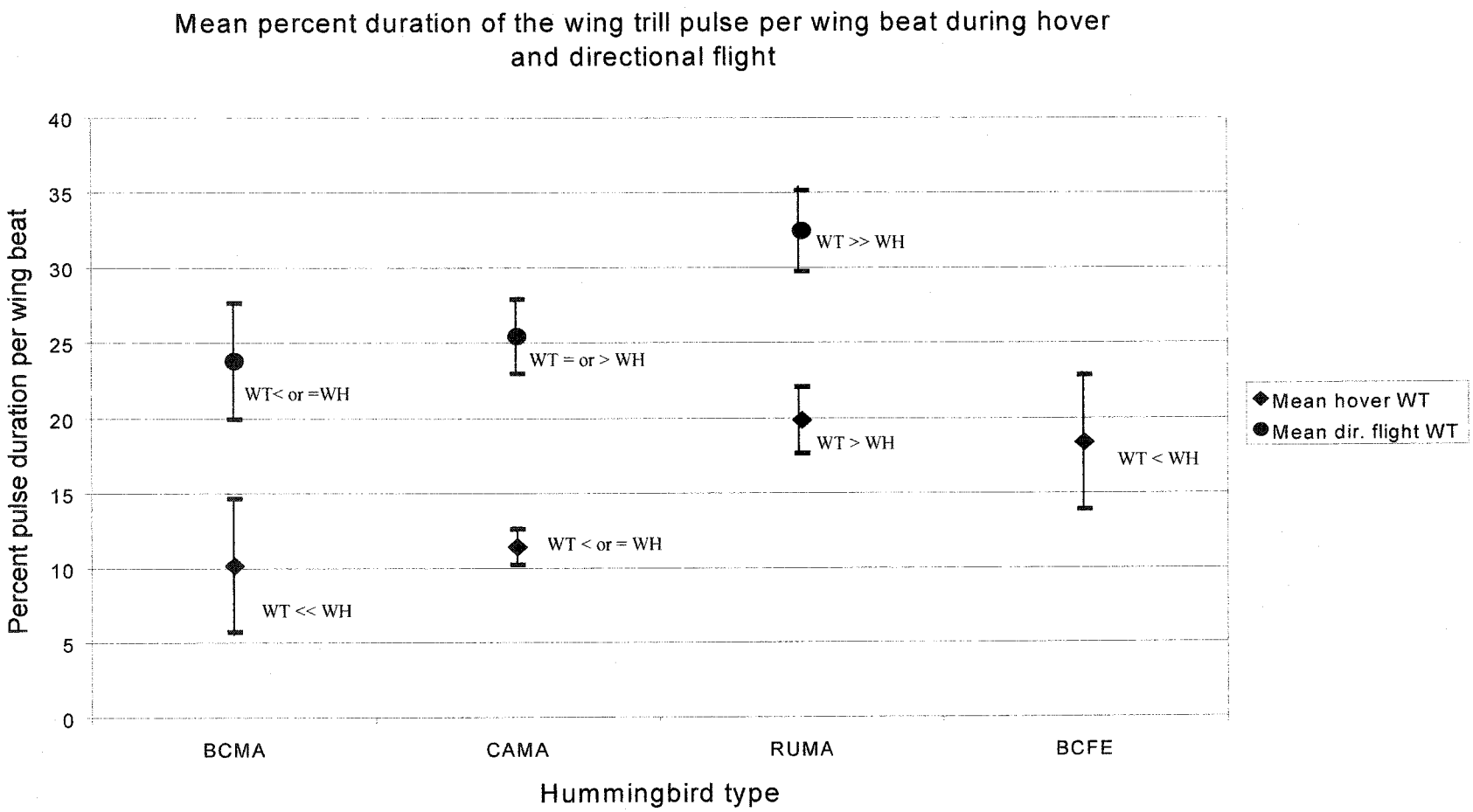

Mean percent duration of the wing trill pulse per wing beat during hover and directional flight
Percent pulse duration per wing beat
40
35
30
25
20
15
10
5
0
WT< or =WH
WT << WH
WT = or > WH
WT < or = WH
WT >> WH
WT > WH
WT < WH
BCMA
CAMA
RUMA
BCFE
Hummingbird type
Mean hover WT
Mean dir. flight WT

Table 1. The estimated marginal means of each species and sex type with associated standard deviations (SD), 95% confidence limits and number of individuals (no. of ind.(n)). Means are based on the GLM of the first five sound segments of the first visit of each individual with three replicates per segment.

| Type | no.of ind. (n) | Mean wing hum (Hz) | SD (+/-) | 95% confidence interval Lower bound (Hz) | Upper bound (Hz) |
|---|---|---|---|---|---|
| BCFE | 12 | 44.17 | 1.22 | 41.78 | 46.56 |
| BCMA | 13 | 50.45 | 1.02 | 48.45 | 52.45 |
| RTFE | 12 | 54.16 | 0.76 | 52.67 | 55.65 |
| RTMA | 11 | 63.03 | 0.89 | 61.28 | 64.77 |
| RUFE | 21 | 52.46 | 1.3 | 49.91 | 55.01 |
| RUMA | 23 | 62.06 | 1.84 | 58.45 | 65.67 |
| CAFE | 27 | 55.55 | 0.94 | 53.71 | 57.39 |
| CAMA | 25 | 67.2 | 0.94 | 65.36 | 69.04 |

Table 2. A summary by species and sex (8 types) of the mean variability in wing beat frequency (WBF) of individuals during single visits. Mean WBF, standard deviation (SD) and percent change in WBF were calculated for each individual. These individual (ind.) values were averaged and the median calculated by hummingbird type. The minimum (min) and maximum (max) percent change (% +/- Δ) are given to show the range in individual values for each type. The number of individuals (no. ind.) has been listed (n) for each type.

| Type | no. ind. (n) | Mean of the ind. WBF mean (Hz) | Median of the ind. SD | Mean of the ind. SD | Min % +/- Δ in WBF | Max % +/- Δ in WBF | Avg. % +/- Δ in WBF |
|---|---|---|---|---|---|---|---|
| BCFE | 12 | 44.37 | 1.03 | 1.10 | 1.14 | 5.37 | 3.23 |
| BCMA | 13 | 50.10 | 0.89 | 1.04 | 1.51 | 4.85 | 2.86 |
| RUFE | 21 | 52.60 | 1.14 | 1.35 | 0.62 | 8.09 | 3.41 |
| RUMA | 23 | 62.00 | 1.66 | 1.61 | 0.34 | 7.75 | 3.42 |
| RTFE | 11 | 54.57 | 1.64 | 1.52 | 1.10 | 5.98 | 3.65 |
| RTMA | 12 | 64.50 | 1.31 | 1.64 | 0.53 | 8.50 | 3.17 |
| CAFE | 27 | 55.41 | 1.26 | 1.49 | 0.73 | 7.10 | 3.62 |
| CAMA | 25 | 66.52 | 1.32 | 1.36 | 0.18 | 8.94 | 2.67 |
| | | | | | | *Average =* | *3.25* |

Table 3. A summary by species and sex (8 types) of the mean variability in wing beat frequency (WBF) of individuals over multiple visits. Individual mean wing beat frequencies were calculated by taking the mean of the visit averages in order to balance the unequal number of samples per visit. Subsequently, the table presents the hummingbird type averages of the individuals. The standard deviation (SD) between visit averages was calculated for each individual and then averaged by type. The minimum (min), maximum (max) and average percent change (% +/- Δ), based on the total frequency (Hz) range of the individuals, are presented by type along with an overall hummingbird multiple visit average WBF range. The number of individuals (no. ind.) for each type is listed along with the median number of visits per individual. The number of visits by an individual ranged from two to seven with an overall median value of 3 (mean=3.3visits). No multiple visits of RUMA individuals were collected

| Type | no. ind. (n) | Median no. visits per ind. | Mean of individual visit avg. WBF (Hz) | Mean of the ind. between visit SD | Min % +/- Δ in WBF | Max % +/- Δ in WBF | Avg. % +/- Δ in WBF |
|---|---|---|---|---|---|---|---|
| BCFE | 4 | 3 | 45.37 | 1.36 | 4.41 | 8.53 | 5.79 |
| BCMA | 4 | 3 | 48.98 | 1.25 | 3.99 | 11.39 | 5.98 |
| CAFE | 9 | 3 | 54.86 | 1.70 | 5.95 | 15.47 | 9.20 |
| CAMA | 2 | 6 | 65.17 | 1.33 | 8.70 | 9.97 | 9.33 |
| RTFE | 1 | 2 | 60.61 | 0.86 | 6.46 | 6.46 | 6.46 |
| RTMA | 3 | 6 | 61.44 | 2.20 | 6.50 | 14.29 | 9.43 |
| RUFE | 2 | 2 | 50.47 | 2.73 | 6.38 | 10.23 | 8.30 |
| RUMA | 0 | - | - | - | - | - | - |
| | | | | | | *Average =* | *7.78* |

Table 4. Mean wing trill frequency (Hz) for CAMA, RUMA and BCMA as well the BCFE Standard deviation (SD) based on mean of five samples from each individual with the number of individuals (*n*) listed by the species/sex type. The 95% confidence limits are given based on the type average. One-way mixed model ANOVA (alpha = 0.05) run on pairs with similar means. The BCHU (both sexes) wing trill frequencies were unquestionably lower than the other two male species, so statistical analysis was not performed.

| Type | Individuals sampled (*n*) | Species mean (Hz) | SD (+/-) | Lower limit (Hz) | Upper limit (Hz) | P (0.05) / F value |
|---|---|---|---|---|---|---|
| BCFE | 7.0 | 3792.6 | 119.6 | 3558.2 | 4027.1 | P<<0.0001 |
| BCMA | 12.0 | 4322.4 | 193.9 | 3942.3 | 4702.4 | $F_{1,17} = 50.70$ |
| CAMA | 25.0 | 9009.9 | 415.5 | 8195.4 | 9824.4 | P>0.05 |
| RUMA | 23.0 | 9204.8 | 343.8 | 8531.0 | 9878.5 | $F_{1,45} = 3.02$ |

Table 5. The percent increase in wing beat frequency (WBF) from hovering mean for 6 individual (*n*) Calliope female hummingbirds and the duration (s) of the Cobra behaviour measured from the commencement of frequency (Hz) rise to peak and return to base WBF levels. CAFE median, mean and standard deviation (SD) are given.

| Individual (*n*=6) | Mean base WBF (Hz) | Cobra peak WBF (Hz) | Δ WBF (%) | Duration (s) |
|---|---|---|---|---|
| 1 | 54.5 | 71.5 | 31.19 | 1.67 |
| 2 | 58.8 | 73.6 | 25.17 | 1.02 |
| 3 | 57.6 | 77.6 | 34.96 | 1.21 |
| 4 | 57.4 | 77.2 | 34.26 | 0.75 |
| 5 | 57.7 | 70.8 | 22.70 | 1.24 |
| 6 | 52.5 | 70.3 | 33.90 | 2.54 |
| | | **Median =** | *32.55* | *1.23* |
| | | **Mean =** | *30.36* | *1.41* |
| | | **SD =** | *5.20* | *0.63* |

**ACKNOWLEDGMENTS**

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**CHAPTER TWO**: On the role of wing sounds in hummingbird communication

*Abstract.* For the most part there is a paucity of experimental data to support the proposed role of non-vocal avian sounds in communication. Playback of natural and digitally altered wing sounds from both sexes of Calliope (*Stellula calliope*) and Rufous (*Selasphorus rufus*) hummingbirds were used to test whether these stimuli altered the behavior of target hummingbirds. Stimuli played from behind target birds at artificial feeders were used to study responses that characterized the level of threat associated with each wing sound stimulus. Behaviours were classified into one of five response categories and the data were analyzed using log-linear (Poisson) models. The study showed that the wing trill signal of males strongly alters the behavior of the recipient. Females showed stronger responses than males to male stimuli, and stronger responses were elicited by male Rufous stimuli than by male Calliope. I used digitally altered wing sound stimuli to further determine which sound components are used in communication. From this study, in conjunction with previous research that has shown inclusive fitness benefits to the sender of the signal, I conclude that male wing trill is an important component of hummingbird communication. Female wing sounds elicited stronger responses than control sounds but the actual role of these sounds in communication requires further study. As the first playback study using non-vocal avian sounds, these positive results suggest that further research into other non-vocal communication signal forms are warranted.

*Résumé.* D'une manière générale, les données expérimentales manquent pour étayer le rôle proposé des sons aviens non vocaux dans la communication avant vérification expérimentale. Des enregistrements de sons d'ailes, naturels et numériquement modifiés, des deux sexes de colibri Calliope (*Stellula calliope*) et Colibri Roux (*Selasphorus rufus*) ont été utilisés pour vérifier si ces stimuli interspécifiques modifiaient le comportement des colibris cibles. On a fait jouer des enregistrements de stimuli derrière des oiseaux cibles près de mangeoires pour étudier les réponses caractéristiques du niveau de menace associé à chaque stimulus de son d'ailes. Les comportements ont été classés en cinq catégories de réponses, et les données ont été analysées à l'aide de modèles linéaires logarithmiques (Poisson). L'étude a montré que le signal de battement d'ailes des mâles modifiait fortement le comportement du récepteur. Les femelles ont réagi davantage que les mâles aux stimuli mâles, et les stimuli mâles Rufous étaient plus puissants que les stimuli mâles Calliope. À partir de cette étude, conjointement avec des recherches antérieures qui ont montré des avantages du point de vue du fitness inclusif pour l'émetteur d'un signal, je conclus que le battement d'ailes des mâles joue un rôle important dans la communication des colibris. Les sons d'ailes des femelles produisaient des réponses plus fortes que les sons de contrôle, mais le rôle réel de ces sons dans la communication doit être étudié plus en profondeur. J'ai utilisé des stimuli de sons d'ailes modifiés pour déterminer plus précisément quelles sont les composantes du son qui servent à la communication. Les résultats positifs de cette première étude au moyen d'enregistrements de sons aviens non vocaux justifient la conduite de recherches plus poussées sur d'autres formes de signaux de communication non vocaux.

## INTRODUCTION

The fundamental difficulty in the study of animal communication is our inability to speak the language of our study subjects. We are left to devise experiments that investigate the behavioral responses of recipients to signals and the behavioral context in which the sender employs them. Research in the avian field has focused on vocal communication (Catchpole 1978, Goldberg and Ewald 1991, Hurd 1996), although birds may be using various other signal forms to communicate (Bleiweiss 1994, Pytte and Ficken 1994, Rusch et al. 1996). Playback of avian vocalizations has been the standard method of eliciting behavioral responses and in attempt to decipher the contextual message of the signals. Generally, responses of the recipient to playback stimuli are characterized by a combination of the following behaviors: proximity of their approach to the sound source, latency of response, time spent near the source and number and type of their vocalizations (Martin et al. 1996, Catchpole 1978, Rice 1978, Falls 1982. In contrast, the role of non-vocal avian sounds, such as the drumming of woodpeckers (Jellis 1977), the boom of the Nighthawk (Miller 1925) and the wing sound of the Flappet lark (Bertram 1977), has received little attention.

The beating wings of a hummingbird produce a non-vocal sound form that has been posited to be a communication signal (Armstrong 1963, Pytte and Ficken 1994, Rusch et al. 1996). The term 'wing sounds' encompasses two types of sound produced by the wings. The first, *wing hum* (WH), is the low frequency (<100Hz) sound produced by the movement of the wings through the air. The frequency of this sound is that of the wing beat, and varies accordingly. Both sexes produce this sound during all types of flight. The second sound is wing trill (WT), which is produced primarily by the males of

some species in which the 9th and 10th primaries are thinned to allow air to rush over them, producing a high frequency 'trill' during flight (Armstrong 1963). This form of wing sound shows greater variability in terms of amplitude and temporal duration and occurrence with the assumption that wing trill is under individualistic control (Hunter 2004). This sound component has been discovered in the females of some hummingbird species (Hunter 2004), but it only occurs during a certain type of flight or a specialized behaviour (Cobra) and its intensity is much reduced compared to males. Of the two wing sounds, WT is thought most likely to function as a means of communication because it is perceived to be a key component of the ritualized displays of male hummingbirds (Armstrong 1963, Ortiz-Crespo 1980, Rusch et al. 1996) and serves no other known function.

For a signal to be part of a communication system, it must affect the behavior of the recipient and provide benefit to the sender (Catchpole 1979). Although it has been suggested that hummingbirds use the ultra violet reflectance of the gorget (Bleiweiss 1994) and non-vocal wing sounds (Pytte and Ficken 1994) to communicate, in only one study have these suggestions been examined. Miller and Inouye (1983) silenced the wing trill of territorial male Broad-tailed hummingbirds. They discovered that silencing wing trill reduced the aggressiveness and territorial defense abilities of the silenced male which when compared to sham control males demonstrated the importance of the wing trill to the sender. This experiment did not however determine if wing trill altered recipient behavior.

Avian playback studies have focused historically on intraspecific responses (Slabberkoorn et al. 2002), but as our understanding of avian communication has grown,

there has been a greater focus on interspecific responses (Hurd 1996, Møller 1992, Catchpole 1978, Rice 1978). These studies have advanced our understanding of interspecies territoriality and the role of vocal communication in hybrid populations (Ceugniet and Aubin 2001, Kort et al. 2002).

Often several hummingbird species are found cohabiting a given area in some form of hierarchical structure. Previous studies of this social structure have suggested that interspecific identification occurs, but wing sounds have not been included among the hypothesized means by which hummingbirds distinguish different species (Powers and McKee 1994, Lyon et al. 1977). Given the frequent association of wing sounds with ritualized behavior (Armstrong 1963, Ortiz-Crespo 1980, Rusch et al. 1996), the proven ability of birds to detect small changes in frequency (Dooling 1982), and their strong aural memory skills (Jellis 1977), it is surprising that the role of these prominent sounds in communication has not been investigated.

The purpose of this interspecies study was to determine if wing sounds have a specific and reproducible effect upon the behavior of the recipient. Calliope (*Stellula calliope*) and Rufous (*Selasphorus rufus*) hummingbirds were chosen as the study species because they overlap extensively in their breeding range and season, making them ideal subjects for this interspecies playback study. The two species also differ in their relative aggressiveness and territoriality, with the Rufous being the more intensely territorial (Calder 1993, Calder and Calder 1994).

I hypothesize that if wing sounds are used for inter- and intraspecific communication, that receivers will respond in a predictable manner to specific wing sound stimuli. From this, the following predictions can be made: 1) multiple stimuli of the same wing sound

type should produce consistent responses in a given type of target bird, 2) responses to the collective female stimuli and the collective male stimuli should be stronger than responses to the non-threatening control sounds, 3) the presence of wing trill in males should elicit stronger behavioral responses to grouped male wing stimuli than to the grouped female wing stimuli which lack this sound component, 4) female target birds should show more high level responses than males to grouped male stimuli since females, which are less territorial, should be more threatened by male stimuli since males are highly territorial and aggressive, 5) males should show slightly stronger responses than females to grouped female wing sound stimuli because of their greater territoriality and courtship interests, 6) due to the high overlap in wing hum frequencies of the females of the two species (Hunter 2004), responses by target birds to female Calliope and Rufous wing sounds should not be significantly different, 7) responses should be stronger to male Rufous stimuli than to those of the naturally less aggressive Calliope male , 8) finally, responses to altered stimuli should show that wing trill has a greater role in communication than wing hum.

## METHODS

### STUDY SITES

Playback experiments were performed on Calliope and Rufous hummingbirds at ten sites within the Okanagan Valley region of British Columbia (N43.3, W75.8) between 15 April and 15 May, and 2-9 July, 2003. Sites ranged in elevation from 350m (valley floor level) to the sub-alpine meadow areas of Kilpoola at 837m. Multiple sites were used in order to increase the number of unique individuals being studied. The average minimum inter-site distance was 8.1 km (range 2.3 to 18 km). Private landowners provided

established artificial feeder sites and the only selection criteria was that the area held a large hummingbird population, was undisturbed by significant ambient noise, and that the site was >2.0 km from any other site.

This interspecies study required samples of both sexes of both species. For purposes of this study, the first two letters of the traditional four-letter AOU banding code describe the species and the second two the sex. Thus, Rufous males and females are respectively RUMA and RUFE and Calliope males and females are CAMA and CAFE. The term 'stimulus' is used when referring to a playback track and 'target' or 'recipient' to refer to the bird receiving the stimulus.

## RECORDING OF STIMULI

A Compact Disc recording of 18 wing sound stimuli tracks in WAV format was produced from selections of wing sound recordings collected in 2002 and April 2003. The original high quality recordings were made using an Audio Technica 3035 condenser microphone placed 20cm from an artificial feeder spout. A Midiman Audiosport Duo pre-amp supplied phantom power for the microphone and amplified the analogue signal before converting to digital form, which was recorded directly through USB using Soundstudio software running on an Apple ibook (OsX). This avoided the sound degradation and frequency alteration inherent to portable computer soundcards. A more detailed explanation of the recording process is found in Hunter (2004).

Each of the 18 stimuli tracks (Table 1) was a 10-second excerpt from a longer recording of a unique individual during hover flight with a 0.5 second fade used to smooth the start and end of each selection. The excerpts were selected on the basis of their having a high signal to noise ratio, minimal directional flight movement, minimal

background sounds and the absence of vocalizations. Three versions of each of the following four stimuli were made: CAMA, CAFE, RUMA and RUFE. The use of three versions represents a compromise between the need to allow for the qualitative variation among the population in the production of, and the response to, the stimulus (Kroodsma 1989), and the limits imposed by the number of potential variables in this initial study. It was considered that the relative simplicity of the sound compared to song justified this approach. The three versions per stimulus type included the mean and two extremes (+/- 5Hz) of wing hum mean frequency. Two control stimuli were made using the song of American Goldfinch (AMGO) and of Say's Phoebe (SAPH). These species were chosen because they are common local residents, sing frequently and do not appear to show aggressive behavior towards hummingbirds or to compete for the same resources. Single versions were made of the unaltered CAFE Cobra stimulus and digitally altered RUMA wing trill only, RUMA wing hum only, and RUFE with low frequencies (<1000Hz) removed. The CAFE Cobra is a sudden and brief, one to three second, increase in wing beat frequency of 10-20Hz, which was observed during the approach of another individual, but prior to any confrontation or agonistic interaction. The observation of this highly energetic behaviour with no other visible reason for being, suggested that it might be communicating a signal beyond that of the regular CAFE stimulus (Hunter 2004). RUMA without wing trill was produced by digitally dropping all sounds above 1kHz by 50db. The RUMA wing trill only and the RUFE no wing hum stimuli were produced by dampening frequencies below 1kHz by 50db. The resultant RUFE with no wing hum track was too quiet and was therefore amplified by 15db.

PLAYBACK EQUIPMENT AND SET-UP

A single Realistic Minimus 7 speaker, which contains a relatively small woofer that approximates a hummingbird in sound source size, provided exceptional undistorted, high definition, low frequency (<100hz) sound playback. A solar-power-supplemented, 12-volt car battery powered an 80-watt car amplifier, and the tracks were played with a Phillips portable CD player held at a constant volume that roughly matched the natural sound intensity of hovering hummingbirds. Variation in playback amplitude was minimal, and between track variation was the result of natural hummingbird species and sex variation in wing sound amplitude. Preliminary testing revealed that moderate variations in volume level had a minimal effect on responses, and that characteristic behavior was independent of volume within natural bounds. The playback set-up was held constant and the speaker set up was left in place during all recording and non-manipulative testing so as to decrease any effect of its presence during playback trials.

The same four-spout, saucer-bottom cylinder feeder, stripped of its perches and with three of the feeding holes covered, was hung between 1 and 1.5m from the ground at each site. The tripod-mounted speaker was placed 60cm behind and 10cm below the available spout, and angled towards the spout, thus allowing a clear flight path for the birds entering and exiting the feeder area. Having the sound behind the target birds decreased immediate visual identification of its origin, and increased the requirement of body position change to investigate the source of the sound. A 33% sucrose solution by volume was used, rather than the standard 20% concentration, in order to compete with the high concentrations used by many feeder operators in the Okanagan Valley, and because higher concentrations decrease sampling behavior (Stromberg and Johnsen 1990, Blem et al. 2000).

CLASSIFICATION OF BEHAVIOURAL RESPONSE

A playback trial commenced after the target bird had been feeding normally for 2-3 seconds and was showing no signs of uncertainty (twitchy flight, vocalizations, long feeding pauses). Although individuals varied, feeding was usually a fluid back and forth movement from feeding at the spout in a horizontal body position to pauses in the normal 45 degree hovering body position 5-10cm back from the feeding spout. Small, usually rapid, head turns were common during pauses, but the duration of the feeding and pause intervals, as well as the number of cycles, showed great variation, but the individual feeding style tended to remain consistent unless the bird was disturbed.

The aforementioned behavioral responses that were used in two previous hummingbird vocal-playback studies (Goldberg and Ewald 1991, Ficken et al. 2002) were not suited to the playback of wing sounds. Wing sound stimuli were presented once a bird was feeding normally, and the sudden occurrence of the sound was predicted to represent a level of threat, which would vary with the sex and species of the sender, and with the sex and the species of recipient. After preliminary trial observations, behavioral responses to playback were classified into one of five categories from 'no response' to 'exit response'. Easily defined actions were used to separate the categories because of the rapid movement and reactions of hummingbirds so as to avoid questions of classification. However, the separation of groups 1 and 2 remained somewhat subjective.

*Category 1: No response-* No visible change from the baseline normal feeding behavior.

*Category 2: Mild response-* Bird remains in the immediate area of the spout but changes feeding behavior; characteristically by increased duration of the pause portion and by

increased vigilance. More marked mild responses include brief head turns to look behind or change to a brief upright, vertical, body position before continuing to feed.

*Category 3: Mid Response-* The essential behavioral component is that the bird moves away from the immediate spout area (generally 15-50cm) but returns to feed normally as the playback continues. Associated behavior generally shows one or more of the following: upright vertical body position, twitchy nervous flight, orientation towards sound source, and on occasion vocalization.

*Category 4: High Response-* Bird rapidly ceases feeding and flies away from spout area and speaker, and pauses in an upright body position at a distance of about a meter. Associated behavior frequently shows one or more of the following: twitchy agitated flight (most common), flared tail, or vocalization. Birds then depart from the area without returning to feed. On rare occasions (<2%) a bird returned briefly to the spout and fed for less than 0.5sec before leaving the study area. These patterns were classified as category 4, whereas a return to feeding with longer duration, or on repeated occasions, were considered category 3 responses.

Category 5: Exit Response- Characterized by immediate rapid flight from the study area, generally (but not required) in the opposite direction of the sound source.

TRIAL CONDITIONS

All observations were performed by the author from a distance of 5-6m and usually from within a blind. A trial was begun once a target bird was identified to species and sex, and had been feeding normally for 2-3 seconds in the absence of any other hummingbird within a 3m radius of the feeder. A stimulus, selected using a random numbers table, was then played in its entirety (10sec). The target bird's response was then described in

words and assigned an appropriate behavioral classification number (1-5). The first 200 trials were recorded using a Sony Mini DV TRV 33 video camera to allow for later verification of the on site classification. Video taping was discontinued once consistent classification was demonstrated. Trials were limited to daylight hours, light winds, and precipitation-free conditions.

## IDENTIFICATION OF INDIVIDUAL BIRDS

Identification of individual hummingbirds in the field is difficult (Lyon et al. 1977, Gass 1979, Tamm et al. 1989, Powers and McKee 1994, Rusch et al. 1996). The risk of within stimulus pseudoreplication was reduced by the use of multiple sites, each with sizeable populations, and by maintaining an inter-site distance greater than 2 km ($\mu$ 8.1 km) Stromberg and Johnsen (1990).

In order to prevent individual habituation to a given stimulus, sites were frequently rotated ($\mu$ 1.7 sites/day) and playback periods were kept to a short duration ($\mu$ 2.07hrs). Goldsmith and Goldsmith (1979) found that individuals average only 1.37 visits per hour to a feeder, and Miller and Inouye (1983) confirmed that many males are non-territorial and fail to return to feeders on a regular basis. During this study 35 CAFE were marked at one site and they were re-sighted relatively infrequently. Given the high background rate of natural inter- and intraspecies interactions, and the fact that this was an interspecies study with four subject types (CAMA, CAFE, RUMA, RUFE), 18 different playback tracks, and an average of only 20.1 playback trials per period, the likelihood of habituation is remote. This random approach was chosen over attempting to run trials on each of the 18 stimuli on marked individuals because of the practical difficulty (field hours) of marking a sufficient percentage of the population. The relatively infrequent

resighting of the 35 CAFE's I marked at one site validated this concern. Many marked males are satellites and would fail to return on a regular basis as shown in the study by Miller and Inouye (1983) in which 79% of the male population were non-territorial. Use of a remote ink spray system to mark birds after testing, as described in Henderson et al. (2001), was not possible as the application would affect the behavioral responses under study. Further, collecting response data for each of the 18 stimuli on a given individual, in the field, was deemed impractical and the risk of habituation to the set-up, greater.

### STATISTICAL ANALYSES

The target of the study was to collect 15 independent responses for each of the 18 stimuli on each of the four hummingbird subtypes (1080 responses). A total of 1076 successful trials were completed. Categorical behavior response data was analyzed using log-linear (Poisson) models. A highly conservative level of significance ($P \leq 0.0025$) was used because of the large number of models tested (15) and to cover the possibility of some level of pseudoreplication, although the test's assumption of independence was probably met.

## RESULTS

### NATURAL INTERACTION OBSERVATIONS

From observing normal agonistic interactions at feeders I found that the individual that instigated an attack was the winner in 93% of interactions (128 of 137). The individual that attacked took control of, or remained at the feeder, regardless of whether it was the intruder or was originally feeding. In 69% of cases the attack was instigated by the new

arrival. In 36 additional interactions the attacking bird chased the other bird from the area but because birds were unmarked, the final outcome was unknown.

## LOG-LINEAR MODELS

Table 1 lists the 18 types of stimuli being tested, and describes groups and subgroups by which they are referred to below. For example, Group B refers to the three RUMA and the three CAMA wing trill stimuli. Table 2 summarizes the significance of the within and between group interaction of stimuli and responses as determined by appropriate independent log-linear models for these categorical data. For example, Model 1 is the comparison of the responses of all birds to the two different control songs, and the results show no significant difference. The model numbers used in the table are used throughout the subsequent text. In order to reduce the presentation of redundant results due to the use of certain data groupings in multiple models, only the results of interactions relevant to the prediction in question are shown. Figures 1 to 3 summarize the mean responses for each stimulus but are for visual presentation of data only.

## WITHIN STIMULI TYPES

A separate log-linear model was applied to each group of three variations of the four main wing stimulus types and the two control bird songs (Figure 1) in order to test the prediction that behavioural responses would be consistent within each playback stimulus of the same wing sound type. The control stimuli (Table 1, Group C; Table 2, Model 1), the CAFE (Table 1, Subgroup I; Table 2, Model 2) and the RUFE (Table 1, Subgroup II; Table 2, Model 3) yielded consistent intra-stimulus responses. Therefore, responses to each of the separate stimuli in each of these three groups were lumped to give single

stimulus response groups. Responses to the three CAMA stimuli (Table 1, Subgroup III; Table 2, Model 4) were significantly different. Pair-wise assessment showed that stimulus 7 gave significantly higher responses than stimuli 8 or 9, which were not significantly different from each other (Figure 1). The within stimulus interaction for RUMA (Table 1, Subgroup IV; Table 2, Model 5) did not quite reach the level of significance set for the study ($P=0.028$), but because of the potential importance of within-wing-sound stimulus variation on behavioral responses, it was treated as significant. Pair-wise analysis demonstrated that stimulus 11 elicited lower responses than either stimulus 10 ($P=0.011$ or stimulus 12 ($P=0.028$), which did not differ significantly from one another ($P>0.71$). In order to reduce the potential bias from intra-stimulus variability in response, weighted average CAMA and RUMA responses were used in Model 12 (Table 2). In the former, I derived the average CAMA group by using an equivalent number of samples of randomly selected responses by each target bird to the single strong stimulus from the two weak stimuli responses. In the latter both strong stimuli were randomly sampled.

RESPONSE TO CONTROL, FEMALE AND MALE STIMULI

The consistent lack of response (96% Type 1) to the two bird-song controls demonstrated that hummingbirds do not simply respond to sudden sounds behind them while they are feeding. By contrast, female stimuli (Table 1, Group A) produced a significant stimulus-response interaction that was significantly greater than the response to control stimuli (Figure 2; Table 2, Model 6). Grouped male stimuli (Table 1, Group B) caused dramatically stronger responses than controls (Figure 2; Table 2, Model 7).

RESPONSE TO MALE VERSUS FEMALE STIMULI

The grouped female (Table 1, Group A) and male (Table 1, Group B) stimuli were compared against the response by each sex (Models 8a and 8b). There was a highly significant three-way interaction between sex, stimuli and response. The responses differed by stimulus group, and by the sex of the recipient (Table 2, Model 8a). As summarized in Figure 2, the response of both sexes to male stimuli is greater than their responses to female stimuli, but males show a stronger response than females to female stimuli (Table 2, Model 9; $P=0.007$), and females a stronger response than males to male stimuli (Table 2, Model 10; $P<0.0001$). Further analysis (Model 8b) shows clearly that it is the sex-of-stimulus to response interaction, rather than the sex of recipient, that accounts for the great majority of the deviance in Model 8.

WING SOUND SPECIFIC COMPARISONS

*Unaltered stimuli*

Responses to CAFE stimuli (Table 1, Group I) did not differ statistically from those to RUFE stimuli (Table 1, Group II; Table 2, Model 11). The response of both sexes to RUMA stimuli was significantly greater than that to average CAMA stimuli (Table 2, Model 12; Figure 3). Responses to the CAFE Cobra stimulus (Table 1,18) were found to be significantly stronger than to regular CAFE (Table 1, Subgroup I) stimuli (Table 2, Model 15; Figure 3).

*Altered stimuli*

The dramatically stronger responses elicited by male stimuli than female stimuli suggested that the wing trill of males might be the key element in wing-sound

communication. The digitally altered RUMA stimuli (Table 1, 16 and 17) were produced in order to test this hypothesis. The wing-trill-only (Table 1, 17) stimulus elicited significantly stronger responses than the wing-hum-only (Table 1, 16) stimulus (Table 2, Model 13). The wing-trill-only track response is comparable to, if not greater than, the grouped RUMA stimuli, whereas the response to the RUMA wing-hum-only track was comparable to the RUFE stimulus group (Figure 3).

Notwithstanding the key role of the wing trill, the responses to female stimuli were significantly higher than to control sounds, leaving open the possibility that wing hum does play some part in communication. In order to address this question a stimulus was generated by digitally filtering out all wing hum sounds (<1kHz) from a RUFE sample. The remaining 'noise', with its indistinct frequencies, was digitally amplified so as to present a stimulus of normal intensity. The resultant wing noise stimulus that had no wing hum components or associated harmonics (Table 1, 15) was found to elicit a significantly stronger response than RUFE wing hum (Table 1, Subgroup II; Table 2, Model 14). Indeed the responses were comparable to those elicited by CAMA (Figure 3).

## DISCUSSION

Observation of natural interactions suggests that birds respond strongly to sounds that are perceived as a threat. The attacking bird, regardless of species or sex of the attacker or the target, usually wins the interaction, and it therefore follows that the initial response of a target bird should be to move from the immediate area of danger. The outcome of interactions appears to be largely dependent on which bird attacks first, and the overall hierarchy of cohabiting hummingbirds is likely a result of a greater frequency of attacks

instigated by the more aggressive and territorial species and sex. The same reasoning could explain individual differences in territoriality and aggressiveness. The distinct responses by sex and species to different wing sounds observed in this study are probably a behavioral adaptation to the threat associated with the sex and species of the source.

## WITHIN STIMULUS TYPE VARIABILITY

Where the intra-stimulus-type variability in behavioral response was low, this allowed the data from each stimulus Subgroup to be lumped when assessing the behavior attributable to that species. In turn this increased the respective stimulus sample size and decreased the number of pair-wise comparisons that were required to test the different predictions. Likewise the lack of response to the two control species was expected because they do not compete with or show aggression towards hummingbirds, and this allowed their data to be combined.

Although the CAFE and the RUFE wings hum stimuli Subgroups covered a range of 49 to 59Hz and 44 to 54HZ respectively, the responses were, as predicted, consistent within each stimulus type. This suggests that the stimuli were representative of the stimuli produced by the general population of the females of these species. However, the three CAMA stimulus variations elicited different responses, which suggests that the recipients perceived a difference between the signals. The 10Hz in variation in wing hum is identical to that noted among the female stimuli, and it is therefore improbable that the variability in wing hum frequency was responsible for the different responses. What remained was to reinvestigate the wing trill component of the CAMA wing sound stimuli. As shown by Hunter (2004), the overlap in the frequency of wing trill between individuals of a given species is broad enough to suggest that this is an unlikely

explanation for variation in behavioral response. It became evident upon listening again to the three versions of the CAMA stimulus, even with the naked ear, that the differences lay in the temporal structure of the wing trill. By studying the waveforms I discovered that the structure varies in three ways: 1) the overall intensity of each wing trill pulse relative to the wing hum level varies from essentially absent to extremely prominent, 2) the relative duration of the wing trill pulse varies in relation to the total duration of the wing beat. These two variables appear to be related in that with rising amplitude of the pulse sound, the pulse duration within a given wing beat increases. 3) Wing trill sounds are of greater intensity during rapid changes in body position. Therefore recordings with more changes in position tend to have a greater number of distinct wing trill sections. The two versions of CAMA stimuli that elicited low level responses contained less audible and distinct wing trill sections than those found within the stimulus that caused a strong response. The results were the same for RUMA where the single stimulus that elicited a strong response contained more prominent and temporally constant wing trill components than the two stimuli that contained only short portions of less intense and distinct wing trill, and resulted in less marked behavioral response.

CONTROLS AND MALE/FEMALE COMPARISONS

The lack of response to the playback of passerine songs confirmed that the sudden appearance of a non-threatening sound from behind does not alter hummingbird behavior. This is what would be expected under natural circumstances because responding to songs of non-competitive local passerines would be wasteful of energy, and it supports the view that the responses to wing sound stimuli are not indiscriminate reactions to noise. Both male and female wing sounds generated significant behavioral responses that were not

seen with the control sounds, providing evidence that they communicate a degree of threat.

Overall, feeding hummingbirds of both species responded with greater intensity to the wing sounds of the male than to those of the female. This was anticipated because males are more territorial and aggressive, and therefore present a greater level of threat during natural interactions. That there was some response to female stimuli suggests that their wing sound does function as a communication signal. The wing trill, which is limited to males, could be the key to the greater response to male wing sounds.

Analysis of the interaction of sex, stimulus and response indicated that the response varied by the sex of the recipient and with the stimulus used. A separate model was run within each stimulus group to analyze the response by sex of the recipient. When presented with male stimuli, females were significantly more likely to show the maximal Type 5 exit behavior than males, suggesting that, regardless of species, they are more threatened than males by male wing sounds. The lower rate of exit responses in males could be attributed to their higher level of territoriality (Kodric-Brown and Brown 1978). A number of the responses by males during playback were characteristic of aggression, such as approaching the speaker, vocal chatter, and agonistic body positions (Ficken et al. 2002, Stiles 1982). These observations give further credence to the view that males tend to respond in a territorial manner when threatened, whereas females are more likely to respond by fleeing to safety. Within the female stimulus group, the sex response interaction was not statistically significant but the general trend was for males more often to respond than females to female stimuli (*vide infra*).

Both species gave similar responses to the stimuli, indicating that they perceived an equivalent level of threat. Generally, responses to heterospecific playback are of lower intensity than to conspecific sounds (Evans 1972, Catchpole 1978, Rice 1978, Ceugniet and Aubin 2001), but some studies have found equivalent responses (Rice 1978). The results of this study probably reflect the highly territorial feeding behavior of these two species that compete for sources of food.

## SPECIFIC COMPARISONS AMONG WING SOUNDS

### *Unaltered*

Two stimuli that are fundamentally similar in structure and frequency should evoke similar behavioral responses even if the source species differ. The CAFE and RUFE show substantial overlap in wing hum frequency (Table 1) and in their responses to playback. Wing hum is a by-product of flight and during hovering it is temporally constant and relatively stable in frequency and intensity. The major source of variation is the fundamental wing beat frequency. If wing hum is a communication signal, the similar behavioral responses elicited by the two species stimuli in this study is expected because they produce essentially the same wing hum, and thus it follows that they are conveying the same information.

The responses to male stimuli did vary with by stimulus species type. A weighted average was used for both the CAMA and RUMA stimuli to reduce any bias that might have arisen from an unequal number of responses to the low and high intensity stimulus types that were discovered in both species. Overall, the RUMA stimuli elicited a greater average response. RUMA hummingbirds are naturally more aggressive than CAMA hummingbirds during territorial disputes (Bené 1947, Kodric-Brown and Brown 1978,

Calder 1993), although CAMA hummingbirds do chase both male and female Rufous (Cody 1966). This supports my prediction that the male wing sounds are honest signals of threat, and that the playback of RUMA wing sounds should elicit stronger behavioral responses than the CAMA stimuli.

Large increases in wing beat frequency are energetically expensive, which would suggest that they should have some biological benefit. Chai and Dudley (1999) showed that Ruby-throated hummingbirds (*Archilochus colubris*) have reserve capacities to maintain an increase in wing beat frequency of only 4-6%. The CAFE Cobra sample used in this experiment showed a very rapid and brief 34% increase in WBF from a hovering average of 53.5Hz to a peak of 71.5Hz. This peak exceeds the maximum WBF recorded for CAFE hummingbirds by 7.5Hz. Hunter (2004a) stated that though the Cobra can be seen in conjunction with a change to an agonistic posture, the posture is not required to produce the sound and in most cases the Cobra occurs without any perceptible change in body position. Therefore, the Cobra is not a by-product of specific changes in body or flight position, leaving open its possible role in communication.

Though statistically different, biologically, the behavioral responses to the Cobra were not much stronger than to regular CAFE stimuli, and so I studied how Cobra maneuvers were used during natural interactions at feeders. Three key points emerged: 1) this sound was produced by the feeding bird upon the arrival of another individual, 2) the sound was only produced if the new arrival remained at a distance (roughly 1m) from the feeding bird, 3) once the sound was produced, the new bird usually moved in slowly to share the feeder, and did not display aggressive behavior. Therefore, this display may have a

greater defensive, than aggressive or antagonistic function, which may not be captured adequately by a playback study that was designed to test responses to threatening sounds. However, only one example of Cobra was used in the study and it may not have been representative and so further research is suggested.

*Altered*

Since the wing sounds of the male hummingbirds were composed of two distinct sound types, it was important to determine whether the wing trill or the wing hum was the key communication signal. By digitally altering RUMA stimuli the two components of wing sound from the same individual could be tested for behavioral response. The low pass filter was set at 1kHz in order to ensure that the wing hum test-sound included all harmonics and was completely natural except for the lack of wing trill. For the wing trill version, the high pass filter was set at 1kHz to ensure that all harmonics of the wing hum were eliminated but that all higher frequency wing trill and noise were included. The results showed that wing trill is clearly the more important signal of threat, as it elicited responses comparable to the unaltered RUMA stimulus, whereas the constructed wing hum produced responses similar to RUFE stimulus. Altered CAMA stimuli were not tested, but the strong responses to CAMA stimuli, as well as the within CAMA variation associated with differing wing trill intensity, suggest that wing trill is the key signal in this species as well.

Although wing trill is the predominant male signal, there is a behavioral response to female wing sounds, which do not contain a distinct wing trill. While this suggests that wing hum has some role in communication, I think that indistinct, low amplitude, and higher frequency female wing noises might be responsible for the mild responses

elicited by the female playback stimuli. The altered RUFE stimulus in which wing hum was eliminated and the remaining higher frequencies were amplified caused behavioral responses comparable to those obtained using CAMA stimuli. Although the altered stimulus was not natural because the normally quiet high frequencies were amplified to provide a signal level comparable to regular stimuli, the results suggest a possible role for subtle indistinct wing noises in females. It must be remembered that computer software compares all frequency amplitudes on an equivalent scale whereas biologically, the auditory sensitivity varies with frequency, which would dictate which frequencies are actually perceived with greater or lesser amplitude by the individual.

## ROLE OF SPECIFIC SOUND TYPES

### *Wing Trill*

WT may make a bird more conspicuous to predators, and its production requires a modification to the outer primaries that has no other known function, but does result in a slight reduction in wing surface area; two features that would be expected to cause a selective handicap. Thus a role in communication could be the compensatory fitness benefit that would explain the presence of wing trill.

Wing trill has been described frequently in the context of the highly ritualized displays of male hummingbirds (Armstrong 1963, Ortiz-Crespo 1980, Rusch et al. 1996, Hurly et al. 2001). Debate continues as to the fundamental function (courtship or aggression) of certain displays (Stiles 1982, Tamm et al. 1989, Calder 1993, Hurly et al. 2001), but it is known that the WBF, and the temporal intensity and amplitude of wing trill sounds can dramatically increase during these displays. For example, CAMA may increase its wing beat frequency from its normal hovering average of 65Hz up to 95Hz, with a

simultaneous increase in wing trill intensity, during the close proximity 'shuttle' display (Ortiz-Crespo 1980, Hunter, unpublished data). This brief increase of roughly 45% in wing beat frequency unquestionably has an energy cost, and suggests that the associated explosive wing trill must send a message to the recipient.

The control of production of wing trill during non-ritualized flight is not fully understood. Individual CAMA and RUMA stimuli produced consistently different responses, indicating that wing trill variation modifies behavioral response (Figure 1). How an individual controls the temporal intensity and amplitude of its wing trill remains unknown. Increases in wing beat frequency, wing stroke amplitude, and stroke-angle have been suggested as possible factors controlling wing trill (Ortiz-Crespo 1980, Chai and Dudley 1996). High intensity wing trill often occurs during ritualized displays in conjunction with dramatic increases in wing beat frequency, but Hunter (2004a) has shown that it is not due to a simple relationship to WBF as it can occur at average WBFs and be essentially absent during higher WBF hover flight. This suggests that WBF may occur in parallel to wing trill production, but that it is unlikely to be sole factor in its production.

*Wing Hum*

The responses to female stimuli, which contain only the wing hum component, were relatively mild with a significant proportion of recipients showing no response. It should be noted that wing hum includes not only the fundamental frequency (equal to wing beat frequency), but also the associated harmonics, of which the first was often of equivalent

or greater amplitude than the fundamental. The responses to wing hum were stronger than to the controls indicating that some level of challenge was being conveyed.

These results suggest two possible explanations. Firstly, wing hum may signal that the source of the sound is female, and because females are less aggressive than males, the signal is accorded a weak response. That males responded more strongly than females to the female stimuli, though not statistically significant at this highly conservative level, requires further investigation but could represent the increased level of male territoriality and/or their greater interest in courtship opportunities. Though not directly transferable because of the physiological differences between species, Pytte's (personal communication) work on Blue-throated Hummingbirds revealed that males and females possess different hearing response levels at frequencies below around 2.5kHz. This difference in sensitivity could account for the sex difference in response. It should be noted that this sex difference in hearing sensitivity is not seen at higher frequencies and as such does not transfer to explaining sex response differences to wing trill.

The low responses of target females may partially be explained by observations made of females interacting at feeders. I found that feeding females often showed no response to intruding females within their field of view until the intruder showed threatening behavior, such as vocal chatter, agonistic body position, or with a direct flight attack (Ficken et al. 2002, Stiles 1982). However, the simple presence of males in the area was often sufficient to elicit rapid exit responses in feeding females. The less aggressive nature of females may result in their maximizing feeding times by waiting for evidence of definite aggression before they respond to other females.

The second interpretation is that target birds are not responding to the wing hum itself, but to indistinct high frequency wing noises. The strong response to the wing trill of males showed that these high frequency sounds are important signals. The altered RUFE stimulus in which the amplified high frequencies elicited CAMA stimulus level responses suggests that recipients may be responding to the faint wing noises of the female stimuli. Though not known at the time of this study, I discovered that the Cobra sound contains indistinct high frequency sounds in a wing trill pattern similar to males. Therefore, the higher responses to the Cobra sounds could be attributed to the sudden appearance of a low amplitude wing trill type sound (Hunter 2004). This possibility is further supported by the additional discovery that female Black-chinned hummingbirds (*Archilochus alexandri*) can produce a distinct wing trill, similar in frequency but of lower amplitude than conspecific males (Hunter 2004).

For wing hum to be an effective signal, it would require that the sender have some level of control over its production. Wing hum is a direct by-product of the wing beat (Armstrong 1963) that can only be varied by a change in wing beat frequency. Thus it is relatively constant compared to the selectively pulsed wing trill of males. Despite the ability of most bird species to detect frequency changes of only 1-2% (Dooling 1982), the variation in normal wing hum frequency between female stimuli had no apparent effect in this study. The wing hum frequency is relatively constant during normal hovering flight, which suggests that it be under insufficient individual control to be a specific form of communication beyond possibly conveying the base information that the individual is present and its sex. Though the Cobra display appears to be subject to individual manipulation, the discovery that wing trill type sounds are produced within this wing

hum burst eliminates this behaviour as supporting evidence for the communication role of wing hum itself.

Finally, through his work on the auditory sensitivities of the RTHU, Lohr (personal communication) states that the hearing range of this species is from 500-4000Hz, with hearing under 1000Hz being questionable. Though requiring further behavioural experimentation, as all work thus far has been physiological, Lohr's work does lend support to my belief that wing hum frequencies are not being used as communication signals but rather responses are elicited by the higher wing noise frequencies.

ROLE IN COMMUNICATION

Results from this study have added to the initial observation of Miller and Inouye (1983) that wing trill is used in hummingbird communication. To conform to the definition of true communication, a signal must alter the behavior of the recipient and, in so doing, must benefit the sender (Morton 1982, Catchpole 1979). Miller and Inouye (1983) removed the wing trill signal from male hummingbirds and showed that their overall aggressiveness and ability to hold territory was diminished, thus documenting that the signal was important to the sender. In this study I have shown that the recipients interpret the signal as threatening. Furthermore, the responses differed depending upon the source of the sound and the sex of the target bird, confirming that the signal contained enough information to define the level of threat. Although the control of wing trill requires further study, the fact that it appears to be under greater individualistic control is an indication of its functional importance. The presence of wing trill components within the Cobra sounds produced by females and the subsequently stronger responses by target birds to these sounds further supports that wing trill is the key communication signal.

Finally, as is true for other better-documented forms of communication, such as avian vocal sounds (Beer 1982), the wing trill (Armstrong 1963) and the Cobra maneuver have no other known function than communication.

The role of song in birds has long been linked to territoriality and mate attraction (reviewed in Searcy and Andersson 1986) but the males of both hummingbird species in this study do not sing (Ortiz-Crespo 1980, Calder 1993, Calder and Calder 1994). Singing entails some increase in expenditure of energy and risk of predation, but most noticeably it takes time away from other activities essential to inclusive fitness (Goldberg and Ewald 1991). As a replacement for song, wing trill would dramatically decrease these costs. WT drives other birds from an area, thus reducing the number of direct agonistic interactions with their inherent risk of injury and demand for energy, thereby increasing the inclusive fitness of the sender while allowing territory to be maintained. The extremely rapid pulse that forms the wing trill produces a note of constant narrow band frequency. This concentration of energy into a narrow band frequency may increase its amplitude, thus increasing the distance that the signal is transmitted and reducing the sound degradation associated with broad-frequency-range sounds (Slabbekorn et al. 2002). Prolonged constant tones are also more omnidirectional and make the sound source more difficult to locate by predators. Wing trill thus allows hummingbirds, at a low expenditure of energy, to produce loud and far-reaching sounds while they simultaneously forage and patrol their territories, thus reducing the need for song.

The role of wing hum in communication on the other hand can not be fully explained. The importance of wing hum to the sender has yet to be studied. Wing hum is a by-product sound of the beating wings and as such has a fundamental role other than

communication. It is possible that receivers are opportunistically responding to these by-product sounds of flight without the intent of, or benefit to, the sender. Regardless, the low amplitude of wing hum compared to the more distantly traveling and audible wing trill would only allow wing hum to function as a very close range signal. The use of energetically costly Cobra type displays by individuals suggested that wing hum was a signal holding benefit for its sender. However, due to the simultaneous appearance of a low amplitude wing trill patterned sound within the Cobra, it can not be used in support of wing hum as a communication signal, but rather reinforces the importance of wing trill. Finally, further work on the hearing range of hummingbirds may aid in eliminating wing hum as a communication signal.

The lack of a distinct wing sound with which females can be identified to species may explain the indiscriminate nature of males performing ritualized displays. The primary role of displays has been related to both aggression and to courtship (Stiles 1982, Tamm et al. 1989, Mulvihill et al. 1992, Calder 1993). The argument for the aggressive function of displays is generally supported by the fact that males of a given species will often perform these displays towards females of other species of hummingbirds, passerines or even inanimate objects. With females being difficult to separate morphologically and with no evidence that they can be separated through wing sounds, I propose the idea that male courtship is indiscriminate in nature. This could further explain previous observations of males attempting to mate with juvenile conspecifics (Armstrong 1988), which due to their female coloration and lack of wing trill, could easily be mistaken for females. Hybridization in hummingbirds is relatively common compared to other avian families (Armstrong 1963, review in Ortiz-Crespo 1980, Kaufman 1990) so it may follow

that the cost of a possible heterospecific mating is not great enough to outweigh the cost of missed mating opportunities with female conspecifics.

Male hummingbirds do not invest energy in nesting and rearing of young and so it follows that the females are the selective sex in terms of mate selection. It seems probable from the results of this study that wing trill is another cue, likely in addition to species-specific displays, body coloration and vocalizations, which females may be using to identify conspecifics for mating. Forced copulation attempts with heterospecifics (Wells et al. 1978), juveniles (Armstrong 1988, Stiles 1982) and even male conspecifics while perched (personal observation) do occur but it is only during appropriate conspecific mating that female receptivity in terms of body position and vocal chips has been documented (Stiles 1982, Ficken et al. 2002). This suggests that females play a greater role in species identification during mate selection.

## FUTURE STUDY

This study has determined an important role for wing trill in communication, but many questions remain about the relationship between the intensity of these sounds and the level of the responses elicited. Future study should take a comprehensive look at Cobra displays, in natural and computer altered forms, using experiments designed to gauge responses on a finer scale under a playback set up that would better test the likely defensive nature of this sound. There may be value in revisiting studies that have looked at attempted copulation with juveniles (Armstrong 1988), and the increased ability of juveniles to avoid detection by territorial adult males (Ewald 1980), because juveniles do not possess self advertising and male distinguishing wing trill. This study dealt primarily

with recordings from hovering individuals. I noticed that the response by target birds often followed immediately a sudden wing sound change on the playback, which were due to the rapid body position changes of the source bird during recording. These changes in flight direction generally result in a stronger wing trill and a brief increase in overall amplitude, and further study of behavioral responses to wing sounds from various types of flight may lead to a greater understanding of the information carried in wing sounds.

It would also be of interest to study the interactions associated with wing sounds between species of hummingbird that share a geographical area but do not overlap in their time of arrival or of breeding, and hence should be less competitive for territory. In the area of this study the Black-chinned hummingbird would be suitable.

Figure 1. The mean responses (1-5 categories) of the grouped target hummingbird types to multiple versions of each of the four main playback stimulus types and the control sound group. The '*' indicates a significant difference based on results from a log linear model.

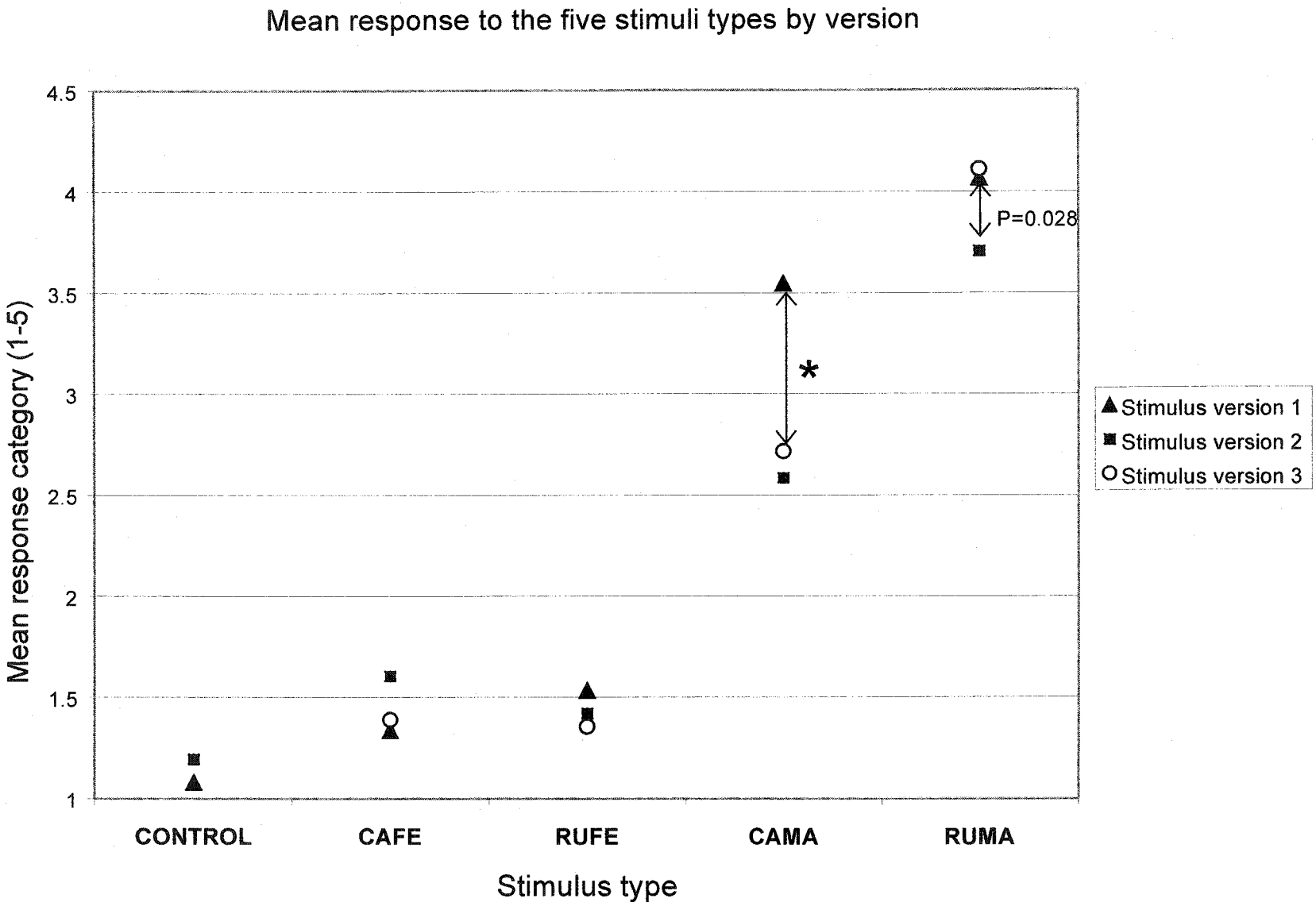
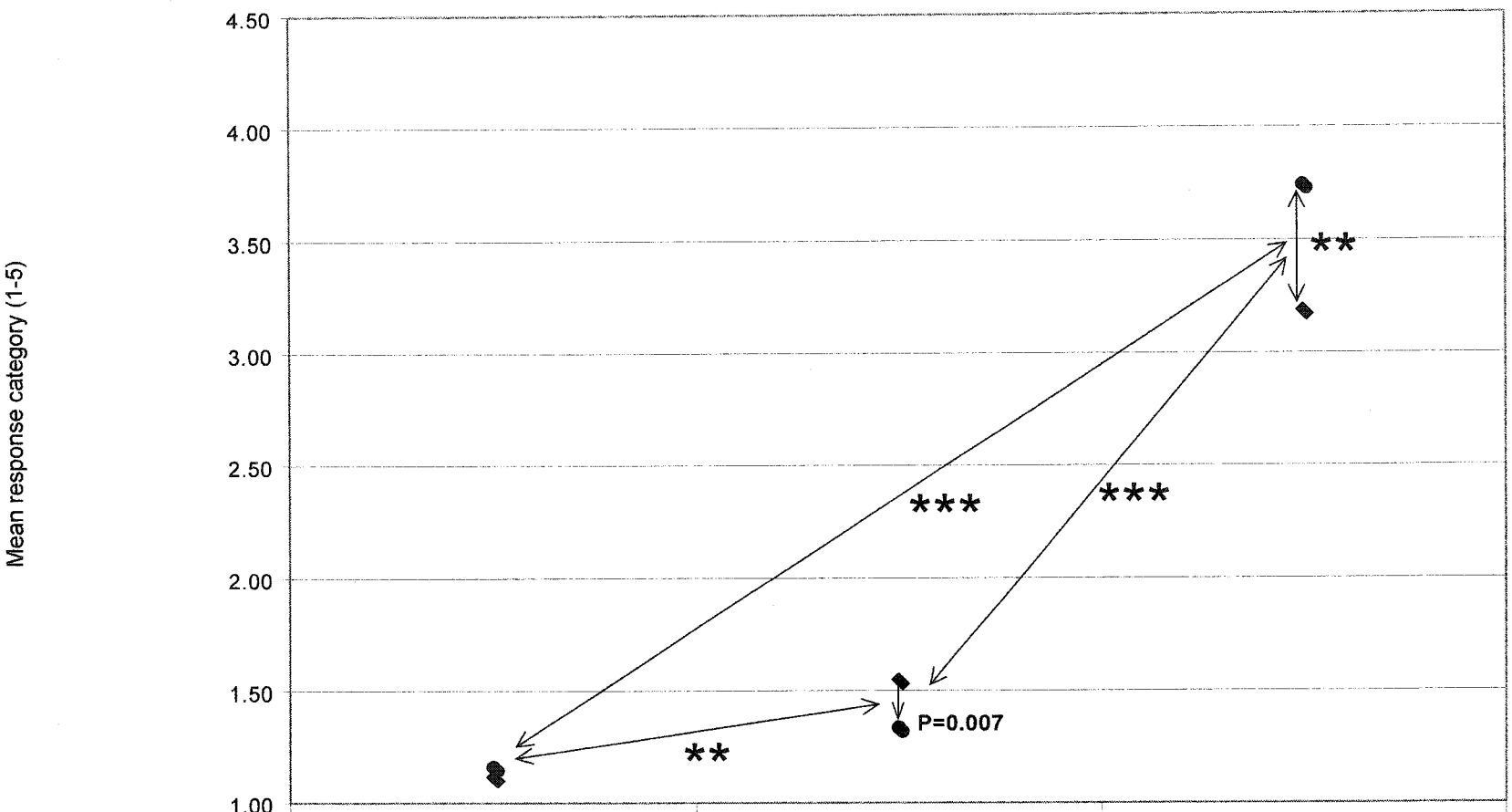

Mean response to the five stimuli types by version
Mean response category (1-5)
4.5
4
3.5
3
2.5
2
1.5
1
P=0.028
*
CONTROL
CAFE
RUFE
CAMA
RUMA
Stimulus type
Stimulus version 1
Stimulus version 2
Stimulus version 3

Figure 2. The mean responses (1- 5 categories) of hummingbird types by sex (male and female receivers) to the grouped control sounds (two versions), the female stimuli (3 CAFE + 3 RUFE stimuli) and the male stimuli (3 CAMA + 3 RUMA). The '**' indicates a significant difference with a $P<0.0001$ and '***' indicates $P<<0.00001$ based on log linear models.

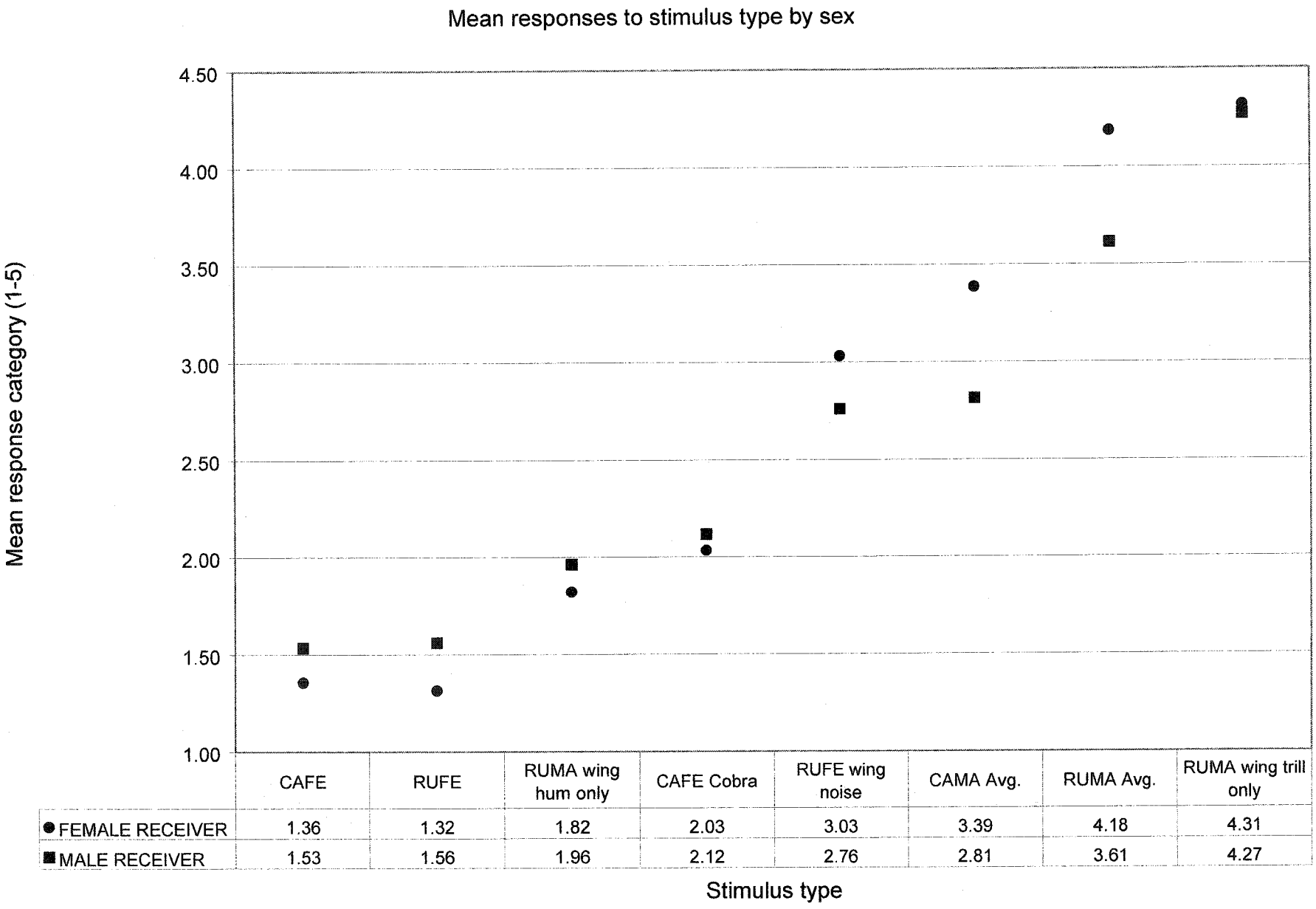
Mean responses to grouped stimuli by sex




| | CONTROL (2) | FEMALE (6) | MALE (6) |
|---|---|---|---|
| ● FEMALE RECEIVER | 1.16 | 1.34 | 3.74 |
| ◆ MALE RECEIVER | 1.12 | 1.55 | 3.19 |

Stimuli group

Figure 3. The mean responses of male and female receivers (CAHU and RUHU grouped) to eight different stimulus types.




| | CAFE | RUFE | RUMA wing hum only | CAFE Cobra | RUFE wing noise | CAMA Avg. | RUMA Avg. | RUMA wing trill only |
|---|---|---|---|---|---|---|---|---|
| ● FEMALE RECEIVER | 1.36 | 1.32 | 1.82 | 2.03 | 3.03 | 3.39 | 4.18 | 4.31 |
| ■ MALE RECEIVER | 1.53 | 1.56 | 1.96 | 2.12 | 2.76 | 2.81 | 3.61 | 4.27 |

Table 1. The 18 stimulus types with associated fundamental wing beat frequencies (WBF) and wing trill frequencies (WT-males only) divided in to stimulus groups used for log linear modeling.

| Sex grouping | Species grouped by sex | Stimulus | Stimulus Wing Sound Type | Fundamental WBF/WT (Hz) |
|---|---|---|---|---|
| Group A *(Female)* | Subgroup I *(Calliope)* | 1 | CAFE | 49 |
| | | 2 | CAFE | 54 |
| | | 3 | CAFE | 59 |
| | Subgroup II *(Rufous)* | 4 | RUFE | 44 |
| | | 5 | RUFE | 49 |
| | | 6 | RUFE | 54 |
| Group B *(Male)* | Subgroup III *(Calliope)* | 7 | CAMA | 62/WT |
| | | 8 | CAMA | 67/WT |
| | | 9 | CAMA | 72/WT |
| | Subgroup IV *(Rufous)* | 10 | RUMA | 53/WT |
| | | 11 | RUMA | 58/WT |
| | | 12 | RUMA | 63/WT |
| Group C *(Control)* | | 13 | AMGO | Song |
| | | 14 | SAPH | Song |
| *Altered stimuli* | | 15 | RUFE wing noise | >1000HZ |
| | | 16 | RUMA wing hum only | <1000HZ |
| | | 17 | RUMA wing trill only | >1000HZ |
| *Natural wing hum burst* | | 18 | CAFE Cobra | Base =53.5 Peak =71.5/WT |

Table 2. The 15 log linear models tested with the stimulus types used and the key interaction of interest given in each case. Each models null deviance and degrees of freedom are given along with the interaction terms deviance and degrees of freedom. P values are listed with an alpha level set at P=0.0025 to correct for the number of models (15).

| Model number | Stimulus types being modeled | Interaction | Null deviance | Null degrees freedom | Term deviance | Δ Degree freedom | P value | Significance level* |
|---|---|---|---|---|---|---|---|---|
| 1 | Within Controls | Stimulus x Response | 304.55 | 9 | 2.81 | 4 | P>0.25 | ns |
| 2 | Within CAFE | Stimulus x Response | 302.70 | 59 | 8.21 | 8 | P>0.25 | ns |
| 3 | Within RUFE | Stimulus x Response | 327.18 | 59 | 3.36 | 8 | P>0.25 | ns |
| 4 | Within CAMA | Stimulus x Response | 138.15 | 59 | 29.0 | 8 | P<0.001 | s |
| 5 | Within RUMA | Stimulus x Response | 181.18 | 59 | 17.14 | 8 | P=0.028 | s** |
| 6 | Controls vs Female stimuli | Stimulus x Response | 999.04 | 39 | 24.61 | 4 | P<0.0001 | s |
| 7 | Controls vs Male stimuli | Stimulus x Response | 568.64 | 39 | 293.71 | 4 | P<<0.00001 | hs |
| 8a | Female vs Male stimuli | Sex x Stimuli x response | 687.92 | 39 | 35.64 | 4 | P<<0.00001 | hs |
| 8b | Female vs Male stimuli | Stimulus x Response | 687.92 | 39 | 426.44 | 4 | P<<0.00001 | hs |
| 9 | Within Female stimuli | Sex x Response | 561.95 | 19 | 14.09 | 4 | P=0.007 | ns |
| 10 | Within Male stimuli | Sex x Response | 125.90 | 19 | 26.65 | 4 | P<0.0001 | s |
| 11 | RUFE vs CAFE | Stimulus x Response | 574.84 | 39 | 4.46 | 4 | P>0.25 | ns |
| 12 | CAMA vs RUMA | Stimulus x Response | 161.82 | 39 | 28.13 | 4 | P<0.0001 | s |
| 13 | RUMA trill vs RUMA hum | Stimulus x Response | 137.45 | 39 | 96.62 | 4 | P<<0.00001 | hs |
| 14 | RUFE vs RUFE noise | Stimulus x Response | 393.89 | 39 | 82.23 | 4 | P<<0.00001 | hs |
| 15 | CAFE vs Wing Hum Burst | Stimulus x Response | 396.54 | 39 | 19.0 | 4 | P<0.001 | s |

*ns = not significant, s= significant, hs= highly significant

** Not significant by set P<0.0025 standard but because of the biological significance of stimuli eliciting different behavioral responses, this result will be considered significant and will be dealt with in the same manner as CAMA stimuli of Model 4.

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