THE USE AND FUNCTION OF THE RUFFED GROUSE *(BONASA UMBELLUS)* NON-VOCAL DRUMMING DISPLAY ACROSS THE BREEDING SEASON

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DEDICATION

This thesis is dedicated to my late grandfather (Papa) Mike Dermyer, one of my biggest supporters throughout my MSc career and perhaps the best story teller I've ever known. I finished like I promised I would.

ABSTRACT

The use of sonations in avian courtship displays is described for many species, however, the function and variation with these non-vocal acoustic displays has rarely been investigated. Perhaps the only well studied sonation used by a bird is the wing snap display of the golden-collared manakin. My thesis focuses on the use and function of a non-vocal drumming display used by male ruffed grouse during the breeding season. This thesis presents data that the non-vocal drumming display of the ruffed grouse is used in similar fashion to bird song and calls. That is, drumming peaks in activity during the morning hours much like a dawn chorus. Additionally drumming appears to function in part like a contact call, attracting potential mates and marking a male's location within the environment. This is to the best of my knowledge, the first report of a daily change in a display performance reported for sonations.

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LIST OF ABBREVIATIONS

4P – four parameter
A – after
AICc – Akaike information criteria correlations
ANOVA – analysis of variance
ATV – all terrain vehicle
B – before
Ca – California
D – during
FF – fundamental frequency
g – grams(s)
GPS – global positioning satellite
Hz – hertz
m – meter
mm – millimeter
Ma – Massachusetts
N – north
OHV – off highway vehicle
PC – principal component
PCA – principal components analysis
pers. – personal
RUGR – ruffed grouse
sec. – second(s)
SPL – sound pressure level
spp. – species
W – west

CHAPTER ONE: GENERAL INTRODUCTION

Vocalizations are commonly used in the courtship displays of birds. Of all the various vocalizations used in courtship, learned song in songbirds is perhaps the most heavily investigated. While song can be defined in many ways, it is often differentiated from other vocalizations by its greater length, complexity and amplitude as well as being derived, in part, from some learned component, at least in songbirds (Gill, 2007; Spector, 1994). During the breeding season, male songbirds sing loudly to attract females and defend territories from other males (Brumm, Robertson, & Nemeth, 2011; Catchpole, 1983). Species, populations and individuals vary in the structure of their songs and this variation enables species, dialect and individual recognition (Brooks & Falls, 1975; Dooling, Leek, Gleich, & Dent, 2002; Mathevon et al., 2008; Nelson & Soha, 2004). In fact, individual variation in song structure has been compared to that of human speech (Naguib and Wiley 2001). Females of many species appear to use song to assess the relative quality of males. For example, in the java sparrow (*Lonchura oryzibora*), trill performance is indicative of male physical quality (Kagawa & Soma, 2013). Through eavesdropping on male song, females can also assess the dominance and quality of competing males (Amy et al., 2008; Bartsch, Wenchel, Kaiser, & Kipper, 2014; Bradbury & Vehrencamp, 2011; Mennill, Ratcliffe, & Boag, 2002). Song is also used by males to establish territories, identify neighboring males, estimate distance and assess ‘winners’ in song contests (Bartsch et al., 2014; Brumm et al., 2011; Brumm & Slater, 2005; Naguib, Klump, Hillmann, Griessmann, & Teige, 2000). Finally, the ability to perceive differences among individuals and species is supported by a discrete and specialized system of brain regions referred to as the song system (Knudsen & Gentner, 2010).

Regions within the song system are tuned to individual and species differences in song, including the male's own song (Knudsen & Gentner, 2010), which supports the discriminative abilities outlined above. In sum, there is a lot of information on song, how it varies and how it is used in songbirds.

A variety of other vocalizations in non-songbirds serve the same functions as song (Spector, 1994), namely mate attraction and territory defense. For example, the duet call of the slender-billed prion (*Pachyptila belcheri*) is used for both mate attraction and territory defense in a similar fashion to songbird song (Bretagnolle, Genevois, & Mougeot, 1998). Similarly, the soft calls of the corncrake (*Crex crex*) play an equivalent role to that of soft song in songbirds; they are quieter signals used in aggressive encounters and/or courtship (Rek & Osiejuk, 2011). Calls are also greatly important for mate attraction in lek breeding species, such as greater sage grouse, (*Centrocercus urophasianus*; Gibson, 1989), greater prairie chicken (*Tympanuchus cupido*; Hale, Nelson, & Augustine, 2014) and black grouse (*Tetrao tetrix*; Hovi, Alatalo, Halonen, & Lundberg, 1997). In a similar fashion to songbirds, non-songbirds are also capable of individual discrimination based on the structure of calls used in courtship (Cornec, Hingrat, Rybak, & Fusani, 2014; Peake et al., 1998; Puglisi & Adama, 2004). In Japanese quail (*Coturnix japonica*) crowing not only elicits female approach behavior, but females can distinguish among birds, thereby allowing mate identification based on crowing behavior alone (Goodson & Adkins-Regan, 1997; Mills, Crawford, Domjan, & Faure, 1997). Courtship calls can also indicate male quality in various non-songbirds species, like the Eurasian eagle owl (*Bubo bubo*; (Penteriani, 2003) and the Adélie penguin *(Pygoscelis adeliae*; (Marks, Brunton, & Rodrigo, 2010). While these calls function in the same way as song, the neural control of courtship vocalizations in non-songbirds is still poorly understood (Gahr, 2000).

Vocalizations are only one type of sound used in avian courtship behavior. Various ‘sonations’, defined as non-vocal acoustic signals created by mechanical means, are rather common, but poorly understood. Bostwick (2006) describes avian sonations as modulated, communicative sounds produced by non-syringeal structures such as the bill, feet, and feathers. Much of the research regarding sonations used in courtship has focused on how these sounds are produced. For example, the ‘tick-ting’ courtship display of the male club-winged manakin (*Machaeropterus deliciosus*) is made by the rapid pronation and adduction of the wings causing a collision of the secondary feathers of the right and left wings (Bostwick & Prum, 2005). Similarly, modified wing feathers and retrices enable a number of different sounds to be produced by hummingbirds during courtship flight (Clark, 2008; Clark & Feo, 2008). Despite this recent interest in sonations and the mechanisms by which they are produced, little is known about how these sounds are used in courtship and the extent to which they share similarities with song and other courtship vocalizations. The golden-collared manakin (*Manacus vitellinus*) is perhaps the only species in which the production, function and proximate control of sonations have been studied in detail (Fusani, Barske, Day, Fuxjager, & Schlinger, 2014). Male golden-collared manakins, hereafter ‘manakins’, have a complex courtship display that comprises vocalizations, acrobatic movements and sonations (Fusani, Barske, et al., 2014). The ‘roll-snap’, which consists of repeated wing claps, is used along with a vocalization to mark males’ position within a lek as well as to attract females (Fusani, Barske, et al., 2014). Males also produce a “wing snap” display within the lek that is judged by females in a courtship arena (Barske, Schlinger, Wikelski, & Fusani, 2011; Fusani, Giordano, Day, & Schlinger, 2007). Female manakins visit male 'courts' (male display sites) to assess males based on the production of their wing snap display and can differentiate individual differences in their performances by tens to hundreds of milliseconds (Barske, Schlinger et al. 2011). Higher speed displays are thought to show the energetic investment and cardio-muscular capacity of the performer and therefore indicate male 'quality' (Barske et al., 2011). Young males are believed to also visit male courts to learn the acrobatic maneuvers required for courtship from successful adults (Fusani, Barske, et al., 2014). Last, there are neurochemical and neuroanatomical specializations that enable the production (Day, Fusani, Kim, & Schlinger, 2011; Feng, Katz, Day, Barske, & Schlinger, 2010; Fusani, Donaldson, London, Fuxjager, & Schlinger, 2014; Schultz & Schlinger, 1999) and possibly the perception (Day et al., 2011) of these sonations and other components of their display are similar to that of the songbird song system. Thus, in the case of this manakin species, sonations used in courtship displays are analogous in function to song and courtship calls, but rely upon different neuorochemical and neuroanatomical specializations than in the oscine song system.

The manakin is the only species in which these aspects of sonation use and function have been studied in detail. Non-vocal sounds are important to study because they address different ways communication and signals have evolved to convey information. Feather-generated sonations have evolved independently across many species and play an important role in communication, yet research is still needed to identify the similarities and differences between sonations and vocalizations (Bostwick, 2006). One such example of a mechanical display is the courtship display of the male ruffed grouse (*Bonasa umbellus*).

The non-vocal drumming display of male ruffed grouse is a series of swift downward wing strokes produced by a stationary bird perched in a perpendicular posture on a log, resulting in a series of pulses that resemble a ‘drumming’ sound (Archibald, 1974; Aubin, 1972; Hjorth, 1970). Drumming is typical of the spring months during the breeding season of ruffed grouse. This display is performed throughout the day with the highest frequency usually occurring just prior to sunrise (Archibald, 1976; Palmer, 1969; Zimmerman & Gutierrez, 2007), with shifts to nocturnal drumming being attributed to moonlight (Archibald, 1976). Ruffed grouse use a variety of logs (and sometimes other structures such as large rocks and live tree roots) for their drumming display, often having one primary log and a few alternatives to switch between through the season (Archibald, 1976; Aubin, 1972; Gullion, 1967). These logs can be transient, changing season-to-season, but many are considered perennial as different males will use the same log year after year (Gullion, 1967). Sometimes these logs are clumped together, suggesting a type of lekking behavior (Aubin, 1972). Although the drumming display may sound relatively uniform to the human ear, it does vary among individuals (Aubin, 1972; Garcia, Charrier, Rendall, & Iwaniuk, 2012) and drumming from one male is thought to stimulate nearby rival males by affecting how frequently they drum, (Archibald, 1976; Aubin, 1972). For example, Archibald (1976) reported two types of drumming interactions between adjacent males. The first of these was ‘interval copying’ in which a male copies the interval length between successive drummings of another male. The second he called a ‘fast response’ when a male immediately followed a neighbor's drumming. Although these drumming interactions were uncommon, they were not random behaviors. Fast responses and/or interval copying were more likely to occur in succession, one after another, rather than as a single and/or random event, indicating non-random behavior. The fact that these interactions do occur, is consistent with some sort of inter-male communication, but the data are largely anecdotal and based on only a single pair of males. Thus, the extent to which the drumming behavior of one male is influenced by another is unclear.

Although numerous studies have examined the habitat requirements of ruffed grouse, characteristics of drumming log sites and counts of drumming males as a censusing tool (Archibald, 1974; Gullion, 1966, 1981; Jones, Harper, Buehler, & Waruburotn, 2005; McDonald, Storm, & Palmer, 1998; Zimmerman & Gutierrez, 2007), little is known about how the drumming display is used, variation among and within individuals or whether some aspect of drumming behavior reflects male quality. It is widely accepted that the drumming display is an acoustic signal used for mate attraction and territorial defense (Archibald, 1976; Brander, 1967; Gullion, 1967; Johnsgard, 2008). Purportedly, females respond to male drumming and will travel to various drumming sites before copulating (Brander, 1967). However, it is unclear whether females select males based on individual variation in their drumming (Archibald, 1976). Brander (1967) suggests that hens visit multiple males in a season and speculates that females are more likely to mate with persistent drummers. Although this could be evidence supporting female selection of males based on drumming activity, it was based on interpreting movement patterns of females with radio transmitters and not direct observations. What characteristics of the display might influence female selection therefore remains unknown. Similarly, it is unclear if males are able to distinguish among one anothers' drumming displays or even respond to drumming by other males in ways that would support the use of drumming to defend a territory. Archibald (1976) mentions that the drumming behavior of a male can influence the drumming of another male, suggesting some form of inter-male communication, but it remains unclear if males are capable of distinguishing among each other based solely on acoustic signals. A recent analysis of the display showed temporal components (pulse rate and pulse number) varied significantly among individuals, so individual recognition is possible, but as yet, untested (Garcia, Charrier, & Iwaniuk, 2012). The inter-individual variation may also reflect information about the male, but this too is unknown. Detailed research is needed to better understand the features of the display and how this information may be used in territorial establishment and mate selection.

The first aim of my thesis was to determine if males respond to playback recordings of drumming. To determine if males use drumming in contest-like behavior drumming recordings were played to 65 male ruffed grouse. I also tested if the speed of the drumming in the playbacks affected the response of the males by presenting both a slow and fast drumming signal on separate days as part of a two playback design. For all playbacks, the likelihood of an approach was no different than would be expected from chance and the speed of drumming in the playback had no effect on male responses. Bioacoustic analyses of the drumming of males that received playbacks showed that they consistently increased interval length between displays; however, drumming rate did not change in any consistent manner. Even though interval length did consistently increase this was no different than from normal drumming behavior as males decrease drumming activity throughout the morning increasing the time between displays. Changes in drumming rate were less consistent, however, with some males increasing drumming rate during and/or after playbacks while others decreased or showed no change. Overall my data suggest males do not consistently respond to drumming in a way to suggest its use as a territorial signal. Instead, the drumming display is most likely used as a advertisement signal to broadcast a male's location to nearby females and other males.

As mentioned above, temporal variation in the drumming display, namely number of drumbeats and drumming rate, vary significantly among individuals in a given season and vary between seasons (Aubin, 1972; Garcia, Charrier, & Iwaniuk, 2012). However, it is not known whether these differences are consistent throughout the day or season because in both studies, males were only recorded over the course of a few days. Thus, it remains unclear if males alter their drumming behavior throughout a day or from one week to the next. In addition, the relationship between male phenotype and drumming behavior has never been tested. It is possible that the drumming display may convey some information about body condition. Drumming is driven by the pectoral muscles of the birds so it is likely that body size may have some effect on drumming behavior, such that larger birds may drum faster than smaller birds. The second part of my thesis was to determine how much temporal variation there is within the drumming display across a day and throughout a season as well as whether individual variation in drumming behavior reflects body size. To look at seasonal drumming activity 15 male ruffed grouse were analyzed across the 2013-2015 seasons to see when drumming activity peaks. Seasonal drumming activity peaked during week 18 of the calendar year (approximately last week of April). Daily drumming activity peaked in the morning approximately an hour before sunrise. 12 of the 15 males sampled from 2013-2015 had enough measurable data to test temporal variation within individuals drum beats and drumming rate across the morning (0000 – 0900 MST) for a single day and multiple weeks. Both drum beats and drumming rate changed across a single day and varied among weeks. However, changes in drumming rate across the day revealed an increase throughout the morning up to a peak speed for all males. Specifically birds start off drumming slowly and increase drumming rate through the morning until reaching a peak performance level. To test the relationship between body size and drumming behavior, 23 male ruffed grouse were recorded drumming and trapped. Overall there was no significant relationship between measures of body size and drumbeats and drumming rate. In sum, my data corroborates previous findings showing seasonal and daily trends in drumming activity while also showing that temporal variation within a male's drumming display is not as consistent as previously thought. Even though drumming rate appears to hold consistent trends throughout the day such as maximum drumming rate, there was no evidence of correlation between drumming behavior and measures of body size.

CHAPTER TWO

EXPERIMENT ONE: THE RESPONSE OF MALE RUFFED GROUSE (*Bonasa umbellus*) TO PLAYBACKS DOES NOT SUPPORT A TERRITORIAL FUNCTION FOR THE DRUMMING DISPLAY

Abstract

Ruffed Grouse (*Bonasa umbellus*) are well known for their ‘drumming’ display during the breeding season, but little is known about how this display is used. Prior research suggests that drumming not only attracts females and marks a male’s location, but may also be used to defend a drumming log through ‘contest-like’ behavior. To test whether male drumming behavior is affected by the drumming sound of another male, I played back the drumming recordings of males from previous field seasons to 65 male ruffed grouse so that the signal would be form an unknown individual. Throughout each playback, we recorded the drumming behavior of target males so that we could test if the drumming activity/pattern changes following a playback as well as whether males change the number of beats and/or speed of their drumming display. Males did not approach the source of playbacks more than would be expected from chance and the speed of the drumming played back to males did not affect the likelihood of an approach. Drumming rate of focal males did not change during or after playbacks in a consistent fashion with males showing both increases and decreases in drumming rate during or after playbacks relative to before playbacks. The interval length between drumming displays did show consistent significant changes during and after playbacks with the interval length increasing over time, but this behavior is consistent with normal diel variation in drumming as males drum less frequently as the morning progressed. Our results therefore fail to support a strictly territorial function for drumming. Instead, we suggest that the primary function of drumming is to advertise a male’s location to potential mates.

Introduction

In birds, courtship displays are performed by males during the breeding season as a means to attract females and/or defend territories (Brooks & Falls, 1975; Brumm et al., 2011; Catchpole, 1983; Dooling et al., 2002; Mathevon et al., 2008). Courtship displays typically include visual signals and/or vocalizations, but much of the research on avian courtship has focused on vocalizations. Vocalizations are not, however, the only sounds that birds produce during courtship. Non-vocal acoustic signals created by mechanical means (i.e., using their beak, wings or tails) are, in fact, commonly used in avian courtship displays (Bostwick, 2006; Clark, 2016), but are not as well studied. Much of the research on non-vocal acoustic signals used in courtship has focused on how these sounds are produced (Bostwick & Prum, 2005; Clark, 2008; Clark & Feo, 2008), with little known about how these sounds are used in courtship and the extent to which they share similarities with song and other courtship vocalizations (Clark, 2016). The golden–collared manakin (*Manacus vitellinus*) is perhaps the only species in which the production, function and proximate control of sonations have been studied in detail (Fusani, Barske, et al., 2014). Golden-collared manakins perform a ‘roll-snap’, which consists of repeated wing claps, used along with a vocalization to mark males’ position within a lek as well as to attract females (Fusani, Barske, et al., 2014). Males also produce a “wing snap” display within the lek that is assessed by females in a courtship arena (Barske et al., 2011; Fusani et al., 2007). Female manakins visit male ‘courts’ to assess males based on the production of their wing snap display and can differentiate individual differences in their performances by tens to hundredths of milliseconds (Barske et al., 2011; Fusani et al., 2007). However, apart from these studies of the manakin, very little is known about how non-vocal sounds are used in courtship. Examining non-vocal sounds involved in courtship in other species could provide insight into their biological function, how they are perceived by receivers and why they evolve in the first place.

Although many species incorporate non-vocal sounds into their courtship, relatively few species rely almost entirely on non-vocal sounds. One such species is the ruffed grouse (*Bonasa umbellus*), a medium-sized game bird distributed across most of North America (Bump, Darrow, Edminster, & Crissey, 1947; Hjorth, 1970). Males perform a wing beat display during the breeding season by perching perpendicularly on a fallen log (or other structure) and producing a series of swift downward wing strokes, which creates a ‘drumming’ sound (Amy et al., 2008; Archibald, 1976; Hjorth, 1970). Unlike other grouse species, ruffed grouse are largely non-vocal and no vocalizations are incorporated into their courtship (Allen, 1934; Atwater & Schnell, 1989; Rusch, Destefano, Reynolds, & Lauten, 2000). Thus, the drumming display is the only sound produced in the context of courtship. Research on drumming in ruffed grouse has primarily focused on the selection of drumming logs and census methods using drumming counts for population estimates (Archibald, 1974; Gullion, 1981; Jones et al., 2005; McDonald et al., 1998; Zimmerman & Gutierrez, 2007), with very little known about the drumming display itself (but see Garcia et al. 2012a,b). It is thought that the drumming display is used to mark a male’s location, attract females, and defend drumming log territories from intruding males (Archibald, 1976; Brander, 1967; Gullion, 1967). However, it is unclear if males can distinguish among males’ drummings or even respond to drumming by other males in ways that would support the use of drumming to defend a territory. Although the drumming display may sound relatively uniform to the human ear, it does vary among individuals (Aubin, 1972; Garcia, Charrier, Rendall, et al., 2012) and drumming from one male is thought to stimulate nearby rival males by affecting how frequently they drum (Archibald, 1976; Aubin, 1972). For example, Archibald (1976) reported two types of drumming interactions between adjacent males. The first of these was ‘interval copying’ in which a male copies the interval length between successive drumming of another male. The second he called a ‘fast response’ when a male immediately followed a neighbor’s drumming. The fact that these interactions occur supports some sort of inter-male communication, but the data are largely anecdotal and based on only a single pair of males.

One means of determining whether a male’s drumming behavior is affected by the drumming of other males is to play back drumming sounds to a male while he is occupying his log (or other drumming structure). To date, there have been two playback studies conducted in ruffed grouse (Aubin, 1972; Naidoo, 2000). In both cases, the responses of males to playbacks were inconsistent, but there are several problems with the two studies. First, both studies relied on few individuals (six males in each study). Second, in both cases, there are insufficient details on the speaker. Drumming is a low frequency signal with most of the energy between 35 and 90 Hz (Garcia, Charrier, Rendall, et al., 2012) that is difficult to recreate accurately without a speaker capable of producing a low frequency sound. Third, there was no standard distance or positioning of the speaker relative to the focal male. Naidoo (2000) placed speakers from 13 to 45 meters from the focal bird and Aubin (1972) makes no mention of the speaker distance. The varying responses across males could therefore be attributed to the perceived distances of the drumming signal (Naguib et al., 2000). Because of these problems, it is not possible to make any conclusion on the behavioral responses of male grouse to playbacks and the function of drumming remains unclear.

The aims of this study were to gain insight into how ruffed grouse use their drumming display during the breeding season using standardized playbacks of drumming sounds. More specifically: 1) do males respond to the drumming display of other males; 2) does the behavioral response vary relative to the temporal components of the stimulus (i.e., number of drum beats and drum rate); and 3) are responses affected by male grouping (i.e., solitary males or males in an exploded lek) or color phase (grey or red morph). If males are responsive to other males drumming we would expect approaches towards the speaker broadcasting a novel drumming stimuli to vary based on perceived condition of the individual, which may be represented by drumming rate. Additionally, it is possible that males that remain solitary during the breeding season are less tolerant of nearby males than males grouped in exploded leks. Indeed, for these solitary males, the playback stimulus could be perceived as an intruder and therefore they would be expected to exhibit more aggressive responses, such as approaching the stimulus, than grouped males.

Materials and Methods

Male ruffed grouse were studied near Buck Lake, Alberta, Canada (52.97º N, 114.77º W) from 2012-2015 during the months of April and May. Males were located by ear and their drumming logs were marked with a handheld GPS unit (GPSMAP 64s, Garmin, Olathe, KS, USA) so they could be found at a later date. Song Meters (SM2 and

SM2+ models, Wildlife Acoustics Inc, Maynard, MA, USA), set at a sampling rate of 64,000 Hz, were placed within 10 meters of their main drumming log for at least one full day (24 hours) prior to playbacks and left in the same location throughout the experiment to record the focal male's drumming behavior. Some males do have alternate logs that they may switch to during the breeding season, but they are usually located within close proximity of their primary log (Gullion, 1967). Males were not individually marked, but given that they maintain the same drumming log(s) during a breeding season (Archibald, 1976; Aubin, 1972; Berkeley, 2014; Gullion, 1967), it is reasonable to assume that the same bird was recorded from the same log.

Playback procedure and stimuli

Playbacks occurred between 18 April and 11 May over four field seasons (2012-2015), after sunrise (0500-0900 hrs MDT) so that the experiment could be video-recorded and males could be seen approaching the sound source. For each playback test, the speaker (see below) was placed at a distance of 35-40m from the focal male's drumming log (mean: 38.8 +/- 0.55), the precise distance from the displaying male relied on available cover to conceal the observer and equipment. Playback stimuli were presented using a Snow-Cro Pro 2 digital game caller (FOXPRO INC., Lewiston, PA, USA) connected to a Bazooka bass tube speaker (BT6014, Southern Audio Services, Baton Rouge, LA, USA). Most of the energy in the drumming display is concentrated between 35-90 Hz, which falls well within the frequency response of this speaker (39-1500 Hz). Prior to initiating a playback, the volume of the subwoofer was calibrated with a sound pressure level meter (Extech Instruments, Nashua, NH, USA, model 407732, ±

1.5 dB, range 35-130 dB), at slow weighting, to ensure that the drumming series were played at a natural amplitude of 60 dB at a distance of one meter (Garcia, Charrier, & Iwaniuk, 2012; Garcia, Charrier, Rendall, et al., 2012).

All males used in playback trials were first verified to be drumming on their log prior to the commencement of the playback. Each playback trial consisted of a previously recorded drumming track repeated 10 times, with random intervals of 1.5-7 minutes between each drumming. By having these random intervals, the playback more closely resembles the natural drumming behavior of a displaying male. At the end of the playback stimulus, the speaker was turned off and a 10-minute period of silence was observed before quietly packing up and leaving the area.

A total of 65 males were provided 110 playbacks from 2012 – 2015. From these, 33 males received a single stimulus playback (drumming with a rate of 4.981 Hz, i.e., 4.981 beats/sec) and 32 males were provided two playback sessions with 2 different stimuli: one with a fast drumming rate, and another one with a slow rate. Stimuli used in the playback tests were drummings recorded from males in the 2011 field season and represented opposite ends of drumming rate range for all males recorded (Garcia, Charrier, Rendall, et al., 2012). Thus, the ‘fast’ drumming stimuli consisted of drumming rates of 5.287, 5.326, or 5.451 beats/sec, whereas the ‘slow’ drumming stimuli consisted of drumming rates of 4.460 or 4.876 beats/sec. Males that received the two playback stimuli were left undisturbed for at least one day between playback trials and the position of the speaker relative to the drumming log varied between the two playback trials. This reduced not only the likelihood of the males becoming habituated to the playback but also the chance of the males becoming overly stressed by repeated activity around their drumming log, which often results in them abandoning a log and moving to another site (Gullion, 1967). The playback order in which individuals received the two playback stimuli was balanced such that half of the males received a "fast" drumming first and the other half received the "slow" drumming first.

Acoustic Analyses

Drummings were analyzed using Avisoft SASLab Pro (v5.1, Avisoft Bioacoustics, Berlin, Germany). Playback signals were distinguished from each focal male's drumming display (see Figure 1; visualized using R package Seewave; Sueur et al., 2008) and focal male's displays were analyzed 1 hour prior to and 1 hour following each playback trial, as well as during the playback itself. The number of drumming displays produced by the focal individual was not used in our analyses. Indeed the number of displays does not necessarily yield accurate information on how frequently males are displaying. Sometimes males would wait before beginning to display after the playback begins or, if males approached, they would not return to their log to resume drumming for some time after the playback. These behaviors would often reduce the total number of drumming displays produced by males, resulting in inaccurate estimates of how often males are displaying during or following playbacks. Further, prior research suggested that the interval between drumming displays was altered after hearing another male drumming (Archibald, 1976). To more accurately determine if males are changing how often they are drumming, we therefore measured interval length between drumming displays to the nearest second for the same three time periods (1 hour before, during, and 1 hour after the playback).

In addition to simply drumming more often in response to the playback, males could also potentially alter their drumming rate (beats per second, Hz). To test for change in drumming rate, we randomly sampled six drumming displays for each of the three time periods (1 hour before, during and 1 hour after playback). Drumming rate (in Hz) was measured using Avisoft's pulse train analysis tool, which calculates the average distance between pulses (wing beats) over time throughout the drumming display. For drumming rate analyses the first quartet of the drumming display (see Figure 2.1) was not included as it is often obscured by background noise or is not picked up by the recorders (SM2 and SM2+) at all. Only drumming displays with high signal-to-noise ratios were included in the pulse train analyses. Weather (i.e., wind and/or rain), movement between primary and secondary logs, and changes in position of the male relative to the recorder reduced sample sizes such that for some males, only three drumming displays could be used in these analyses. Last, males that approached the speaker during playback trials and/or stopped drumming completely were excluded from our analyses of drumming rate and drumming interval length because there were no recordings to analyze.

Statistical Analyses

A number of factors could potentially affect the likelihood of a male responding to drumming playbacks. Two that I could specifically test for are color morph and grouping pattern. Ruffed grouse have two color morphs (red and grey), most noticeable in their tail feathers. In birds, color morph has been related to aggressive behavior and dominance in some species (Pryke & Griffith, 2006). Additionally some males tend to group together in a way suggesting lekking behavior (Archibald, 1976). However unlike the other lekking grouse species, male ruffed grouse are spaced out suggesting an ‘exploded’ lek system (Foster 1983) similar to that of bustards (Morales, Jiguet, & Arroyo, 2001). Exploded leks differ from traditional leks in that they cover more area and have a lower density due to males spacing themselves farther apart (Foster, 1983). Because the boundaries of ruffed grouse drumming court remain undefined and it is unclear whether they form true leks, I labeled birds as ‘grouped’ or ‘solitary’. For males to be considered grouped we relied on whether or not I could hear neighboring males drumming from a focal male’s log. As such, 27 males were considered to be grouped, and the average distance to neighbors for these grouped males was 238.1m (+/- 148.6m).

As an initial sorting of the behavioral responses of males to the playbacks, I noted if males approached the playback speaker or not. ‘Approach’ meant that the males left their drumming log and approached the speaker during the playback trial. ‘No approach’ meant that males did not approach the speaker, continued or ceased to drum, or, in some cases, they left the drumming log in an opposite direction from the speaker. To test for differences in approach behavior, I used Fisher’s exact test across all males. When comparing responses across all males, individuals provided two playback trials were categorized as approaching if a single playback trial resulted in an approach. To investigate more deeply, a second Fisher’s exact test was then performed only on males that received two playback stimuli (2014-2015 playback trials), and individuals were separated into 3 categories: never approached, approached once, and approached twice.

To test for differences in behavioral response between drumming rates (fast/slow), color morphs (red/grey) and grouping pattern (solitary/grouped), Fisher’s exact tests were also performed. As described above, these tests were conducted across all males, scoring those individuals that received two playbacks as approaching if they approached in at least one trial. Similarly, I ran the tests again only on males that received two playback stimuli.

Finally, to test for differences in inter-drumming duration and drumming rate, an analysis of variance (ANOVA) was performed on interval length and drumming rates within each individual with the three time periods as grouping variables (1 hour before, during and 1 hour after playback). If a significant difference was detected, this was followed by a post-hoc Tukey-Kramer HSD test to determine the significant pair-wise differences.

Results

Approach behavior

Overall, 57% (37/65) of the males approached the speaker during playbacks. In a 'typical' approach, the male begins towards the speaker after the first or second drumming is played within a trial. Males would often stop in between each of the drumming displays within a playback and then start moving towards the speaker as soon as the next drumming display was heard. Once within the vicinity of the speaker, males would walk around the area of the speaker, in some cases circling the speaker several times. Some individuals would drum after approaching the speaker during playbacks from either their original log (n = 9) or from a new location (n = 4). For males presented two playback trials, three individuals drummed and approached the speaker during one trial and then only approached in the other trial. Of the 37 males that approached, 5 males approached immediately, did not drum during the playback trial at all and returned to their logs after the playback had ended. Last, two of these same 37 males produced a full tail fan display while approaching the speaker (Figure 2.3). This display, called the ‘cum Ruff Display’ by Hjorth (1970), consists of males extending the long dark upper neck feathers that form the ruff and raising/fanning their tail. The two males exhibiting this ‘cum Ruff display’ also pecked at the ground vigorously as they approached the speaker. This display is considered very aggressive (Hjorth 1970), but given that it only occurred in two males in our entire study, it is atypical of male response behavior to drumming in isolation of other cues.

As mentioned above, just over 50% of males approached the speaker and this was not significantly different than what would be expected from chance (Table 2.1). We then tested whether a male approaching or not was related to color morph (red or grey) or grouping pattern (solitary or grouped males). Although red males appeared to be more likely than grey males to approach the speaker, no significant difference was detected (Table 2.1). Approach behavior between solitary and grouped birds also did not differ from chance (see Table 2.1). In other words, red or grey birds approached the speaker in the same proportion, as well as solitary or grouped males.

Thirty-two males were presented two different drumming stimuli (fast and slow drumming). Of these 32, only 11 males approached the speaker during both playbacks. With respect to approaches towards the two different stimuli, 16 individuals approached the slow stimulus and 14 approached the fast stimulus. Approaches on the first and second playbacks were 17 and 13 approaches respectively. Overall, these 32 males did not differ in their response to the fast and slow drumming stimuli (table 2.2). Similarly, how often a bird approached across the two playbacks did not differ from what would be expected from chance and there were also no differences between color morphs and grouping patterns (table 2.2).

Inter-drumming interval duration and drumming rate

Enough data were available to analyze interval duration between drumming displays for 34 males during playback trials. Interval length was measured before, during and after the playback stimuli. A total of 45 playback trials were available for analysis. These trials were split up into birds with data available for two playback trials (n =11; Table 2.3) and males that were only presented one trial or only had data available for one playback trial (n = 23; Table 2.4). Out of the 34 males analyzed for differences in interval duration between drumming displays 16 showed significant differences between before and during playbacks and during and after playbacks (Tables 2.3 and 2.4). For males with data available for 2 playback trials significant differences between before and during playbacks and during and after occurred in 8 trials (Table 2.4). Additionally, comparisons of interval lengths before and after playbacks resulted in significant differences for 15 males (Tables 2.3 and 2.4). Significant changes in interval duration showed the predominant response in interval duration is longer after a playback compared with during or before playbacks (n = 19, Tables 2.3 and 2.4).

Drumming rates could be analyzed for 46 birds before, during, and after playback stimuli (Tables 2.5 and 2.6). Of the 46 males available for analyses, only 15 males had enough data to analyze both playback trials (Table 2.5). Out of the 46 males analyzed, 15 showed a significant difference in drumming rates between: before and during; during and after (Tables 2.5 and 2.6). Seven significant differences were observed in males with data available for two playback trials and 8 significant differences were observed in males presented one playback trial. Males both increased and decreased drumming rate with 16 significant drumming rate increases and 9 significant decreases total across all males.

Discussion

Overall, my results indicate that there is no consistent response of male ruffed grouse to playbacks of drumming. Although I had a limited number of replicates in playback experiments, this represents a significant improvement over previous playback studies in ruffed grouse (Aubin, 1972; Naidoo, 2000). For example, I used a standardized protocol for distance of the speaker to the drumming log, a portable speaker capable of generating low frequencies and calibrated the speaker using the appropriate SPL (Garcia, Charrier, & Iwaniuk, 2012). In addition, by having random intervals between drummings, my playback design was more representative of what would be heard from a male. Finally, the lack of difference with respect to slow versus fast drumming suggests that additional replicates would yield similar results. Thus, despite having some single stimulus presentations, I am confident that the results accurately represent the responses of males to drumming playbacks.

In contrast to Aubin (1972), I found no consistent effect of playbacks on a male’s drumming behavior. Aubin (1972) describes a type of communication between drumming males, namely a fast response by one male to another’s drumming and interval matching between birds. For this to happen a drumming male would have to change the timing (interval length) between displays. Our analyses of changes in the temporal components of males’ drumming displays shows no evidence for males changing the timing between displays in response to playbacks. Gullion (1967) also discusses challenge sites during periods of intense drumming activity, where males would temporarily move to a log not typically used to engage in drumming “duels” with other males. During five of the playback trials the focal male repositioned himself on a new log, in one case within 15 meters of the speaker, to begin displaying again. However, this was not typical of behavior, most trials resulted in birds continuing to drum or approaching. The changes in drumming rate that were observed in some individuals could be due to intra-individual variability in drumming behavior rather than a distinct response to the playbacks. This would also explain why significant changes in drumming rate were detected in only a few males.

Although some grouse appear to be tolerant of other males drumming in close proximity, grouped males were just as likely to approach the speaker as solitary males. Archibald (1976) suggests ruffed grouse may exhibit an exploded lek pattern. That is, males tend to cluster together within a larger space, even when seemingly favorable habitat with suitable drumming logs is present. Exploded leks, like a standard lek, involve displaying males performing in defined courts throughout a habitat; however, exploded leks cover larger areas than a typical lek with lower densities of displaying males (Foster 1983). An example of species displaying in exploded leks are the bustards (Morales et al. 2001), where males have large territories causing males to be further spaced apart. The difficulty with placing ruffed grouse into an exploded lek system is that the exact boundaries of ruffed grouse drumming territories are unknown. Males in our population were spaced out at varying distances from one another with some of the closest males displaying 30m apart. If males are in an exploded lek arrangement it would be expected for there to be uniform responses towards playbacks. Additionally it would be expected that more individuals would appear to be grouped. This lack of a uniform response from all males to playbacks and occurrence of solitary males suggest that some ruffed grouse are simply grouped and not in an exploded lek.

Irrespective of whether ruffed grouse are truly in an exploded lek or not, one of the presumed functions of drumming is territorial defense. In fact, this function is often suggested as a reason for fall drumming; males are defending their territory in advance of the next breeding season (Gullion 1967). Based on my data, however, males do not react to hearing a drumming display in a manner that would suggest that drumming is used as a territorial signal. The frequency of approach responses did not differ from that expected by chance and only a handful of individuals showed changes in the temporal components of their drumming (drumming rate and interval length between displays). If drumming is used for territorial defense, responses to playbacks should have been more uniform as seen in playbacks on songbirds (David Hof & Hazlett, 2010; D. Hof & Podos, 2013). For instance, even if males did not respond in an approach it would be expected for them to alter their drumming in a such a way that an intruder will keep out, such as increasing the amount of displays performed and/or increasing their drumming rate. Further, one might have also expected more males to express the highly aggressive cum Ruff display. Instead only two males exhibited the full cum-ruff display, suggesting this behavior is not typical. A possible explanation for the seemingly random nature of the responses may be that the focal males perceive the sounds of the playback as an individual of different dominance status to themselves. Gullion (1966) discusses ‘satellite’ males that were observed around established drumming males. In his study area, a satellite male would occasionally take over when a drumming male was removed, suggesting some sort of establishment of dominance between males prior to the breeding season. However, a general lack of social interactions between males makes it almost impossible to determine if there is some sort of establishment of dominance between males. More recently, a study by Berkley (2014) revealed no log turnover across the breeding season; once males established themselves they were never displaced by other birds. In cases where we have removed grouse for anatomical studies (Corfield, Krilow, Ligt, & Iwaniuk, 2013; Krilow & Iwaniuk, 2015), we have also observed no other males drumming at those logs for the rest of that season or the subsequent year. An absence of displacement amongst drumming males would suggest little competition for logs, further arguing against the need for drumming to be used in territorial defense. A second possible explanation for males not responding consistently to playbacks may be that display territories are smaller than a 30-40m radius and the playback was not being perceived as a territorial intruder. As mentioned above, I do not have any information on the size of drumming territories. If males have varying territory sizes, as in some having larger territories that place the speaker within their territory and others having smaller territories placing the speaker out of their territory, it would explain the seemingly random approach responses.

Rather than having a strictly territorial function, it is more likely that the drumming display is used primarily to attract mates and advertise a male’s location within the forest. Ruffed grouse are typically found at low density in forested environments (Rusch et al., 2000), making it difficult for males and females to find one another. Through the use of this low frequency drumming(Garcia, Charrier, Rendall, et al., 2012), a male can advertise his presence over long distances to potential mates. This means that the more time a male spends drumming, the better chance that male has of being detected by a female and thus of attracting a female to his log. Females then likely select a mate based upon morphological features the male displays in the full ‘cum Ruff display’. On two occasions, a female was observed approaching a drumming male. In both instances, the male left the log before the female was within 20 m. He rushed up to her with tail fanned and then into the cum Ruff display, which he maintained for at least 30 minutes. In neither case did this result in a copulation attempt, but these anecdotal observations highlight the importance of the visual display over drumming once a female approaches a drumming male.

Although my study provides some insight into how males use the drumming display, there are still many unknowns. First, do females prefer certain drumming signals and visit those males first? While the data suggest that males do not respond to different speeds of the drumming display it is possible that females are picking up on the drumming rate. It has been shown that females cover a large distance during the breeding season and may be traveling between males to assess them individually (Brander, 1967). Due to females being difficult to differentiate from males it is nearly impossible to tell if non-drumming birds are male or female without having them in hand. The few cases of males displaying to females is the only evidence I have of females attending a males drumming log, and these are too few to infer preferences for drumming rate. Second, do males that drum the most have higher reproductive success? Presumably a male that can drum more frequently has a higher chance of attracting a female to his log, improving his chance of copulation and reproductive success. Any time spent off of the drumming log may impose a cost on the individual if a female is in the area and they are not drumming. This would suggest that responding to nearby males (as in approaching) may not be beneficial, as the male has to stop drumming to locate an intruder reducing his drumming and chance of attracting a potential mate. In sum my data suggest that the drumming display of male ruffed grouse is primarily used to attract mates and mark a males' location within the forest.

CHAPTER THREE

EEXPERIMENT TWO: SEASONAL AND INDIVIDUAL VARIATION IN THE RUFFED GROUSE (*Bonasa umbellus*) DRUMMING DISPLAY

Abstract

Non-vocal sounds, or sonations, are commonly used in avian courtship displays, however, most of the research on them has focused on how these sounds are produced. Thus, the extent to which sonations are variable among and within individuals or if they reflect body size or condition has remained largely unexplored. The male ruffed grouse's (*Bonasa umbellus*) non-vocal drumming display exhibits individual variation allowing the possibility for individual identification, yet it is unknown if individual variation is consistent over time or if this variation reflects body size. 15 drumming male ruffed grouse were recorded over the 2013 – 2015 drumming seasons to determine when males are most active during the day and across seasons. I then analyzed the drumming behavior of 12 of these individuals across the day and multiple weeks to determine if individual variation in the drumming display is consistent. In 2016, 23 drumming males were recorded and trapped to compare drumming to measures of body size. My data corroborates previous reports of seasonal and daily peaks in drumming activity; however, individual variation in drumming behavior is not as consistent as previously reported. The temporal components of male drumming varies across the day with drumming rate increasing up to maximum drumming rate. While individual males reached a consistent maximum drumming rate, I found no correlations between drumming behavior and several measurements of body size. Overall my research shows seasonal and daily patterns in drumming behavior, while also describing a novel warm up pattern in the performance of a sonation across the day.

Introduction

Non-vocal sounds, or sonations, are commonly used in avian courtship displays (Bostwick, 2006; Clark, 2016). Despite how common non-vocal acoustic signals are, most of the research on them has focused on how these sounds are produced (Bostwick & Prum, 2005; Clark, 2008; Clark & Feo, 2008), with little known about how these sounds are used in courtship (Clark, 2016). In contrast to avian vocalizations, the amount of variability in sonation frequency or bioacoustics among and within individuals is largely unknown (but see Garcia, Charrier, Rendal, et al., 2012; Barske et al., 2011) . Similarly unclear is whether sonations reflect some aspect of a bird's body size or condition, as is the case with vocalizations. For example, lower frequency modulation in the Adélie penguin's (*Pygoscelis adeliae*) ecstatic display call is typical of larger males in better condition, which are also more successful in acquiring mates than smaller males (Marks et al., 2010). Similarly, constraints on syllable repetition and frequency bandwidth in birdsong are attributed to beak and body size in Darwin's finches (Podos, 2001). Although relationships between vocalizations and body size and/or condition are widespread, relating avian sonations with individual 'quality' or phenotype is the golden-collared manakin (*Manacus vitellanus*, hereafter manakins). Individual variation in the manakin's display is associated with cardiovascular function and motor skills (Barske et al., 2011). More specifically, males in better condition are faster at returning to a 'beard-up' posture in between wing-snaps than less successful males (Barske et al., 2011). Both display activity and aspects of 'choreography' of male manakins were significantly correlated with mating success, however, morphological measurements, such as body size or beard length, were not associated with mating success at all. Thus, females appear to be attending to performance of the display and not size or plumage of the male, but female attendance to sonations is unknown.

The ruffed grouse (*Bonasa umbellus*) is a useful species for understanding how sonations are used and the possible inter- and intra-individual variability in their production because they are largely avocal (Allen, 1934; Atwater & Schnell, 1989; Rusch et al., 2000). Unlike most other galliforms, male ruffed grouse do not vocalize as part of their courtship. Instead, they perform a wingbeat display known as ‘drumming’ during the breeding season, which consists of a stationary male rapidly producing a series of downward wing strokes over approximately 10-11 seconds (Archibald, 1976; Hjorth, 1970). Ruffed grouse drumming behavior is easy to observe and analyze due to site fidelity within individuals. Once a male has established himself on a drumming structure he will remain there for the entirety of the season, occasionally switching to a nearby, alternate log (Archibald, 1976; Aubin, 1972; Gullion, 1967). This allows the opportunity to record an individual’s drumming behavior over long periods of time to determine daily and seasonal variation within a sonation. Previous reports of when and how much males drum are based on relatively small data sets with inconsistent sampling methodology. For instance some authors only conducted fieldwork in the morning hours (Gullion, 1966; Palmer, 1969; Zimmerman & Gutierrez, 2007) or only on favorable days (Palmer, 1969). Archibald (1976) recorded male drumming activity across the day, but he relied on modified radio telemetry gear to monitor and record drumming behavior with little, if any, field observations. This was problematic due to the telemetry relying on rapid movements to detect when males where drumming, additionally inclement weather would affect radio reception limiting recordings in poor weather. Determining how much ruffed grouse drum throughout a day or season is important for relating drumming behavior with condition because males and/or females may be able to use the drumming display as a means of assessing the quality or body condition of a male.

A prerequisite for drumming behavior to reflect body size or condition is that it varies among individuals. Garcia, Charrier, Rendal, et al.(2012) documented that males vary in the number of wing beats produced within a display and the drumming rate of the display (wingbeats/sec.). Despite these initial findings, males were only recorded for 1-3 days and the bioacoustics analyses were limited primarily to early morning hours. Thus, whether the drumming is truly consistent within individuals throughout a day or the season is unknown. If drumming is inconsistent throughout the season, this could have implications for how the display is used during the breeding season and the extent to which drumming reflect a male's size or condition.

Given the lack of quantitative data on ruffed grouse drumming, the goals of this study were to address three main questions: 1) How much do ruffed grouse drum throughout a day and season? 2) How much does the drumming display vary among and within individuals? 3) Does individual variation in drumming reflect body size or condition? We address these questions through the use of long-term acoustic recordings of males over several breeding seasons.

Methods

Male Ruffed Grouse were studied near Buck Lake, Alberta Canada (2013-2015; 52.97º N, 114.77º W) and Castle Special Management Area, Alberta Canada (2015 - 2016; 49.41° N, 114.34° W) during the months of April and May. Males were located by listening for drumming along rural roads and ATV trails. Once located, drumming structures were marked with a handheld GPS unit (GPSMAP 64s, Garmin, Olathe, KS, USA) within 20m to limit disturbing birds (i.e. flushing them off their logs). For years 2013-2015, Song Meters SM2 and SM2+ (Wildlife Acoustics Inc, Maynard, MA, USA), long-term weatherproof acoustic recorders, were placed within 10 meters of the drumming log to record the focal male's drumming behavior for 23.5 hours every day. To minimize disturbance, batteries were changed every 3-5 days during the afternoon when males were typically displaying less or absent from their logs. Males were not individually marked, but they maintain the same drumming log(s) throughout the breeding season allowing the same bird to be recorded with minimal disturbance for extended periods of time (Archibald, 1976; Aubin, 1972; Gullion, 1967). Some males do have alternate logs that they may switch to during the breeding season, but they are often located within close proximity of their primary log (Gullion, 1967) and the drumming could still be recorded.

In 2016, Song Meters were deployed for 2 full mornings to collect acoustic data on the drumming displays of individual males. Once two days of drumming data had been collected, mirror traps (Gullion, 1966), lift nets (Fischer, 1974) and a CO_2 powered net gun (Advanced Weapons Technology Inc., La Quinta, CA, USA) were used to trap males. Several measurements were then made of these males to enable comparisons of body size and condition with aspects of their drumming behavior (see below).

Acoustic analyses

First, drumming displays were counted every hour for 7-37 days for 15 males recorded in 2013-2015 to determine how much males are drumming and when. Second, temporal components of drumming displays were analyzed using the pulse train analysis tool in Avisoft SASLab Pro (v5.1, Avisoft Bioacoustics, Berlin, Germany). For all pulse train analyses, the initial four pulses (quartet) were excluded. The quartet is a series of four low amplitude wing beats at the beginning of each drumming display (Figure 3.1). This portion of the display is often masked by background noise and difficult to analyze from Song Meter recordings and therefore was excluded to increase the sample size across and within individuals. Only drumming displays with high signal to noise ratios were included in pulse train analyses. Both drumming rate (beats per second) and number of drumbeats were measured for each drumming display. As discussed above, these two measurements vary among individual males (Garcia, Charrier, Rendall, et al., 2012) and are therefore likely to reflect body size.

To test for variability in drumming rate and number of wing beats within males, two males were sampled throughout the day (6 drumming displays analyzed per hour) for a week. From these two males, we determined that after 0900, there is little change in drumming rate (see below). Further, males are more active throughout morning hours and signal to noise ratio decreases throughout the day due to wind, bird song and calls, and recreational vehicles in the area. As a result, the recordings are of higher quality during morning hours. Data for afternoon and evening drumming was also much more variable resulting in less consistent drumming data. Recording quality was sufficient to analyze 12 individuals from 0000-0900. For these 12 males, we analyzed 6 drumming displays every hour for each recorded day.

In 2016, 23 males were recorded for 2-3 days in order to then set traps and test for correlations between drumming behavior and body size. For these 2016 males, six drumming displays were analyzed each hour from 0000-0900. The displays analyzed were spaced approximately 10 minutes apart and dependent on a high signal to noise ratio to ensure accurate measurements.

Morphometric measurements

Bioacoustic features of vocalizations are often associated with body size and condition (Kagawa & Soma, 2013; Marks et al., 2010; Penteriani, 2003). To test whether drumming rate and number of drumbeats is correlated with body size, we took several measurements of males that were trapped in 2016. Traditional measures of fitness reflect some measure of body size, often through a multivariate analysis because a single measurement often does not necessarily reflect all components of body size (Rising & Somers, 1989; Telleria, La Hera, & Perez-Tris, 2013). Measurements included body mass as well as wing chord, tarsus and tail lengths (Telleria et al., 2013). Body mass was measured by weighing birds in a bag with a 1000g (±5g) spring scale (PESOLA AG, Schindellegi, Switzerland). Tarsus length was measured using plastic calipers (± 0.5mm) and wing chord and tail length were measure using a wing rule (± 1mm). In addition to these traditional measurements, we also measured chest girth using a soft tailor's measuring tape (±2mm). One end of the measuring tape was placed in a wing pit and then extended across the chest just below the furculum of the bird to the other wing pit.

The wing pit was located by first feeling underneath the wing for featherless skin and then locating the joint where the humerus meets the glenoid fossa. The chest girth measurement was taken twice for all birds. One individual performed all measurements.

Statistical Analyses

Prior to any longitudinal analyses, dates were converted to the Julian calendar system. Within the 12 males for which we sampled 6 drumming displays every hour from 0000-0900, I ran ANOVAs on the number of drumbeats and drumming rate across a single day to see if there was any variation within a day with hour treated as an ordinal variable. The day analyzed for each male was selected during peak activity (approximately last week of April) and based upon the quality of recordings and drumming activity. Four individuals (RUGR527, RUGR526, RUGR430 and RUGR427) did not have recordings during peak activity so days were selected solely upon the quality of recordings and drumming activity. To analyze seasonal trends in data, another ANOVA was performed on drumbeats and drumming rate across the season for individuals with at least two weeks of data (n = 11), using week as a grouping variable. Because week and hour could potentially interact to affect drumbeats and drumming rate, a MANOVA was performed on 7 males (3 males with 4 weeks of data, 4 males with two weeks of data) with week, hour and the interaction term as independent variables.

To compare body size to drumming behavior, I first ran a principal components analysis (PCA) on all body measurements. Principal components 1 and 2 (PC1 and PC2) were retained, having eigenvalues above 1, explaining 47.24% and 22.48% of the variation respectively for measures of body size (Table 3.1). All of the measurements had positive loadings on PC1, indicating that it reflected overall body size (Table 3.1). PC2 had positive loadings on wing chord and tail length measurements, the rest were negative showing that PC2 reflects relative feather length (Table 3.1). Finally, correlations were performed on maximum drumming rate and number of drumbeats against all five body size measurements, as well as PC1 and PC2.

Results

Daily and Seasonal Variation in Drumming Activity

Male ruffed grouse drum throughout the day, with the majority of activity occurring in the morning or evening hours. The total number of drumming displays produced in a day can exceed 300 during the peak week (Figure 3.2). Daily drumming activity peaks approximately 1 hour before sunrise, with a smaller, secondary peak just prior to sunset. Morning drumming activity peaks around 30 drumming displays in an hour between 0500 and 0600. In 2013 and 2014, drumming activity peaked on week 18 (approximately the last week of April), but in 2015 the peak in activity occurred a week earlier (Figure 3.2).

Figure 3.3 shows drumming activity averaged across 5 males recorded in 2015. Peak activity in drumming occurred between weeks 17 and 118 (approximately days 111 – 118). During peak activity two drops can be observed on days 112 and 116, which received heavy rain. An additional drop in activity occurred on day 134, which reflects a long weekend when there was increased camping and off highway vehicle (OHV) activity in the area.

Intra-Individual Variation in Drumming Rate and Drum Beats

Drumming rate and the number of drumbeats varied significantly between the hours of 0000 and 0900 for almost all of the 12 males that were analyzed. 9 out of 12 individuals decreased significantly the number of drumbeats in their display (Table 3.2). The change in drumbeats varied by approximately 0.67 to 3.17 drumbeats (or a 1.6 - 8.1% difference). The drumming rate of all 12 birds increased significantly from 2 – 7.1% (Table 3.2). Thus, males begin each day drumming at a lower rate with more drumbeats and increase their speed and decrease drumbeats as the morning progresses.

Drumming rate and the number of drumbeats also varied significantly across weeks. For males that were recorded for three weeks, the number of drumbeats and drumming rate also changed significantly across weeks (Table 3.3). The number of drumbeats decreased by 0.19 – 0.39 beats for the three birds. Two males decreased their drumming rate by 0.6-0.8%, but the third male increased his drumming rate by 1.1%. For the males with two weeks of data, two individuals significantly decreased their number of drumbeats one of which had a significant change in drumming rate (RUGR502, -0.6% change; Table 3). A third male had a significant change in drumming rate (RUGR402, 0.2% change; Table 3); however, had no change in drumbeats. For individuals in which the interaction effect of hour and week was significant, a Tukey-Kramer HSD post-hoc test was performed (Table 3.4). Post-hoc tests revealed that the majority of significant differences comparing drum beats and drumming rate across weeks was from comparisons of separate hours. For example hour 8 of week 17 was significantly different from hour 4 of week 19. Little to no differences were observed for the same hour compared across weeks (e.g. hour 8 of both week 17 and week 18). In cases where there was a difference in either drumbeats or drumming rate for the same hour across weeks, both positive and negative differences were observed (Table 3.4).

Two males for which we had a large number of high quality recordings for several days (n = 52) were analyzed in greater detail to determine the rate of change in drumming rate. To analyze the rate of change in the drumming rate across the day I first sampled 6 drumming displays from each hour of the day using the same selection criteria for pulse train analyses as above. Following recommendations and examples from Buzatto et al., 2012; Knell, 2009; Wilson, et al., 2014 for fitting non-linear curves, I first plotted drumming rate measurements by hour of the day and determined there was a continuous, non-linear relationship (Figure 3.4). Of the several models that we initially screened, a logistic four parameter model (logistic 4P) provided the best fit to the data based on Akaike Information Criteria correlations (AICc) (Table 3.5). Although the logistic 4P model provided the best fit across both individuals, the model parameters varied across birds (Figure 3.5). I then tested whether the same curves applied to daily changes in drumming rate across weeks based on recordings from 0000-0900 hrs MDT. Days were sampled only from 0000-0900 due to the aforementioned inconsistency of afternoon drumming and that drumming rate remains consistent after 0900 in our analyses throughout the entire day (Figure 3.4a,b). While the logistic 4P model was the best fit for most of the days sampled, it did not fit every day. The logistic 4P model fit 37.5% of the time for RUGR501 and 42.9% of the time for RUGR506 (Figure 4c,d); the next best models were cubic and quartic functions (Table 3.6). Even though the logistic 4P model did not fit the change in drumming rate every day, alternate models, such as the cubic functions in Figure 3.4 (panels E and F), still showed the trend for birds to start slower and increase to a maximum drumming rate before 0900.

Individual Variation in Relation to Body Size and Condition

Although drumming rate decreased with increasing body size (Figure 3.5), no significant correlations were detected between drumming rate and measurements of body size (Table 3.7). Similarly, there was a tendency for larger males to produce fewer drumbeats, but none of these correlations were significant (Figure 3.5; Table 3.7). Drumming rate and drumbeats were significantly correlated with one another; however, there was no significant relationship between the interaction of the two and body size measurements (Table 3.8).

Discussion

Daily and Seasonal Patterns of Drumming Activity

My data corroborates past research suggesting that male ruffed grouse are most actively drumming in the morning, 1-2 hours before sunrise (Archibald, 1974; Palmer, 1969; Zimmerman & Gutierrez, 2007). Daily peaks in morning activity supports a strong photoperiod effect on male ruffed grouse drumming as males have daily cycles in activity relating to sunrise and sunset (Figure 3.3). While the evening peak in drumming is not as defined as morning peaks, there is an obvious increase in activity prior to sunset that recedes sometime after dusk (Figure 3.3). These morning and evening patterns persist across multiple seasons and adjust with the changing photoperiods as sunrise becomes earlier and sunset much later. In addition to daily activity periods corresponding with sunrise and sunset cycles, seasonal peak activity is fairly consistent, with peak drumming activity occurring sometime around week 18 of the calendar year (Figure 3.3). While drumming males in 2015 did show peak activity starting in week 17, day-to-day activity shows there was only a slight shift in average daily activity by a few days (Figure 3.4). This shift in seasonal peak activity is most likely due to the warm winter and early spring experienced that year (Gullion, 1966). While correlations between drumming behavior and weather have yet to be tested, the 2015 field season was 'uncharacteristically' warmer compared to past years and as a result had much earlier snowmelt. This anecdotal evidence would suggest some support for Gullion's (1966) claim that the start of the drumming season coincides with snowmelt. In addition to slight shift in seasonal peak activity we witnessed decreases in daily activity due to rainy weather (Figure 3.4). In sum, drumming males show consistent trends in when peak activity occurs with some variability due to weather.

In addition to effects of weather, microclimate may have some effect on drumming behavior. Specifically, birds may be altering their drumming to deal with slight variations in the immediate area of their drumming structure. Increasing temperatures and humidity levels within nest boxes increase the intensity of chick’s calls to offset the loss of sound pressure due to increased moisture levels in the air (Swaddle, Kight, Perera, Davila-Reyes, & Sikora, 2012). It is possible that ruffed grouse may be altering their own drumming due to changes in temperature as the sun rises.

Currently it is recommended that ruffed grouse drumming surveys be conducted from April to early May, on mornings with favorable conditions and experiencing rapid temperature increases (Zimmerman & Gutierrez, 2007). My results would agree that drumming surveys should be conducted from April to early May as we found birds consistently peaking in activity around the last week of April. However, as I have shown there may be some fluctuation based on seasonal temperatures and snowfall, which could create earlier peaks in seasonal activity. Atwater and Schnell (1989) mention that the time of drumming surveys fluctuates from 35 – 45 minutes prior to sunrise to an hour or two after sunrise with four minute stops every mile. I recommend that surveys begin at least 1 hour before sunrise as this is when males are most actively displaying. In addition, the amount of time spent stopped should be increased after sunrise as males are still actively displaying, but the interval between drumming displays is often greater than four minutes. Our data also suggest that evening drumming counts just prior to sunset may prove useful. Finally, I concur that drumming counts be conducted on favorable days that are free of heavy rain and strong winds. Although grouse will continue drumming in the rain, their activity is greatly reduced and rain/wind can greatly affect the ability to hear the low frequency drumming signal (pers. observation).

Intra-individual Variability

My data reveal that the temporal components of the drumming display are not stable throughout the day; rather drumming rate increases throughout the morning reaching a peak point before stabilizing. Similarly, drumbeats produced in a display change, but they decrease throughout the day as drumming rate increases. While these changes are significant, the actual change is relatively small (less than 10% in most cases). In addition to daily differences, drumbeats and drumming rate varied across weeks for individuals (Table 3.3), but the effect size was much lower and comparisons of the same hour of the day across weeks revealed very few differences (Table 3.4). While the temporal components of drumming do not appear to be as consistent between individuals as previously thought (Garcia, Charrier, Rendall, et al., 2012), males do have consistent changes in drumming rate across the day. For example RUGR501 peaks around 5.05 drumbeats/sec while RUGR506 peaks around 5.22 drumbeats/sec (Figure 3.4). So, while males do change drumming behavior across the day they maintain consistent patterns (maximum drumming rate) retaining individuality in the signal. There may be some variation in the change of drumming rate across the morning for individuals, but this does not appear to be consistent throughout the season as neither individual tested for daily changes in drumming fit any one single curve function.

While daily changes in drumming rate did not consistently fit any single model it did show a similar pattern across the day. That is, all males start at a slower drumming rate and then increase up to a maximum where they appear to remain stable throughout the day and/or morning. This pattern of daily changes in drumming rate appears to be similar to a ‘warm up’ observed in athletes before competitions or sports events, where individuals undergo some preparatory exercise in order to reach some maximum level of performance during competition or training (for review see Fradkin, Zasryn et al., 2010). Male ruffed grouse appear to receive the same benefits as a controlled warm up routine utilized by athletes by slowly building up to a peak drumming rate in the morning and then sustaining that drumming rate. Animals requiring some warm up period to reach a peak performance level, whether it be a display or other behavior, would seem rather intuitive. However, there are few examples in the literature demonstrating a warm up pattern or change in signaling behavior across time. One example can be seen in tungara frogs (*Engystomops pustulosus*), one of the more intensively studied species in animal communication (Baugh, Hoke, & Ryan, 2012). Male tungara frogs begin calling at slower rates, with shorter durations, and lower amplitudes. As their vocal sac inflates, they increase call rates, duration, and amplitude with consecutive calling bouts, which likely increases their attractiveness to females (Pauly, Bernal, Rand, & Ryan, 2006). A second example of daily variation in a communication signal is the occurrence of oscillations in fundamental frequency (FF) and amplitude of undirected song in the zebra finch (*Taeniopygia guttata*) (Wood et al., 2013). Both FF and amplitude of zebra finch song increases throughout the morning, to a maximum during the afternoon and then decreases through the evening. This increase is not, however, correlated with peaks in daily singing behavior. The daily increases in FF and amplitude could be driven by physiological factors, such as body temperature and melatonin, which may drive daily cycles in activity (Wood et al., 2013).

Despite these two examples, daily changes in the structure of communication signals remain relatively unexplored, and to my knowledge no examples have been reported in sonations. Like the change in song observed in zebra finches, daily changes in ruffed grouse drumming activity show males reaching peak drumming rates after early morning when they are most active. While it is possible that physiological conditions controlling daily cycles in motor activity could be acting on the ruffed grouse, it is more likely that males are increasing drumming rate through continuous performance of the exercise. Unlike vocalizations, the drumming display involves most of the body and recruits larger muscles as males adjust posture and wing beat behavior to remain stationary while producing the loud drumming sound. Through continued displaying, males are working their muscles more, very much like a track sprinter would before competing in a race, and can ultimately improve their performance to an individual-specific maximum drumming rate. Additionally males are increasing in drumming rate around the same time they are most actively displaying, which would further support the idea that drumming rate increases from early morning due to continued displaying. While it is presently unknown if males benefit from increasing their drumming rate throughout the morning, it provides an opportunity to further investigate how sonations are used in courtship. This change in drumming rate could improve mating success. Faster male golden-collared manakins achieve higher mating success than slower individuals (Fusani, Barske, et al., 2014), so achieving a maximum drumming rate may be a signal that female grouse select for from potential mates.

If females are using drumming rate for some aspect of mate selection, they are unlikely to be basing their preference on body size. Even though a negative association was observed between both drumbeats and drumming rate with body mass, neither was significant. The lack of a relationship between drumbeat and drumming rate and male body size does not mean that male quality is not reflected in some aspect of drumming behavior. Female ruffed grouse may be able to distinguish subtle differences in drumming rate similar to female golden-collared manakins differentiating subtle differences in the motor performance of the male courtship display (Barske et al., 2011). However, measures of body size may not be appropriate, body condition was not assessed for males and some measure of relative size in muscle mass such as the pectoral muscles might be correlated with faster drumming. Additionally persistence in drumming (the number of displays produced over time and duration of time spent drumming) could be a better cue for females than drumming rate.

Conclusion

In sum, my research corroborates past claims of researchers that drumming activity peaks around the same time of year and is likely affected by snowmelt. However I also demonstrate that males can drum throughout the day and produce a second smaller peak in daily activity in the evening. I also showed that while Garcia, Charrier, Rendal, et al.'s (2012) initial reports of individual variation being stable is not entirely accurate; males do consistently increase their drumming rate up to a maximum and maintain that maximum throughout the day. That is that while drumming rate changes across the day, individual's maximum drumming rate appears consistent. This daily change in drumming behavior, or warm up, is not well reported in the literature and appears to be the first example reported for a sonation. Measures of body size were not correlated with drumming behavior, however, the daily pattern of males increasing drumming rate may still serve some function in mate attraction and/or selection. Even with the lack of a correlation between body size and drumming female grouse may be judging male drumming through selection for subtle differences in motor skills such as a faster drumming rate.

CHAPTER FOUR: GENERAL DISCUSSION

Grouse Biology and Behavior

The results of the playback experiment in Chapter 2 suggests that ruffed grouse do not use the drumming display strictly for territorial defense, as they did not approach more than would be expected from chance and did not change their drumming behavior during and/or after playbacks. However, there is evidence that some males respond to drumming, indicating that the signal may still stimulate males in some form. Approximately half of the grouse studied (38/65) were categorized as grouped, meaning that you could hear one or more drumming males from a focal male's drumming structure. Additionally in the 2016 field season a group of 5 males were drumming within a short distance of each other (mean: 38.8 +/- 0.55 m). As stated by Gullion (1967), this grouping behavior suggests a type of exploded lek behavior. Like truly lekking species of grouse (e.g., sage grouse, *Centrocercus urophasianus*), ruffed grouse have high site fidelity for their drumming structures, where once established, males rarely move structures and if they do, never far from their original log (Gullion, 1967). Further, there is evidence showing the use of perennial drumming structures year after year in which first year males were found using the same logs as males from previous years (Gullion, 1967). The difficulty in determining if ruffed grouse exhibit exploded lekking behavior lies in the undefined boundaries of the drumming territory. Lekking species often have higher densities and smaller territories compared to species considered to be in exploded leks (Foster, 1983). For example male sage grouse occupy display courts between 13-85 m^2 (Wiley, 1973) compared to those of the little bustard (*Tetrax tetrax*) a species found in exploded leks, that has territories of 18.7 +/- 16.2 ha (Jiguet, Arroyo, &

Bretagnolle, 2000). However, this is not the only issue with identifying exploded lek behavior in ruffed grouse. While nearly half of my study population was considered grouped, the rest remained solitary. It is possible that the number of birds grouped together is dependent on population density. Over the 2012-2015 field seasons, groupings were found more frequently with the most grouped birds located in 2015. The 2015 field season also involved a high population density of drumming males compared to previous field seasons.

With what little we know of female ruffed grouse movements during the field season, it appears that they cover a lot of ground visiting multiple males over the course of a drumming season (Brander, 1967). It would be of benefit for males to group together in the hopes of attracting a female to their location, with more males in an area there may be greater odds of females visiting them compared to a solitary male. While no research has been done to investigate propagation distance of the signal, it is bidirectional(Garcia, Charrier, & Iwaniuk, 2012). That is the decibel level is highest in front and immediately behind a displaying male (Garcia, Charrier, Rendall, et al., 2012). This and personal experience in locating drumming males suggests that the signal is limited in propagation distance solely based upon on the direction the male is facing. Often when trying to locate males, we would stumble upon a bird that was much closer than previously thought due to him displaying in a direction perpendicular to our approach path. While galliform birds have exceptional low frequency hearing (Corfield et al., 2013; Freeman & Hare, 2015), making ruffed grouse suited for hearing the low frequency drumming display, they still may have difficulty localizing the signal. The males that approached the speaker in the playback experiment often reached the general vicinity of the speaker rather quickly, but whether they are equally capable of locating a more distant signal is unknown. Given the problems associated with localizing low frequency sounds in general (Bradbury & Vehrencamp, 2011) it would seem that having more males displaying within an area may be beneficial in increasing the chance of attracting a female to surrounding area. However, instead of suggesting that ruffed grouse arrange themselves in an exploded lek system, I would suggest that they behave in a more intermediate stage between solitary displaying and lekking. Specifically, males will perform their drumming as a solitary individual and in loose “groups”. This is most likely dependent on the population size in the given drumming season, with high density years producing more groups of birds. Given that some males do respond to the drumming display, they may be drawn to display around an individual who has already established himself for the season, thus creating groups of birds.

Playback experiments suggest that males do not change drumming behavior in response to an unknown male in any way to suggest territorial defense and further, males have been observed displaying within 30m of each other. Given the basal position of ruffed grouse in the evolution of grouse and ptarmigan (Drovetski, 2002) ruffed grouse may be exhibiting an intermediate stage to lekking behavior; in which tolerance towards other males in grouped display sites and high site fidelity may be necessary precursors for the evolution of lekking behavior.

Individual and seasonal variation results show that males cumulatively reach peak display activity within the same week year after year in consistent fashion (Figure 3.2). As discussed in Chapter 3, the results corroborate previous claims that the peak in daily activity occurs just prior to sunrise (Archibald, 1976; Palmer, 1969; Zimmerman &

Gutierrez, 2007). In addition to morning peak activity, a smaller evening peak in drumming activity was observed, although it is less consistent than morning peak activity. Also within Chapter 3, I showed that individual variation within the temporal components of the display (drumbeats and drumming rate) is not as consistent as previously thought (Garcia, Charrier, Rendall, et al., 2012). Rather, drumbeats decrease and drumming rate speeds up throughout the course of the morning. The drumming rate of individuals exhibits a ‘warm-up’ pattern through the morning hours. Seeing as drumming relies on working pectoral muscles continuously throughout the day, it makes sense that birds warm up to a peak in drumming speed. Very much like a professional athlete, ruffed grouse are likely warming up their muscles and reaching peak performance as the morning progresses. While this pattern is seen amongst individuals, it too is not consistent day-to-day. The rate of increase seems to vary between days and could be a result of variation in morning temperatures as some days experienced little change compared to others; however, this has yet to be tested. Additionally it is unknown if there is a benefit to increasing drumming rate throughout the morning.

Initial analyses failed to show correlations between measures of body size and drumming behavior. There is potentially a correlation between body mass and drumming rate, however this trend was insignificant. Body mass had a negative relationship with drumming rate, so it would not be useful for males to increase drumming rate if this correlation could be heard by other birds (i.e. females looking for a mate, or warding off intruding males). If drumming is indeed useful as an honest signal for body size it would be expected that changing the speed of drumming in playback experiments would result in males consistently changing their approach behavior based on drumming speed. For example, if the speed of the drumming could be used to assess the size of a male and individuals were using it in contest like behavior as described by Gullion (1967), slower drumming rates could potentially indicate a larger male and reduce a male's likelihood of approaching in order to avoid a potentially costly fight. However, the speed of a drumming display played to males had no effect on their likelihood to approach the speaker. This does not necessarily mean that drumming rate and body mass are not correlated; rather it is likely that males are not picking up on these differences and/or association to male size. This also does not mean that there is no benefit in increasing drumming rate throughout the morning. It is possible that by increasing drumming rate, males are increasing the amplitude of their display and increasing its effective distance. As morning breaks, increased background noise affects the propagation of drumming (i.e. increased song/calls from other birds, wind, etc.). If ruffed grouse can improve the amplitude of their drumming it may help increase signal propagation through the environment.

Function and use of Sonations

One of the key questions of studying sonations is determining the function of non-vocal acoustic signals produced in courtship displays and how they compare to vocal signals, such as calls and song. When looking at when ruffed grouse are most actively displaying, the data show that ruffed grouse are capable of drumming throughout the day, up to 21 hours continuously during peak activity (figure 3.2). However, drumming is most consistent 1-2 hours prior to sunrise and then again nearing dusk. These morning and evening peaks in activity resemble those of dawn and dusk choruses observed in songbirds (Dabelsteen & Mathevon, 2002). Similarly snipe (*Gallinago* s*pp*.) winnowing, a non-vocal sound produced during a flight display, follows similar daily patterns peaking in activity during dusk (1900-2200) and late night (0300-0500; Downs and Anderson 1999). These two periods of increased display activity are similar to that of drumming peak activity periods. Increased activity in communicative sound production, whether vocal or non-vocal, has been found to increase signal propagation, as environmental factors affecting signal attenuation through the environment are minimal (Dabelsteen & Mathevon, 2002). This suggests that drumming behavior could have evolved, similarly to birdsong, to take advantage of morning and evening hours to increase the signal effectiveness. The low frequency of the drumming displays helps it to propagate through a forested environment(Bradbury & Vehrencamp, 2011); however this also causes the signal to be masked by background noise as morning progresses. Additionally ruffed grouse may receive benefits displaying most actively during early morning by starting after nocturnal predators (owls) are active and before diurnal predators (hawks) become active.

While sonations have similar patterns in production across the day to vocalizations, there is still the question of whether they serve similar functions to vocalizations. In songbirds, dawn and dusk choruses are typically associated with territory defense and mate attraction (Slagsvold, Dale, & Sætre, 1994). My research shows that males likely do not use their drumming display solely for territorial defense. Instead, drumming is likely used to primarily attract females and mark a male's position within the environment: however, drumming may still serve some function in territory defense as males did respond to drumming. This would make drumming similar in function to contact calls observed in various songbirds during the breeding season. A similar use of a non-vocal display is seen in the golden-collared manakins; the wing snap displays along with vocalizations attract females and mark a male's location within the lek (Fusani, Barske, et al., 2014). Additionally female manakins select for males who perform their wing snap display faster, with males that assume a faster 'beard up display' being selected for (Barske et al., 2011). Ruffed grouse appear to use similar tactics, however relying solely on a non-vocal signal, using drumming to attract a female and then performing an elaborate visual display to court the female (see figure 2.3). It is likely that females are primarily relying on the visual display when selecting for potential mates, however, this remains untested. So, in essence the drumming display acts as a long distance acoustic signal to attract mates to a male's location, after which visual displays are used to entice prospective mates.

Future Research

While this research questions the validity of drumming as a territorial signal, it is possible that drumming playbacks were being perceived outside of a male's territory. Data from displaying males shows drumming males approximately 30 meters apart and most of our playbacks were administered even further than this (38.8 +/- 0.55m). Research in bird song has shown that birds can range signals to determine if an intruder is potentially within their territory (Naguib & Wiley, 2001). It is possible that male ruffed grouse are also capable of ranging the drumming of other males and our speakers were outside of typical territory sizes. During the 2016 field season, playbacks were used to try and trap birds by luring them into a trapping area. To draw males in, the speaker was placed within 25 meters of their drumming structure. Of the four males played back to, all four approached the speaker. This is a small sample size, but hints there may be a ‘comfort’ zone in which a drumming male is deemed too close. Therefore the speakers used in the playback design may have been at the outer limits of established territories, resulting in chance approach behavior. To investigate whether or not ruffed grouse are ranging, a more elaborate playback design would need to be incorporated. Multiple trials over a series of days with the speaker placed at varying distances and locations around drumming males could aid in establishing drumming territory size by determining at what distance males begin to approach. In addition to playback experiments, signal propagation experiments may prove useful in determining the effective distance a drumming signal covers. Signal propagation and the directionality of the drumming display may play a role in how grouped males compare to solitary males in attracting females.

Intra-individual variation within the drumming display is not as consistent as previously thought (Garcia, Charrier, Rendall, et al., 2012), however, it does differentiate between individuals in peak drumming rate achieved. While playback experiments failed to show that males react differently to speed of the drumming display, it is still possible that females may be capable of picking up differences in temporal variation within the display. It is likely that females are using the drumming display to locate males and then selecting potential mates based on their cum Ruff display. However, in instances where there might be two or males within hearing distance of each other, females may be selecting whom they approach first on subtle variation with the drumming displays.

Summary

My thesis research on the drumming display of ruffed grouse provides evidence for a sonation exhibiting daily and seasonal patterns similar to those observed in song. Morning and evening displaying likely has the same benefit for acoustic signals, regardless of the mode of production, by maximizing propagation of the signal through the environment. While my data fail to show support for the drumming display being used in territorial defense, it does stimulate some individuals and can provoke an approach. This suggests that drumming is likely used as an advertisement signal, broadcasting a male’s location and attracting females. While it is unclear if males are able to distinguish differences in drumming behavior (drumbeats and drumming rate) there is potential for some components to relate to body condition as males increase drumming rate throughout the morning up to a maximum speed. It therefore remains possible for females to potentially select for drumming rate speeds while visiting drumming males. Overall, my data suggest that the sonation used by male ruffed grouse shares similarities to vocalizations, such as attracting females and broadcasting a male’s position within the environment. However, sonations may be limited as an indicator of body size as neither ruffed grouse nor golden-collared manakins displays correlated with body size. Instead sonations may give indication to body condition rather than just overall size.

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Table 2.1. Approach data for playbacks performed on 65 males from 2012-2015, total number of approaches were broken down by category (drumming rate, grouping pattern and color morph). Total frequency of approaches and no approaches are reported for each category as well as the p-value for the Fisher's exact tests.

	Approach	**No approach**	**Total**	**p-value**
Overall males	37	28	65	0.48
Drumming rate				
Slow	16	16	32	0.80
Fast	14	18	32	
Grouping pattern				
solitary	13	14	27	0.45
grouped	23	15	38	
Color morph*				
Red	15	7	22	0.18
Grey	19	21	40	

* note that three males could not be observed closely enough to accurately determine color morph and were therefore excluded from this analysis.

Table 2.2. Approach data for 32 males subjected to two playback trials (2014-2015). The number of males that did not approach, approached once or approached both playbacks was not significantly different. Approaches are broken down by category (grouping pattern and color morph), p-values are reported from Fisher's exact tests.

	0 approaches	**1 approaches**	**2 approaches**	**Total**	**p-value**
Overall males	13	8	11	32	0.17
Grouping pattern					
Grouped	10	4	4	18	0.17
Solitary	3	4	7	14	
Color morph					
Red	4	4	7	15	0.30
Grey	9	4	4	17	

Table 2.3. The results of F-tests comparing the mean interval lengths between drumming displays before, during and after playbacks for males with data available for two playbacks. Tukey-Kramer post-hoc tests were performed for p values showing significant differences between groups. Differences between groups are denoted in the post-hoc column using greater than (>) or less than (<) signs to compare interval length between drumming displays before (B), during (D), and after (A) playbacks.

ID	Playback	F	DF	P	Post-hoc
502	slow	0.09	2,23	0.91	
502	fast	1.56	2,22	0.23	
504	slow	12.07	2,17	<0.01	A>D, B<A
504	fast	15.25	2,26	<0.01	B<D, B<A
507	fast	1.59	2,41	0.22	
507	slow	2.31	2,47	0.11	
509	slow	0.31	2,40	0.73	
509	fast	11.26	2,42	<0.01	B<A
514	fast	16.85	2,55	<0.01	B<A
514	slow	10.39	2,59	<0.01	D<A, B<A
522	fast	5.68	2,31	0.01	B<A
522	slow	24.03	2,41	<0.01	B<D, B<A
402	slow	3.09	2,19	0.07	
402	fast	46.54	2,68	<0.01	D<A, B<A
415	slow	10.81	2,49	<0.01	B<D, B<A
415	fast	0.35	2,36	0.70	
423	fast	1.98	2,21	0.16	
423	slow	0.34	2,31	0.71	
430	slow	0.26	2,28	0.77	
430	fast	69.88	2,44	<0.01	B<D<A
431	fast	4.49	2,56	0.02	D<A, B<A
431	slow	2.24	1,24	0.13	

Table 2.4. The results of F-tests comparing the mean interval duration between drumming displays before, during and after playbacks for males with data available for only one playback trial. Tukey-Kramer post-hoc tests were performed for p values showing significant differences between groups. Differences between groups are denoted in the post-hoc column using greater than (>) or less than (<) signs to compare interval length between drumming displays before (B), during (D), and after (A) playbacks. Single asterisks denote that data was not sufficient or unavailable for second playback on the designated individual.

ID	F	DF	P	Post-hoc
503	0.96	2,23	0.40	
505	5.68	2,15	0.01	B<A
506	16.47	2,48	<0.01	B<A
523	20.64	2,42	<0.01	B<D, B<A
524	2.03	2,33	0.15	
526	25.53	2,53	<0.01	D<A, B<A
411	22.80	2,36	<0.01	B<D, B<A
413	1.84	1,14	0.20	
419	30.04	2,26	<0.01	B<D, B<A
424	2.29	2,42	0.11	
309	1.90	2,19	0.18	
310	0.47	2,26	0.63	
312	0.00	1,15	9.89	
314	2.15	2,41	0.13	
317	5.50	2,33	0.01	B<D, B<A
318	2.44	2,34	0.10	
321	0.04	2,56	0.96	
323	0.35	2,47	0.71	
324	1.74	2,30	0.19	
325	3.71	2,72	0.03	B<D
326	0.75	2,37	0.46	
327	1.01	2,66	0.37	
333	10.85	2,41	<0.01	B<D, B<A

Table 2.5. The results of F-tests comparing mean drumming rate before, during and after playbacks for males with data available for two playback tests. Tukey-Kramer post-hoc tests were performed for p values showing significant differences between groups. Differences between groups are denoted in the post-hoc column using greater than (>) or less than (<) signs to compare interval length between drumming displays before (B), during (D), and after (A) playbacks.

ID	Playback	F	DF	P	Post-hoc
502	slow	0.03	2,15	0.97	
502	fast	0.41	2,12	0.67	
504	slow	0.06	2,12	0.94	
504	fast	3.83	2,14	0.05	
506	fast	2.36	2,12	0.14	
506	slow	6.44	2,15	0.01	B<D
507	fast	0.15	2,14	0.86	
507	slow	0.50	2,15	0.62	
509	slow	0.29	2,14	0.75	
509	fast	7.19	2,13	0.01	B<A
514	fast	11.27	2,15	<0.01	B<D, B<A
514	slow	6.43	2,15	0.01	B<A
522	fast	0.20	2,15	0.82	
522	slow	2.13	2,15	0.15	
402	slow	5.09	2,11	0.03	B<D
402	fast	40.34	2,15	<0.01	B<D<A
411	slow	1.40	2,14	0.28	
411	fast	3.78	2,13	0.05	
415	slow	7.31	2,15	0.01	B<D, D>A
415	fast	0.46	2,15	0.64	
423	fast	2.20	2,13	0.15	
423	slow	2.98	2,15	0.08	
430	slow	1.09	2,14	0.36	
430	fast	0.36	2,15	0.70	
431	fast	12.62	2,15	<0.01	B<D, D>A
431	slow	2.17	2,13	0.15	
432	fast	3.64	2,10	0.07	
432	slow	6.21	2,12	0.01	B<D

Table 2.6. The results of F-tests comparing mean drumming rate before, during and after playbacks for males with data available for only one playback trial. Tukey-Kramer post-hoc tests were performed for p values showing significant differences between groups. Differences between groups are denoted in the post-hoc column using greater than (>) or less than (<) signs to compare interval length between drumming displays before (B), during (D), and after (A) playbacks. Single asterisks denote that data was not sufficient or unavailable for second playback on the designated individual.

ID	F	DF	P	Post-hoc
501	4.94	2,10	0.03	B<A
503	9.81	2,15	<0.01	D>A, B>A
505	6.88	2,11	0.01	B<A
523	11.09	2,11	<0.01	B>D, D>A
524	2.23	2,15	0.14	
525	0.33	2,12	0.73	
526	3.11	2,15	0.07	
418	5.96	2,12	0.02	D>A
419	0.59	2,14	0.57	
422	2.69	2,12	0.11	
428	1.21	2,12	0.33	
309	0.69	2,12	0.52	
310	0.10	2,13	0.91	
312	8.87	1,9	0.02	B<A
314	1.26	2,15	0.31	
317	9.41	2,15	<0.01	D>A, B<A
318	1.23	2,15	0.32	
321	1.53	2,15	0.25	
323	7.19	2,15	0.01	D>A
324	2.76	2,13	0.10	
325	0.85	2,15	0.45	
326	0.71	2,15	0.51	
327	4.20	2,15	0.04	
333	4.48	2,15	0.03	B<D
202	3.93	2,32	0.03	B<D
203	0.28	2,14	0.76	
205	0.79	2,15	0.47	
207	7.71	2,17	<0.01	B>D, B>A
209	3.61	2,20	0.05	
211	6.48	2,19	0.01	B<A, D<A
217	3.49	2,13	0.06	
221	3.71	2,26	0.04	

Table 3.1. Body measurement eigenvectors are reported for PC1 – PC5 along with eigenvalues for each principal component derived from a principal components analysis across all five measurements.

Body Measurements	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Wing cord (mm)	0.49	0.33	-0.07	-0.76	0.26
Tail Length (mm)	0.36	0.64	0.27	0.57	0.25
Tarsus Length (mm)	0.37	-0.67	0.23	0.13	0.59
Body Mass (g)	0.52	-0.18	0.44	-0.03	-0.71
Body Girth (mm)	0.47	-0.11	-0.82	0.27	-0.15
Eigenvalue	2.36	1.12	0.63	0.5	0.38
Percent	47.24	22.48	12.68	9.94	7.66

Table 3.2. The results of ANOVAs comparing changes in drumbeats and drumming rate across the day for 12 male ruffed grouse. DFs and p-values are reported for each individual. For all significant p-values (p-value < 0.05) the percent change in drumbeats and drumming rate is reported, both negative and positive changes are reported.

ID	**date**	**DF**	**drum beats**		**drum rate**	
			p-value	**%change**	**p-value**	**%change**
527	132	7,44	**<0.01**	**-0.06**	**<0.01**	**0.04**
526	127	5,29	0.24		**0.01**	**0.02**
506	115	5,35	0.1		**<0.01**	**0.04**
502	109	9,51	**0.01**	**-0.04**	**<0.01**	**0.05**
501	110	9,54	**<0.01**	**-0.05**	**<0.01**	**0.04**
430	131	9,58	**<0.01**	**-0.05**	**<0.01**	**0.05**
427	130	5,30	0.67		**<0.01**	**0.07**
412	115	8,52	**0.04**	**-0.02**	**<0.01**	**0.07**
402	119	9,56	**<0.01**	**-0.05**	**<0.01**	**0.05**
401	115	7,36	**0.01**	**-0.04**	**<0.01**	**0.06**
307	116	9,51	**<0.01**	**-0.08**	**<0.01**	**0.06**
306	120	6,38	**<0.01**	**-0.05**	**<0.01**	**0.03**

Table 3.3. The results of ANOVAs comparing the number of drum beats and drumming rate produced daily across 2-4 weeks for 10 individuals. DFs and p-values are reported each individual. The percent change in either drumbeats or drumming rate is reported for all significant p-values (p-value < 0.05).

ID	**Week(s)**	**days**	**DF**	**Drum Beats**		**Drum Rate**	
				p-value	**%change**	**p-value**	**%change**
401	17,18	5	1,151	**0.01**	**-0.01**	0.61	
402	18,19	8	1,341	0.36		**<0.01**	**0.02**
412	17*,18,19*,20	19	3,672	**0.02**	**-0.004**	**<0.01**	**-0.01**
427	20,21*	7	1,237	0.59		0.85	
430	20,21*	6	1,212	0.70		0.26	
501	17,18,19,20	24	3,114	**<0.01**	**-0.01**	**<0.01**	**0.01**
502	17,18	14	1,542	**<0.01**	**-0.01**	**<0.01**	**-0.01**
506	17,18,19,20	28	3, 1072	**<0.01**	**-0.01**	**<0.01**	**-0.01**
526	19,20	7	1,228	0.38		0.40	
527	19,20	7	1,160	0.30		0.16	

*Only one day of data for week

Table 3.4. The results for MANOVAs comparing the interaction between week and hour on drum beats and drumming rate across 7 males. P-values and DFs are reported for the whole model and effect test (Week/Hour). For significant p–values a Tukey-Kramer HSD post-hoc test was performed to determine how values changed across weeks. Positive (+) and negative (-) signs indicate direction of a significant change for at least one weekly hour that varies.

ID	**Effect Test**	**DF**	**Drum Beats p-value**	**Effect**	**Drum Rate p-value**	**Effect**
401*	Week/Hour	6, 151	**<0.01**	-	0.12	
402*	Week/Hour	6, 341	**0.04**		**0.01**	
412	Week/Hour	23, 672	**<0.01**		**<0.01**	+
430	Week/Hour	27, 212	**<0.01**		**<0.01**	
501	Week/Hour	30, 1114	0.32		**<0.01**	+/-
502*	Week/Hour	9, 542	0.90		**<0.01**	
506	Week/Hour	25, 1072	**<0.01**	+	**<0.01**	+/-
526*	Week/Hour	6, 228	0.43		**0.03**	

*Only 2 weeks of data available for individual

Table 3.5. Akaike information criteria correlation (AICc) and R-Squared reports for logistic 4 parameter (4P), logistic 3 parameter (3P), quartic, cubic and linear curves fit to changes in daily drumming rate for two individuals across a single day.

ID	**Date**	**Model**	**AICc**	**R-Squared**
501	4/25/2015	Logistic 4P	-314.81	0.34
		Quartic	-312.06	0.34
		Logistic 3P	-308.71	0.29
		Cubic	-307.32	0.3
		Linear	-304.73	0.25
506	4/23/2015	Logistic 4P	-443.48	0.69
		Quartic	-431.93	0.66
		Logistic 3P	-409.38	0.56
		Cubic	-415.13	0.59
		Linear	-352.1	0.24

Table 3.6. The models and respective number of days each model was the best fit for the change in growth rate from 0000-0900 for both RUGR501 and RUGR506.

ID	**Logistic 4P**	**Quartic**	**Cubic**	**Logistic 3P**
501	9	0	5	10
506	12	4	10	2

Table 3.7. Results for regression analyses comparing measures of body size to drum beats and drumming rate. DFs, p-values and r² values are reported for all comparisons.

Body Measure	DF	Drum Beats		Drumming Rate	
		p-value	R-Squared	p-value	R-Squared
Wing Chord	1,22	0.8	0.00	0.58	0.01
Tail Length	1,22	0.81	0.00	0.49	0.02
Tarsus Length	1,22	0.73	0.01	0.47	0.03
Body Mass	1,22	0.13	0.1	0.07	0.14
Body Girth	1,20	0.16	0.1	0.36	0.04
PC1	1,20	0.18	0.09	0.54	0.02
PC2	1,20	0.75	0.01	0.28	0.06

Table 3.8. The results for ANOVAs comparing the relationship between different measurements of body size with number of drumbeats, drumming rate and their interaction. DFs and p-values are reported for the whole model and effect tests.

Body Measurement	**Whole Model**		**Effect tests**					
			Drum Beats		**Drum Rate**		**Dumbeats*Drum Rate**	
	DF	**p-value**	**DF**	**p-value**	**DF**	**p-value**	**DF**	**p-value**
Wing Chord	3,20	0.70	1	0.32	1	0.42	1	0.37
Tail Length	3,20	0.51	1	0.23	1	0.15	1	0.67
Tarsus Length	3,20	0.73	1	0.91	1	0.76	1	0.31
Body Mass	3,20	0.70	1	0.30	1	0.33	1	0.70
Body Girth	3,20	0.60	1	0.40	1	0.98	1	0.88

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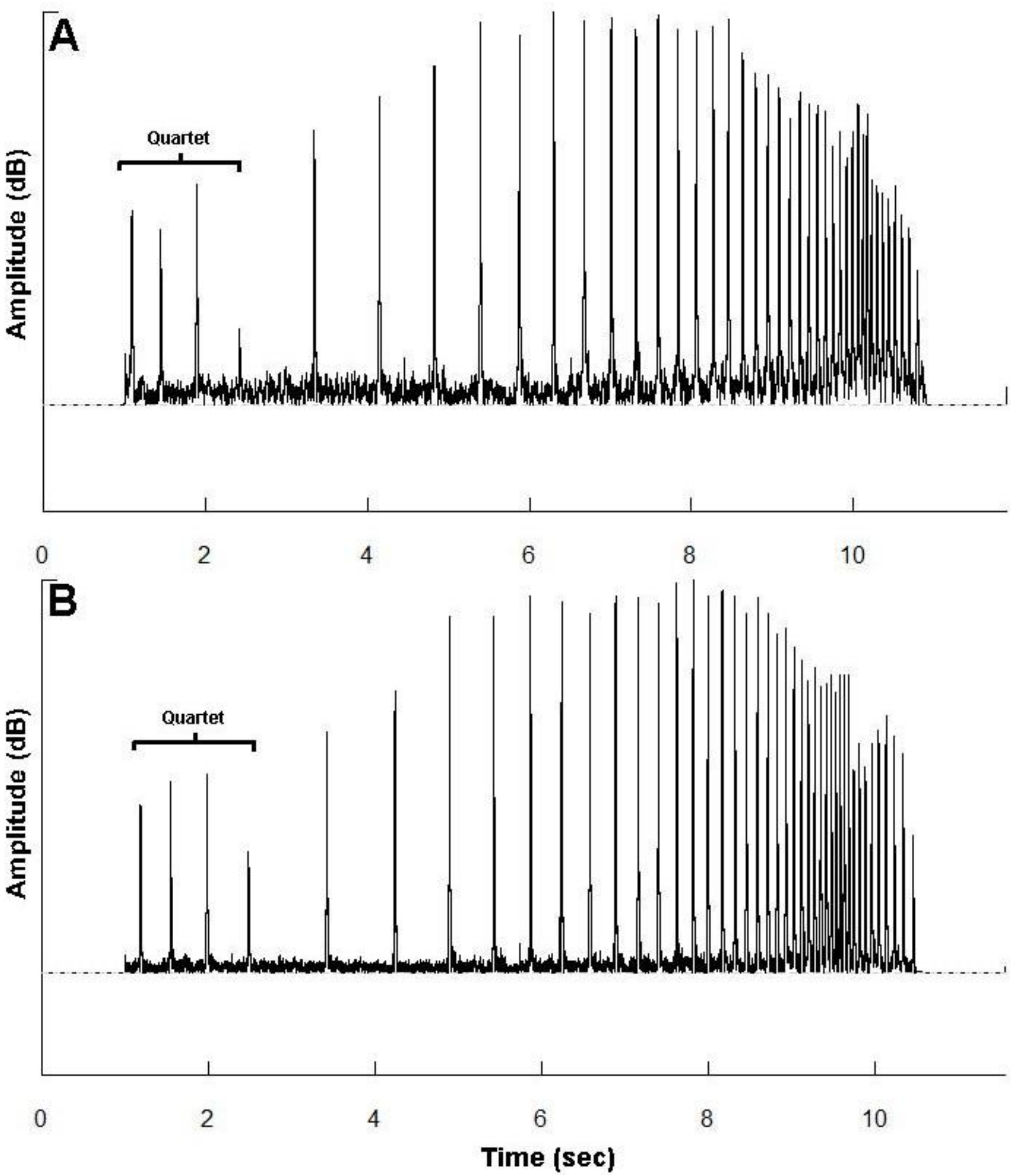

Figure 2.1. The amplitude envelopes of exemplars of the slow (A, drumming rate = 4.876 beats/sec) and fast (B, drumming rate = 5.451 beats/sec) drumming displays used in the playback experiments. In both drumming displays, the quartet is indicated at the beginning of the displays, this is the series of four pulses followed by a brief pause before the rest of the display is performed.

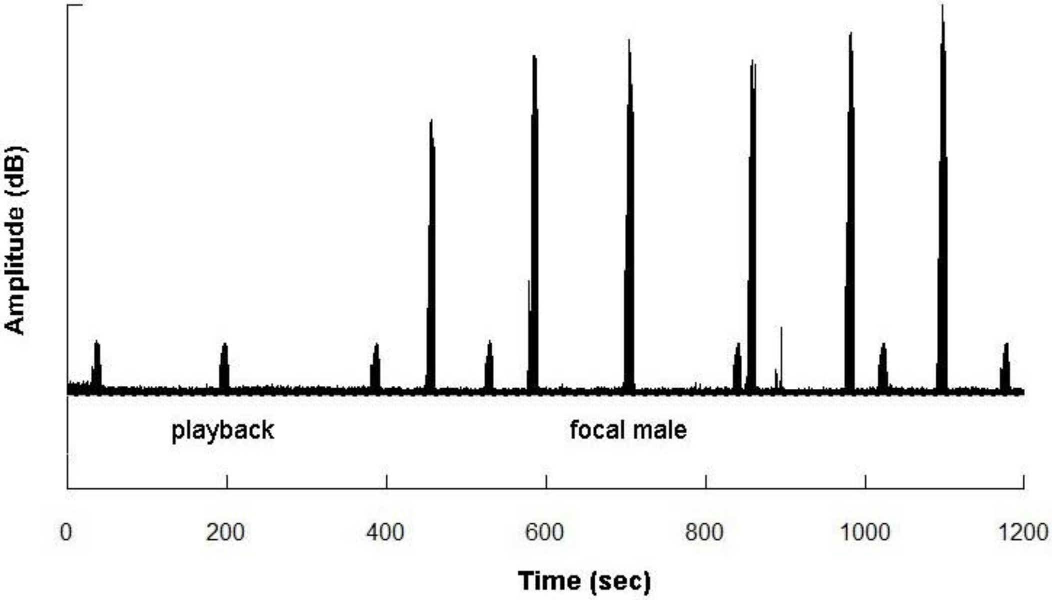

Figure 2.2. An example of a Song Meter recording that contains both playback signal and the drumming of a focal male visualized in an amplitude envelope in Avisoft. Note that the playback signals are the smaller pulses in amplitude and the focal male is represented by the large pulses in the amplitude envelope.

Figure 2.3. Photo of a red-morph male performing Hjorth's (1970) 'full cum ruff' display.

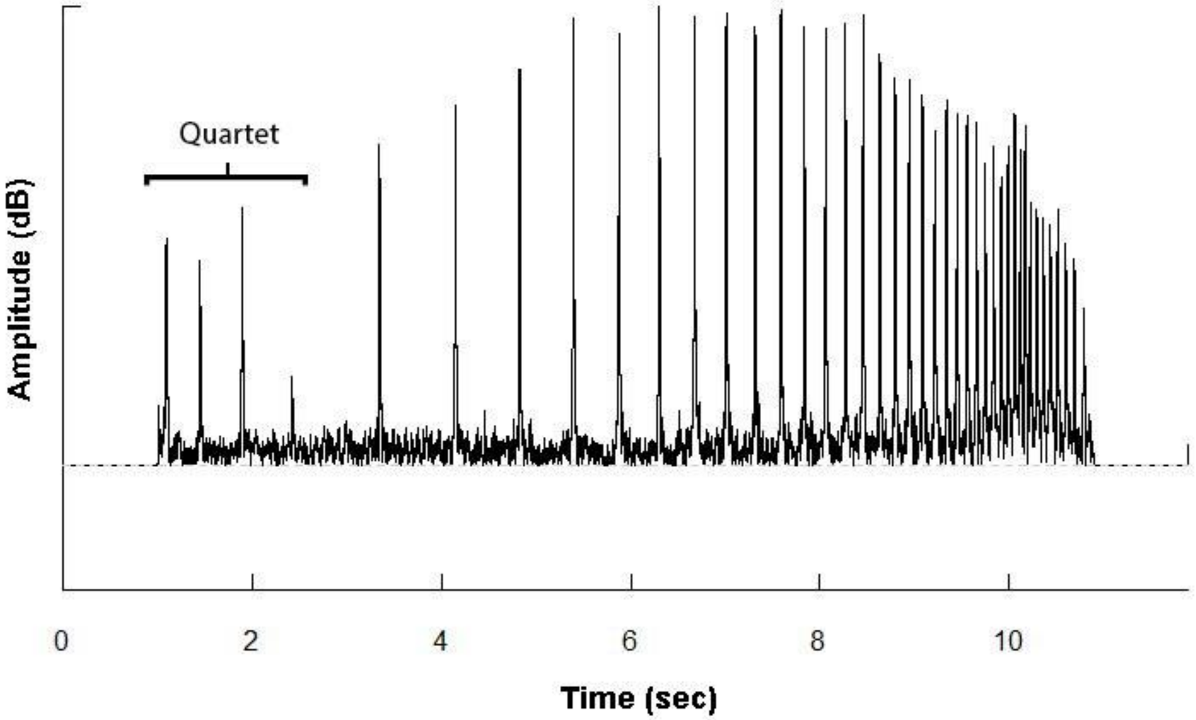

Figure 3.1. Wave envelope of a drumming display exemplar, the quartet distinguished as four wing beats preceding the drumming display is labeled.

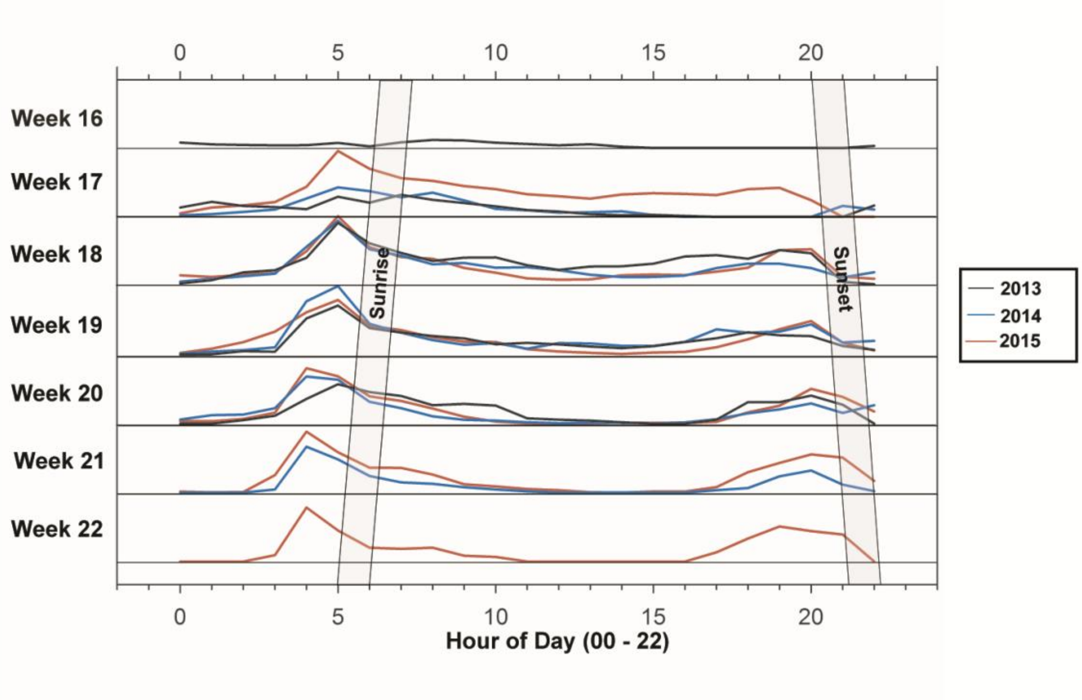

Figure 3.2 Averaged hourly drumming across 7 weeks during the 2013-2015 drumming seasons, weeks are labeled using the Julian calendar system to compare dates across years. Each week bracket (the line below and above average drumming activity) is scaled to 30 drumming displays, during peak activity average drumming across individuals reached upwards of 30 displays per hour. Drumming activity peaked all three years during week 18, with males from the 2015 drumming season showing an increase in activity in preceding week (week 17) due to warmer weather and reduced snow cover compared to the previous years. Daily drumming activity peaks in the morning hours approximately an hour before sunrise and then again in the evening prior to sunset. Afternoon drumming can be observed during peak weeks but is much more variable between individuals.

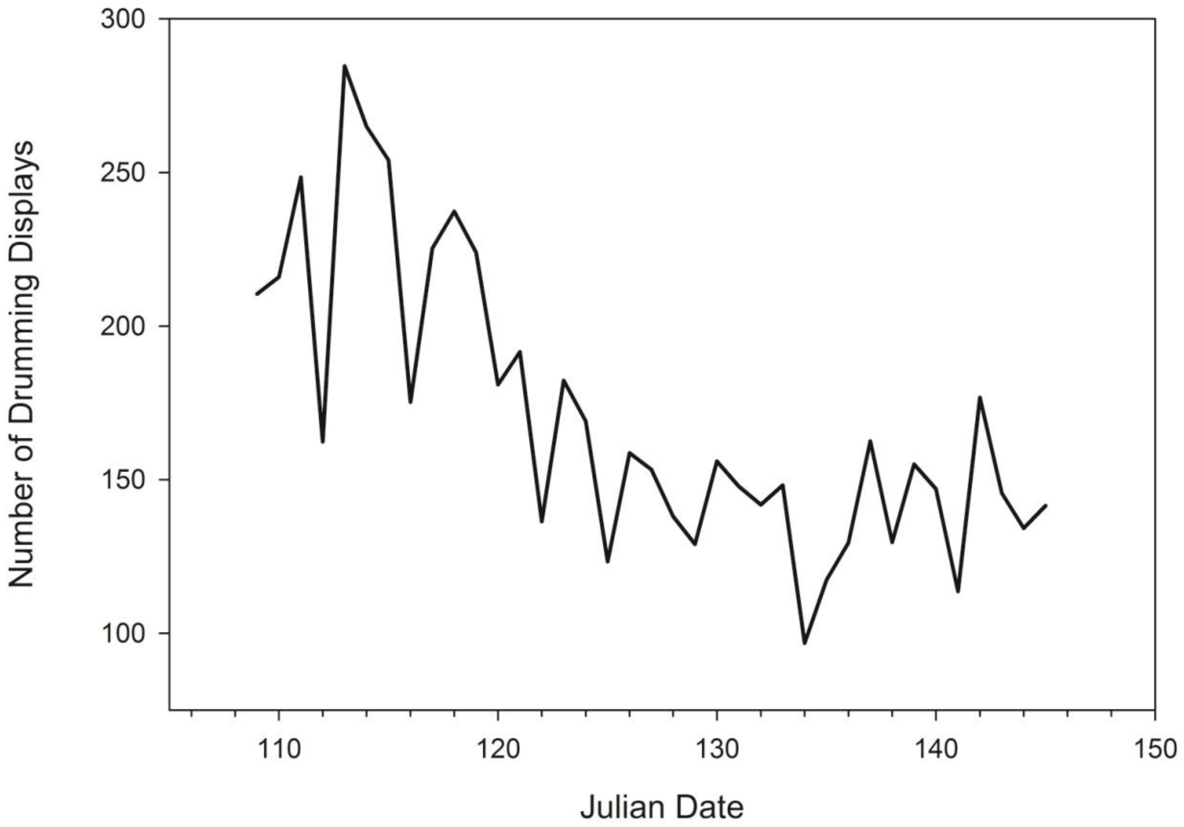

Figure 3.3. Average daily drumming across the 2015 drumming season for 5 male ruffed grouse. Peak activity in drumming occurred between weeks 17 and 18 (approximately days 111 – 118). During peak activity two drops can be observed on days 112 and 116, which received heavy rain. An additional drop in activity occurred on day 134, which reflects a long weekend when there is increased camping and off highway vehicle (OHV) activity in the area.

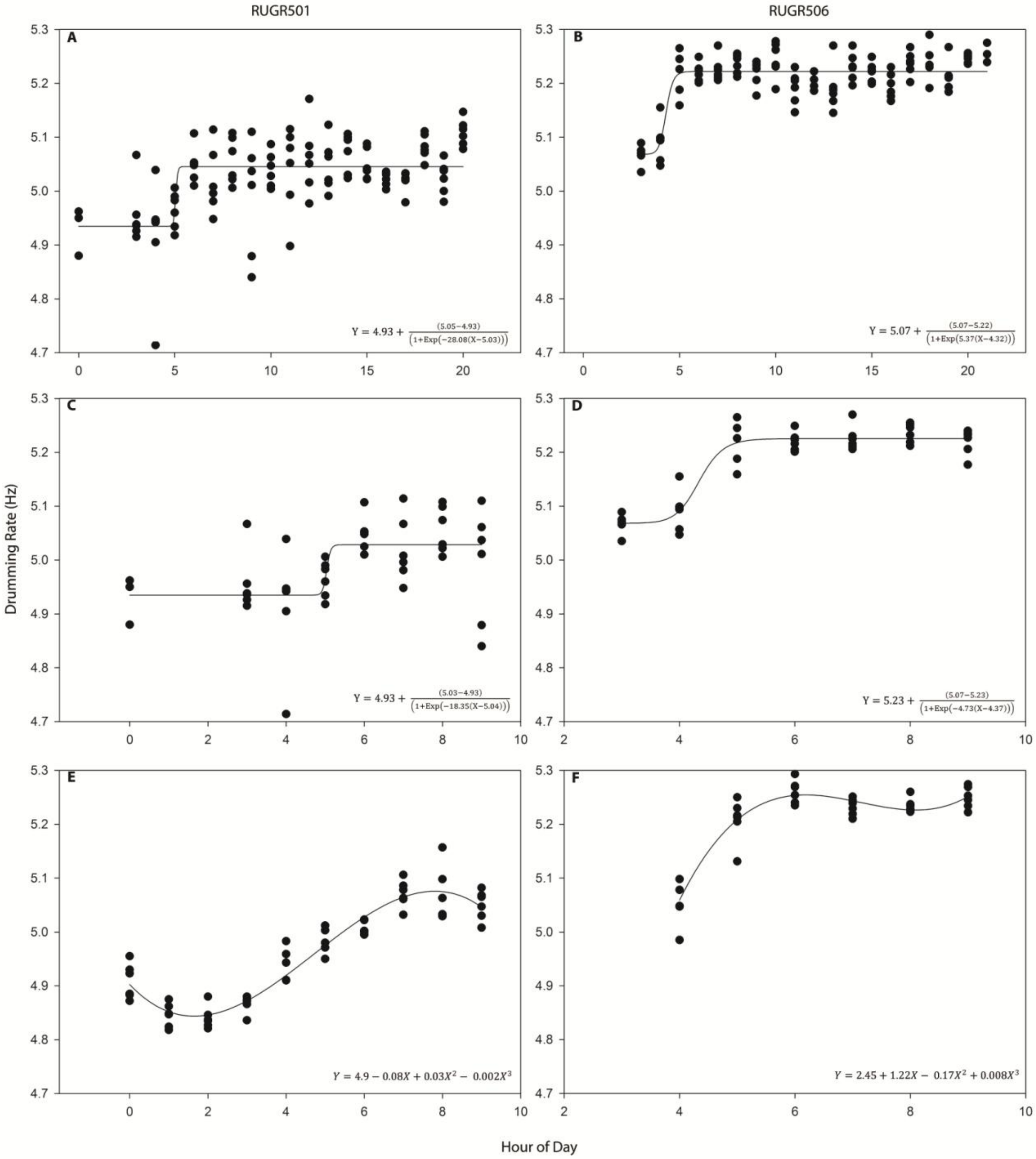

Figure 3.4. Drumming rate across the day for RUGR501 and RUGR506. Panels A and B represent semi-exhaustive sampling fit to a logistic four parameter (4P) model. Panels C and D represent sampling form 0000-0900 with logistic 4P model as the best fit. Panels E and F show exemplars of days for RUGR501 and RUGR506 that do not fit Logistic 4P model, instead fitting a cubic function. Drumming rate increases throughout the morning (approximately 0400 – 0600 hrs MDT). Formulas for each graph are embedded in respective panels.

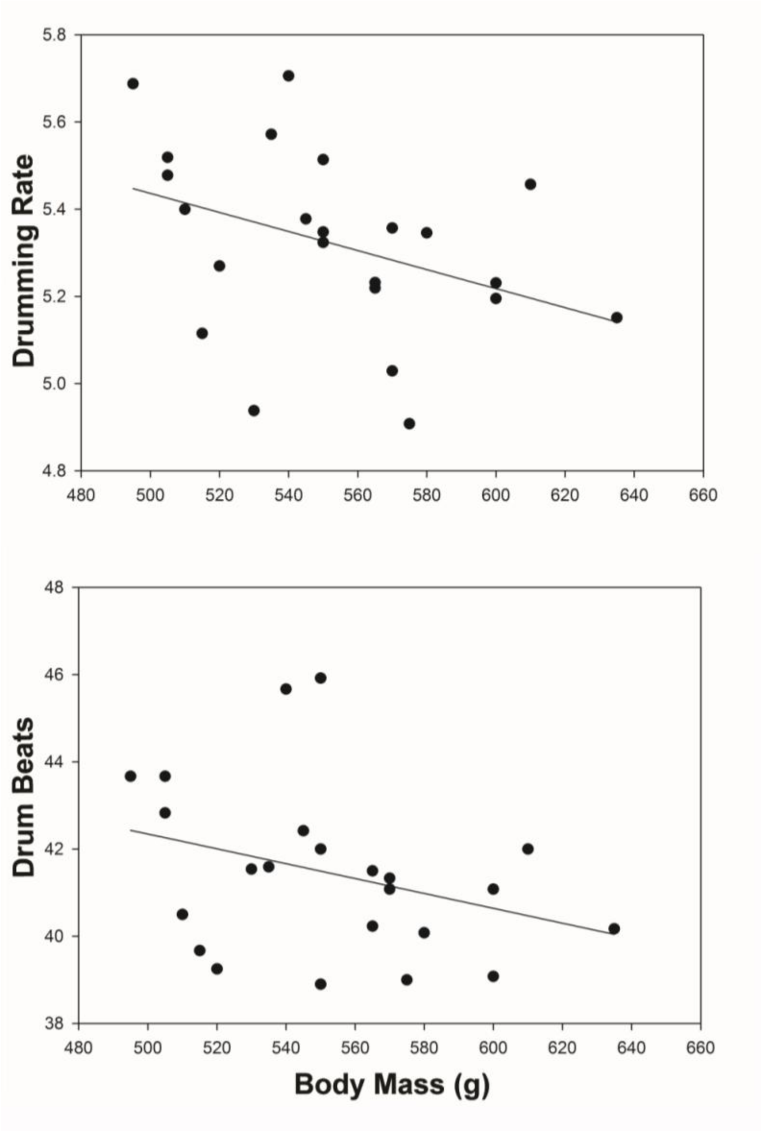

Figure 3.5. Relationship between drumming rate and drum beats against body mass. Both drumming rate and drumbeats have a slight negative relationship with body mass, however, neither is statistically significant across the range of body mass tested.