

Infrasonic and Audible Signals in Male Peafowl
(*Pavo cristatus*) Mating Displays

By

Angela Freeman

A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba

In partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg

Copyright © 2012 by Angela Freeman

ABSTRACT

I recorded audio and video components of Indian Peafowl (*Pavo cristatus*) mating displays at the Assiniboine Park Zoo, in Winnipeg, Manitoba. I determined that males produce infrasound (<20Hz) in their train displays, and played back audible and infrasonic components of these displays to peafowl, to observe their responses. Peafowl responded to infrasonic signals by increasing alertness and locomotory behaviours, while males also responded by calling. Males responded via calling and facing the playback unit in response to audible call playbacks, however, peafowl did not respond to audible signals from the peacock's train display, suggesting the infrasonic signal components are an essential part of the communication signal. Females responded to audible call signals non-vocally via increased locomotion and alertness. Beyond revealing a critical role of acoustic signals in modulating interactions among peafowl, my results provide the first empirical evidence of a bird producing and perceiving infrasound as a signal.

ACKNOWLEDGEMENTS

This thesis and project would not have been possible without the assistance of several individuals and groups.

First and foremost, I am grateful for the support and guidance of my supervisor, Dr. Jim Hare, whose knowledge and patience made this project, and my work, successful. His NSERC Discovery Grant was a major source of funding, and made much of the work possible.

Dr. Darren Gillis' creative mind, in conjunction with Jim's penchant for animal communication, provided the original spark of interest concerning the possibility of peafowl producing infrasound. For their inquisitive nature, I am thankful.

The staff at the Assiniboine Park Zoo (APZ) were of great assistance, especially the veterinary staff: Dr. Charlene Berkvens and Dr. Chris Enright. The keepers and management were helpful in many ways, and provided the essential access to the peafowl, without which, this project would not have been possible.

My primary personal funding was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), in the form of a Canada Graduate Scholarship, which allowed me to focus on the work at hand. The Manitoba provincial government provided a Manitoba Graduate Scholarship in my second year, which was also appreciated. Research costs were supported by NSERC Discovery Grant funding held by Dr. Hare, while funding to purchase infrasonic recording equipment was provided by a University of Manitoba University Research Grants Program grant to Dr. Hare.

Sigma Xi, the scientific research society, also provided funding for this project. Manitoba Hydro graciously provided the transportation and resonance chamber for the infrasonic playback system by donating a cube van to the Assiniboine Park Zoo. Bruce Thigpen from Eminent Technology provided the TRW-17 subwoofer and was exceptional in his service and patience while the playback experiments were ongoing. Dr. Gary Anderson assisted in the assembly of the subwoofer unit, and his help was very much appreciated. Dr. Norm Kenkel provided excellent advice and assistance concerning multivariate statistical techniques used in this project. Dr. Spencer Sealy and Dr. Debbie Kelly both provided valuable comments; improving both the project and the thesis.

Gaby Macklin was an abundant source of humour and provided invaluable assistance in the field for the playback portion of this project.

Finally, this project would never have seen completion without the support of my husband, Matt, who agreed to move to Winnipeg; and my rock-climbing companions, who provided the opportunities to outlet the frustrations and excitement inherent in any field project.

TABLE OF CONTENTS

Abstract	i
Acknowledgements	ii
List of Tables	vi
List of Figures	ix
Chapter I: INTRODUCTION	1
Current Knowledge of Peafowl Mating Behaviour	1
Multimodal Signaling	2
Discord in the Literature	5
Natural Habitat	6
Hypotheses	6
Chapter II: METHODS	7
Recording Design	7
Coding Methods	11
Female Presence	11
Orientation in Relation to Structures	12
Ornamentation Data	14
Playback Scenarios 2011	15
Playback Data Coding	20
Paternity Analysis	22
Chapter III: RECORDING RESULTS	22
Recording Data 2009 and 2010	22
Chapter IV: PLAYBACK RESULTS	35
INFRASOUND	35
Baseline Tests	35
Males Versus Females	37
Pre-Playback	37
During Playback	38
Post-Playback	39
Residents Versus Intruders	39
Pre-Playback	40
During Playback	40
Post-Playback	41
Adult, Juvenile, and Moulting Males	41
Pre-Playback	41
During Playback	42
Post-Playback	42
Territory-Holding Males Versus Floater Males	42
Pre-Playback	42
During Playback	43
Post-Playback	44

Behaviour Changes Between Sections (PRE, DUR, and POST) and Groups	45
Pre-playback Versus During Playback	46
During Playback Versus Post-playback	46
Males and Females	47
Pre-playback to During Playback	47
During Playback to Post-playback	47
Positive Controls and Experimental Tracks	48
Pre-playback to During Playback	48
During Playback to Post-playback	48
Residents and Intruders	49
Pre-playback to During Playback	49
During Playback to Post-playback	50
Territory Holders Versus Floater Males	50
Pre-playback to During Playback	50
During Playback to Post-playback	51
AUDIBLE	53
Baseline Tests	53
Males Versus Females	53
Pre-Playback	53
During Playback	54
Post-Playback	55
Residents and Intruders	55
Pre-Playback	55
During Playback	56
Post-Playback	57
Adult, Juvenile and Moulting Males	57
Pre-Playback and During Playback	57
Post-Playback	58
Territory Holders Versus Floater Males	58
Pre-Playback	58
During Playback	59
Post-Playback	59
Changes in Responses Between Groups	59
Pre-playback to During Playback	60
During Playback to Post-playback	61
Males Versus Females	65
Pre-playback to During Playback	65
During Playback to Post-playback	66
Positive Controls Versus Experimental Playbacks	66
Pre-playback to During Playback	66
During Playback to Post-playback	67
Residents Versus Intruders	68

Territory Holders Versus Floater Males	69
Pre-playback to During Playback	69
During Playback to Post-playback	70
Chapter V: DISCUSSION	70
Infrasound	70
Display Type Selection	73
Resident Signals Versus Intruder Signals	73
Territory Holders Versus Floater Males	75
Audible Signals	77
Territory Holders and Floaters	80
Future Directions	80
References	84
Appendix A	91
Appendix B	97
Appendix C	98
Appendix D	99

LIST OF TABLES

<u>Table 1: Findings From Previous Research Examining the Relationship Between Male Display Characteristics and Male Mating Success (M.S. = Male Mating Success)</u>	3
<u>Table 2: Infrasonic Intensity Versus Display Type</u>	24
<u>Table 3: Approximate Distance of Nearest Female from Male Versus Display Type</u>	26
<u>Table 4: Orientation of Displaying Male Versus Display Type 2009</u>	32
<u>Table 5: Orientation of Displaying Male Versus Display Type 2010</u>	32
<u>Table 6: Orientation of Displaying Male Versus Display Type 2011</u>	33
<u>Table 7: Prior to Playback (Infrasonic) Males and Females Behaviour Proportions</u>	37
<u>Table 8: During Playback (Infrasonic), Males and Females Behaviour Proportions</u>	38
<u>Table 9: Post Playback (Infrasonic), Males and Females Behaviour Proportions</u>	39
<u>Table 10: Prior to playback (Infrasonic Call Playback), Residents Versus Intruders Towards Orientation Behaviour Proportions</u>	40
<u>Table 11: During Playback (Infrasonic Shiver Train Playback), Residents Versus Intruders Walking and Running Behaviour Proportions</u>	40
<u>Table 12: Post Playback (Infrasonic Call Playback), Residents Versus Intruders Behaviour Proportions</u>	41
<u>Table 13: Prior to Playback (Infrasonic Shiver Train Playback), Adult, Juvenile, and Moulting Males Walking and Running Behaviour Proportions</u>	42
<u>Table 14: Prior to Playback (Infrasonic), Territory Holders and Floater Males Behaviour Proportions</u>	43
<u>Table 15: During Playback (Infrasonic), Territory Holders and Floater Males Behaviour Proportions</u>	44
<u>Table 16: Post Playback (Infrasonic), Territory Holders and Floater Males Behaviour Proportions</u>	45
<u>Table 17: Prior to During (Infrasonic Call Playback) Males and Females Changes in Calling Behaviour Proportions</u>	47
<u>Table 18: During to Post (Infrasonic Wing Rotation Playback) Males and Females Change in Behaviour Proportions</u>	48
<u>Table 19: During to Post (Infrasonic Shiver Train Playback), Controls and Experimentals Changes in Alert Behaviour Proportions</u>	49
<u>Table 20: Prior to During (Infrasonic), Residents' and Intruders' Signals Changes in Behaviour Proportions</u>	50
<u>Table 21: Prior to During (Infrasonic) Territory Holders and Floater Males Changes in Behaviour Proportions</u>	51
<u>Table 22: During to Post (Infrasonic Shiver Train Playbacks) Territory Holders and Floater Males Changes in Walking and Running Behaviour Proportions</u>	51

<u>Table 23</u> : Overall Average Peafowl Changes in Behaviour Proportions From Pre-Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Five Infrasonic Playback Types	52
<u>Table 24</u> : Overall Average Male Changes in Display Behaviour Proportions From Pre-Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Infrasonic Playbacks	53
<u>Table 25</u> : Pre-playback (Audible) Males and Females Behaviour Proportions	54
<u>Table 26</u> : During Playback (Audible) Males and Females Behaviour Proportions	54
<u>Table 27</u> : Post Playback (Audible) Males and Females Behaviour Proportions	55
<u>Table 28</u> : Pre-playback (Audible) Residents and Intruders Walking and Running Behaviour Proportions	56
<u>Table 29</u> : During Playback (Audible Wing Rotation Playbacks) Residents and Intruders Walking and Running Behaviour Proportions	56
<u>Table 30</u> : Summary of Kruskal-Wallis Tests, for Adult, Juvenile, and Moulting Males, H values, $df=2.$, where * indicates significance at $\alpha =0.05$.	57
<u>Table 31</u> : Post Playback (Audible Call Playback) Adult, Juvenile, and Moulting Males Towards Orientation Behaviour Proportions	58
<u>Table 32</u> : Pre-playback (Audible Wing Rotation Playback) Territory Holders and Floater Males Behaviour Proportions	58
<u>Table 33</u> : During Playback (Audible) Territory Holders and Floater Males Behaviour Proportions	59
<u>Table 34</u> : Post-playback (Audible Wing Rotation Playback) Territory Holders and Floater Males Walking and Running Behaviour Proportions	59
<u>Table 35</u> : PRE to DUR (Audible) Behaviour Proportions	60
<u>Table 36</u> : DUR to POST (Audible) Behaviour Proportions	61
<u>Table 37</u> : Overall Average Peafowl Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls).	63
<u>Table 38</u> : Overall Average Male Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls)	64
<u>Table 39</u> : Overall Average Female Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls)	65

<u>Table 40</u> : PRE to DUR (Audible Call Playback) Males and Females Calling Behaviour Proportion Changes	66
<u>Table 41</u> : DUR to POST (Audible Wing Rotation Playback) Males and Females Walking and Running Behaviour Proportion Changes	66
<u>Table 42</u> : PRE to DUR (Audible Pulse Train) Controls Versus Experimentals Towards Orientation Behaviour Proportion Changes	67
<u>Table 43</u> : DUR to POST (Audible) Controls Versus Experimentals Behaviour Proportion Changes	68
<u>Table 44</u> : DUR to POST (Audible Wing Rotation Playbacks) Residents Versus Intruders Walking and Running Behaviour Proportion Changes	69
<u>Table 45</u> : PRE to DUR (Audible) Territory Holders Versus Floater Males Behaviour Proportion Changes	69
<u>Table 47</u> : DUR to POST (Audible Pulse Train Playback) Territory Holders Versus Floater Males Alert Behaviour Proportion Changes	70

LIST OF FIGURES

<u>Figure 1:</u> Playback Scenario Flow Chart in Three Parts: Control, Intruder and Resident	18
<u>Figure 2:</u> Frequency of Max Power (Infrasound; Hz) Percentages Per Behaviour 2009	27
<u>Figure 3:</u> Frequency of Max Power (Infrasound; Hz) Percentages Per Behaviour 2010	28
<u>Figure 4:</u> Behaviour Proportions at Female Distance (m) in 2009	30
<u>Figure 5:</u> Behaviour Proportions at Female Distance (m) in 2010	31
<u>Figure 6:</u> Principal Components Analysis of Infrasonic and Audible Components of Pulse Train Displays (points 1-8) and Shiver Train Displays (points 9-15)	34
<u>Figure 7:</u> Principal Components Analysis of Infrasonic Components of Pulse Train Displays (points 1-8), and Shiver Train Displays (points 9-15)	36
<u>Figure 8:</u> Order of Behaviours as Recorded in 2010	81

I: INTRODUCTION

Current Knowledge of Peafowl Mating Behaviour

The peacock's tail provides one of the most popular and long-standing examples of sexual selection, as it is an exaggerated trait that hinders the individual's survival but increases reproductive success (Andersson, 1994; Cronin, 1991; Darwin 1859, 1871). Researchers generally agree that the peacock uses its ornamental train in addition to other parts of its display to attract females for mating (Yasmin & Yahya, 1996; Petrie & Halliday, 1994; Petrie et al., 1991). The ornamentation of the peacock's train has been measured with the number of eyespots (Loyau et al., 2005; Petrie et al., 1991; Manning & Hartley, 1991), train length (Yasmin & Yahya, 1996; Petrie, 1992; Manning, 1989), area of eyespots (Petrie, 1994), density of eyespots (Loyau et al., 2005b), proportion of feathers with eyespots (Petrie et al., 1996), diameter of eyespots (Møller & Petrie, 2002), and eyespot color and iridescence (Loyau et al., 2007). Currently, the consensus is that the peacock's train is a handicap and, thus, an indicator of good genes (Zahavi & Zahavi, 1997). Evidence supporting this assertion includes improved growth of offspring of peacocks with elaborate trains (Petrie, 1994), higher fat reserves in peacocks with longer trains (Petrie et al., 1996), and fewer heterophils (which are released in response to inflammation) in peacocks with elaborate trains and frequent displays (Loyau et al., 2005). Thus, it is believed that the elaborate train of the peacock serves as an honest signal of good genes, reflecting the overall quality of its bearer from the time when the train is grown (spring). As such, displays of the peacock are thought to signal male quality at the time of mating.

Multimodal Signaling

The study of multimodal signaling is important in understanding behaviour, especially with respect to mate choice. Multiple signals can have different messages (multiple message hypothesis), the same message (redundant message hypothesis), alter the meaning of the initial message (metacommunication) and in many cases amplify the message when used at the same time (Partan & Marler, 2005; Møller & Pomiankowski, 1993; Bekoff, 1972). Møller and Pomiankowski (1993) hypothesized that ornaments can spread genetically through female preference, and that these ornaments may not reflect male condition. This is encapsulated in “the unreliable signal hypothesis”, which postulates that ornamentation originally spreads as a by-product of good genes and is then spread through Fisher’s Runaway process owing to female preference (Fisher, 1930). Peacocks have extensive ornamentation which has been studied unimodally to determine which signals are important for female mate choice, including train length (Petrie et al., 2009; Yasmin & Yahya, 1996), eyespot number (Dakin & Montgomerie, 2011; Loyau et al., 2005; Petrie et al., 1991), eyespot density (Loyau et al., 2005), eyespot symmetry (Manning & Hartley, 1991), area of eyespots (Petrie, 1994), eyespot iridescence (Loyau et al., 2007), male mass (Petrie et al., 1996), train mass (Petrie & Williams, 1993), number of call notes (Yasmin & Yahya, 1996), and display rate (Takahashi et al., 2008; Loyau et al., 2005). None of these studies, however, experimentally tested the effects of signals working in concert with one another, though some did consider the interactive effect of a subset of these components (Table 1).

Table 1 summarizes current knowledge concerning mating success and peacock ornamentation and display attributes. Eyespot number is positively correlated with male

Table 1: Findings From Previous Research Examining the Relationship Between Male Display Characteristics and Male Mating Success (M.S. = Male Mating Success)

Source	Train Length	Eyespot Number	Eyespot Iridescence	Eyespot Density	Eyespot Symmetry	Call Rate	Display Rate
Petrie et al. 2009	Highly heritable	Highly heritable					
Takahashi et al. 2008	No detectable relationship to M. S.	No detectable relationship to M. S.			No detectable relationship to M. S.	Low sample of calls with 5 notes or more	More bouts of shivering and increased duration of shivering enhanced M.S.
Yasmin and Yahya 1996	Longer train increased M. S.					Calls >5 notes increased M.S. Call rate had no effect	No correlation to M.S.
Petrie and Halladay 1994		Positively correlated to M.S.					
Petrie et al. 1991		Positively correlated to M.S.					
Manning and Hartley 1991					Eyespot symmetry positively correlated with total # eyespots		
Loyau et al. 2005		Negatively correlated with heterophils					Negatively correlated with heterophils
Loyau et al. 2007			Brightness of eyespot, and maximum change in colour contrast correlated with M.S.				
Loyau et al. 2005, 2005b	Negatively correlated with M.S.	Positively correlated with M.S.		Positively correlated with M.S.			Positively correlated with M.S.
Dakin and Montgomerie 2011		<150 eyespots negatively correlated to M.S.					

mating success as defined by the number of copulations males obtain. For train length and both display and call rate, there is no general trend regarding their correlation to male mating success.

Previously, studies of barn swallows (*Hirundo rustica*) revealed that both song rate and tail length were used in mate choice to determine male quality (Møller et al., 1998). Uetz et al. (2009) determined that in a wolf spider (*Schizocosa ocreata*), females detected males faster when they used both seismic and visual signals. Marchetti (1998) studied yellow-browed leaf warblers (*Phylloscopus inornatus*) and experimentally enlarged male colour patches. Female yellow-browed leaf warblers discerned high-quality males (with large natural colour patches, high body mass, and high call rate) despite plumage alteration (Marchetti, 1998). Females selected mates on the basis of several signals, which aided females in selecting quality males; this supports the redundant signal and multiple message hypotheses. Similar to the species tested in these studies, peacocks likely use multiple signals to convey male quality in mate selection. In barn swallows, females used auditory signals then visual signals to compare highly ornamented males (Møller et al., 1998). Peahens might compare males on the basis of acoustic signals first, and then compare the males' ornamentation (or ornamentation first and acoustic signals secondarily). Peahens might also select males based on a combination of ornamentation and display signals simultaneously.

We can address whether the signal of male quality is enhanced when auditory signals and peacock ornamentation are used together, by examining peafowl behaviour. The existence of ornamented peacocks with low mating success may be explained by studies of multimodal signaling; a study focusing on how audible signals and

ornamentation affect male mating success would bolster current knowledge regarding peafowl mate selection.

Discord in the Literature

Peacocks with the longest train or most eyespots do not always obtain the largest number of mates (Dakin & Montgomerie, 2011, Takahashi et al., 2008, Loyau et al., 2005b). Signals other than those associated with the train, however, may affect mating behaviour in peafowl (Takahashi et al., 2008). Takahashi et al. (2008) have hypothesized that the peacock uses other signals (e.g. calls and display characteristics) in addition to an elaborate or long train to attract mates. I hypothesize that acoustic signals may explain this discrepancy in our current knowledge of peafowl mate choice.

Harper (2006) quoted famous theorist John Maynard Smith as asking, “why [have] ‘birdwatchers’ not studied the obvious auditory signal components during peacock display?” The auditory components of the peacock’s display have not been well studied. Yasmin and Yahya (1996) determined that peacocks broadcasting vocalizations of five notes or more and with longer trains had the greatest mating success, and Manning and Hartley (1991) suggested that the number and length of feathers in the train may affect the audible component of the shivering display. In addition to auditory signals created by the train displays, the vocalizations of the peacock may also serve as signals, and may be used in mating behaviour. Takahashi and Hasegawa (2008) recorded multiple vocalizations from a feral peafowl population and argued that many of these vocalizations are related to breeding, as they occurred only during the breeding season. In their study, however, Takahashi and Hasegawa did not examine any form of train ornamentation or mating success.

Natural Habitat

Indian Peafowl live in the wild from Pakistan through India and into Sri Lanka, with the majority of the wild population in India. In India, the peafowl's preferred habitat is humid to dry open forest with undergrowth consisting of *Zizipus* spp. (Jujube), as well as secondary growth forests and orchards (del Hoyo et al., 1994). In India, the peafowl live in lowland areas up to 2000 m (del Hoyo et al., 1994). Many semi-feral populations exist throughout the world, often in parks, gardens, and zoos. Indian Peafowl may use infrasound (frequencies <20 Hz) in their native shrubby habitat to extend the range of communication, as elephants do (Payne et al., 1986).

Hypotheses

I hypothesized that males use auditory signals in addition to visual displays to advertise both to females, and other males. Based on data obtained through video and audio recordings collected at the Assiniboine Park Zoo in Winnipeg, Manitoba, I determined that infrasound is a part of the shiver train, pulse train and wing rotation displays that are apparent in the breeding season (See Methods for details). Infrasound is produced during communication by Asian elephants (*Elephas maximus*; Payne et al., 1986) and baleen whales (*Mysticeti* spp.; Payne & Webb, 1971), and given the low frequency of these signals, they are conveyed over long distances with little attenuation. The black rhino (*Diceros bicornis* ssp.) also produces infrasound in its vocalizations (Budde & Klump, 2003) as do hippos (*Hippopotamus amphibious*; Barklow, 2004) and tigers (*Panthera tigris*; Walsh et al., 2003). The capercaillie (*Tetrao urogallus*) produces infrasound in its flutter-jump display, but in a previous study females did not respond to infrasound playbacks (Lieser et al., 2006). The subwoofer used in the playback study by

Lieser et al. (2006), however, would not produce frequencies below 23 Hz, which could explain the absence of capercaillie response (Freeman & Hare, 2011). Furthermore, the homing pigeon (*Columba livia*) is known to perceive infrasound, which it uses for orientation (Yodlowski et al., 1977). Similar to these other species, it is possible that peafowl may produce and detect infrasound. I hypothesized that the peacocks' displays are correlated with the presence of infrasound, and that peafowl may respond to the infrasound during playback. Hare and Gillis (personal communication) observed peacocks displaying, and noted that the train might serve as an acoustic radiator during infrasonic production. During infrasonic production, the back wave of the acoustic signal needs to be cancelled for the signal to be propagated effectively. In accordance with this need, males were commonly observed displaying near structures such as buildings and concrete feed bins, presumably promoting the propagation of the signal.

I addressed the following major questions: Do males use acoustic signals as part of their display to attract mates or deter competitors? If so, which parts of the acoustic signals (i.e. infrasound or audible sound) attract females or deter males? In the following sections, I discuss the methods and results of preliminary data collection (recordings of peacock displays, and associated characteristics of those displays), after which I focus on the methods and results of the playback of signals and analysis of peafowl responses, addressing the major questions outlined above.

II: METHODS

Recording Design

In August 2009 Dr. James Hare recorded audio and visual components of nine peacocks displaying at the Assiniboine Park Zoo (49° 52'N, 97° 14'W) in Winnipeg,

Manitoba. In 2010 and 2011, I obtained additional recordings from 15 peacocks in 2010, and 22 peacocks in 2011 using the same methods. These peacocks were individually identifiable based on plumage characteristics or leg bands (Nylon cable ties similar to: TY25-M Thomas & Betts, QC, Canada; and/or wrap-around bandettes: 902-914, National Band and Tag, Kentucky, USA). Audio components of the peacocks' display were recorded using a QTC50 microphone (Earthworks Inc., NH, U.S.A.), which provides near flat frequency response from 3 Hz to 50 kHz, connected to an Earthworks 1021 preamplifier (2 Hz - 100 kHz; Earthworks Inc., NH, U.S.A.), which in turn was connected to a DAQ-6062E PC Card A/D converter (National Instruments, TX, U.S.A.), allowing the digital recording of signals with Avisoft's Recorder software (Avisoft Bioacoustics, Berlin, Germany) on a ruggedized Getac M220 laptop (Getac USA, CA, U.S.A.). Visual display characteristics were recorded with a SONY HDR-XR100 camcorder (SONY, Tokyo, Japan) mounted on a tripod.

The population of peafowl at the Assiniboine Park Zoo is free-ranging over 50 ha of animal enclosures and parkland (Dakin & Montgomerie, 2011), with breeding males holding territories comprising specific lek sites. This population is described by Dakin and Montgomerie (2011), and is similar to the population described by Petrie et al. (1991), as some males hold territories while other males are 'floaters' and follow the females to each lek site. While breeding occurs in early summer (April to July), males continue to display to females who often investigate these displays until August (Hare, personal communication).

In 2010 and 2011, displaying peacocks were recorded between the hours of 07:00 and 15:00 hrs (GMT-6, CDT), as were peacocks in similar studies (08:00-12:00 hrs

(GMT) in Petrie & Williams, 1993; 09:00-17:00 hrs (GMT+1) in Loyau et al., 2005; 05:00 – 09:00 hrs and 15:30-17:30 hrs (GMT+9) in Takahashi et al., 2008). The recording of peacocks is dependent on weather; recording did not take place in rain or when wind speeds exceeded 10 km/h due to the vulnerability of the recording equipment and effect of wind on sound quality, respectively. During recording sessions, displaying males were located and the recording equipment was setup in a convenient location near (<20 m) the males. Males display in zoo exhibits as well as in public areas, and the distance to the displaying males from the recording equipment was noted. When peacocks were displaying in public areas, the distance to the recording equipment was measured with a tape measure (64% of recordings). When peacocks were displaying in animal exhibits (36% of recordings), the distance was estimated in 2010 using known distances to objects (e.g. distances between fence posts), and was measured in 2011 with a Bushnell Sport 850 laser rangefinder (Bushnell Corporation, Overland Park, KS). Only males that could be seen on videotape (i.e. not hidden) were used for audio recordings, so I could associate displays with acoustic components in data collection. Once a male was located, and the equipment was set up, recording continued until the display was finished, or up to approximately 30 minutes. This allowed a selection of males to be recorded, at different times of day without devoting a large portion of recording time to a single display by an individual male (approximately 1000 behavioural events during 77 recording sessions of 15 males from 15 July to 2 August 2010; and 842 behavioural events during 66 recording sessions of 22 males from 6 May to 19 May 2011). The acoustic properties of each behaviour type recorded (e.g. ‘Shiver train’ (vibration of the upper tail coverts from the central feathers to the peripheral feathers), ‘Pulse train’

(Train- rattling; described in Dakin & Montgomerie, 2009, or vibration of the upper tail coverts from the base of the coverts to the ends), ‘Wing rotation’ (Wing-shaking; described in Dakin & Montgomerie, 2009), ‘Hoot-dash’ (described in Petrie et al. 1992), and ‘Call’ (any vocalization other than the ‘Hoot-dash’) was averaged for each individual peacock to minimize pseudoreplication; as I obtained more samples from certain peacocks than from others.

In the Assiniboine Park Zoo population, all adult peafowl are individually marked with colour bands. This (in conjunction with plumage characteristics) allowed for the accurate identification of the recorded individuals. Due to some band loss over the summer of 2010, the peafowl were PIT-tagged with 12 mm AVID microchips (AVID Identification Systems Inc., Norco, CA, U.S.A.), bled, and re-banded by Dr. Chris Enright and Dr. Charlene Berkvens, (Assiniboine Park Zoo veterinarians) when released in spring 2011. The PIT tags were placed subcutaneously on the peafowl’s left breast. While PIT tags cannot be read from great distances (more than 10 cm), these permanent markers ensured individual identification where leg bands were lost. Larger, wrap-around plastic bandettes (National Band and Tag Co., Newport, KY, U.S.A.) were used in 2011 as replacements to reduce band loss, and to allow identification of peafowl from a distance. All audible sound, including calls were analysed spectrographically using SASLabPro (Avisoft Bioacoustics, Berlin, Germany) (See Appendix A for spectrograph examples). Analysis parameters for audible sound were: window type = Hann; FFT length = 512; frequency resolution = 93 Hz; time resolution = 2.688 ms.

Furthermore, spectral attributes of infrasonic signals were analyzed, including bandwidth of the signal, bandwidth of the frequencies of maximum power, and the

frequency of maximum power. Analysis parameters used for infrasound were: window type = Hann; FFT length = 128; frequency resolution = 372 Hz; time resolution = 0.168 ms. Power spectra, which were used to determine the frequency of maximum power, were analysed using a logarithmic Fourier transformation in a Hann window (frequency resolution = 0.006 Hz).

All recordings were filtered with the built-in anti-aliasing filter in Avisoft SASlabPro (Avisoft Bioacoustics, Berlin, Germany) to prevent frequency artefacts (Blumstein & Armitage, 1997). Using an anti-aliasing filter can limit these artefacts from appearing in the final, digitized signal (Hopp et al. 1997).

Coding Methods

I analyzed the peacock video recordings and recorded the presence of infrasound, as well as the association of infrasound with display type (calls, pulse train, shiver train, and wing rotation), orientation to any building or structure, presence of a female, and approximate distance to the nearest female.

Infrasound was coded as “0” for infrasound absent or at background sound pressure level, “1” or low for >10 dB but <30 dB above background level, and “2” or pronounced for >30 dB above background levels.

Female Presence

A peahen was considered present when she was within approximately 30 m of the peacock. Distances instead of presence/absence were used, as it was impossible to determine when individual males perceived a female as ‘present’ or ‘absent’, and most males were observed displaying when females were 30m away or closer. Maximum distance to the closest female was estimated from the video recordings in 2009 and

confirmed from field notes, and was scored as approximately 1 m, 2 m, 3 m, 4 m, 5 m, $5m < x < 30$ m, or >30 m (female away). From reviewing video recordings in 2009, it was difficult to ascertain how far a female was from a displaying male after 5 m. These categorical scores were used for analysis in 2009, as continuous values for female distance were not available from those recordings and notes. When recordings were continued in 2010, female distance was recorded to the nearest meter. The 2009 categorical values were analyzed using a Kolmogorov-Smirnov test, to determine if display type was dependent on female distance. The 2010 values are presented in graph format, and are similar to those from 2009.

Orientation in Relation to Structures

From 15 July to 2 August 2010, and from 6 May to 19 May 2011 I collected the following data from field observations, audio, and video recordings: the identity of the displaying male, the number of females or males that approached (within 30 m), the distance to which other peafowl approached (estimated to nearest m), observed copulations, if the male displayed near (within 3 m) a structure (i.e. buildings, walls, solid fences), and if so, the orientation to the structure, and the presence of infrasound with different display behaviours. These data were used to test the hypothesis that males might use structures to absorb the back wave of the infrasound and promote the propagation of the signal. Observed copulations have been used in previous studies as a measure of male mating success (Petrie et al. 1991). Female approach was also measured by Takahashi et al. (2008) as a behavioural indicator of female "interest" in displaying males. Orientation of the peacock was recorded according to the same criteria established in 2009. The orientation of the peacock was recorded as 'towards' during the emission of calls, and

when pulsing or shivering his train when the male was facing the structure and the vertical plane of the peacock's train was parallel to the structure. 'Away' was defined as the orientation when the peacock was not facing the structure during the emission of calls and displays and the vertical plane of his train was parallel to the structure.

'Perpendicular' orientation was recorded when the peacock displayed or called with the vertical plane of his train approximately 80-100° to the structure. During wing rotation, however, males were coded as displaying towards the structure when his wings were closest to the structure, and his head was oriented away from the structure. Most data were collected in the field; however, infrasound presence was determined through spectrographic analysis. Peacocks often display quickly, switching between different display behaviours. Thus, reviewing video recordings of displays allowed for accurate coding of the peacock's display.

From these data, I determined whether males tend to display close to structures, and how they prefer to orient themselves to those structures, via a contingency table analysis. Orientation was determined from both field notes and from video recordings, as outlined above. I determined whether females approach males more closely if they have pronounced levels of infrasound in their displays. I used the program R to conduct a principal components analysis to compare acoustic properties of different display behaviours (R 2.12.2 for Mac OSX, package: "VEGAN"). I also used a multivariate discriminant analysis to test for differences between the display behaviours. In addition to answering these research questions, these recordings supplied audio samples for playback in 2011.

Data in 2010 were collected prior to moult (first moulting male seen 24 July 2010) for most (13 of 15) individuals. All recording data from 2011 were collected prior to moult. If some moulting or feather loss through human/animal interaction occurred, it was recorded in my field notes.

Ornamentation Data

To compare the ornamentation data with results from previous studies, I measured train length, eyespot number, density, and symmetry (methods described below). Studying coloration or iridescence could also aid in comparison to previous studies, however, the process of analysing multiple eyespots for colour variation is extremely time-consuming and is difficult to measure. Background colour spectra of the environment must be obtained, and in a varied environment such as the Assiniboine Park Zoo (where leks can be in shaded or sunny areas, near concrete or vegetation) determining accurate background characteristics would be difficult (Loyau et al., 2007).

In order to determine train length, I used a metre stick as a reference in video analysis, and inferred the height of the peacock from the video recording. A metre stick was placed near the displaying male during recordings, and through the ratio of the male's train length on video and the metre stick's height on video. I also used landmarks in the field to estimate the peacock's train length, and found that both methods gave results within 5cm. While this method of train length determination is not the method used in previous studies (which involved direct measurement of the train from the base of the upper tail coverts to the end of the longest feather), it allows for an effective comparison of train length between the individuals at the Assiniboine Park Zoo. Eyespot

number and symmetry were determined through analysis of photographs of displaying males. Eyespots were enumerated by visual inspection of digital photos. Displaying males' trains were photographed from as close as possible (2 - 15 m) while documenting the eyespots on the entire train, with a digital camera (Fuji Finepix S1700, FUJIFILM Global, Tokyo, Japan: Setting; AutoSR). Photos were taken from at least 3 different angles to ensure all eyespots (including those obscured by the peacock's head) could be counted from digital photographs. Total eyespot numbers for the left and right sides of the train for each individual were averaged based on the photographs. I calculated symmetry scores for the peacock by subtracting the number of eyespots on the right side from the number of eyespots on the left side of the peacock's train, using the line of ocelli above the peacock's head as the midline (Manning & Hartley, 1991). Eyespot density was calculated using train length as radius; assuming the train was semicircular (See Loyau et al., 2005b). These measures, as well as train length estimated via video analysis were indicators of male ornamentation. Ornamentation data were collected to compare ornamentation and male mating success to previous studies, however, male mating success was not quantified owing to nesting failure. These ornamentation data are provided as an appendix without interpretation (Appendix D) for the potential use of other researchers.

Playback Scenarios 2011

Prior to the breeding season of 2011 (May), I created audio tracks for a playback experiment at the Assiniboine Park Zoo. These tracks were 8 minutes long, as determined from the average display length from recordings in 2010. There were sixteen tracks (a total of 128 minutes, from 13 males) played at each of the 7 sites (Figure 1 summarizes

the design of the playback study). All the tracks (experimental and controls) were played at each lek site once, which reduced pseudoreplication, as territory-holding peacocks received each treatment only once. All audio tracks were acoustic signals from either 'resident' or 'intruder' individuals, where resident signals were from the territory holder of the lek site, and intruders were signals from territory-holding males from leks at least 50m away, but still within the APZ population, as peafowl may respond differentially to familiar versus unfamiliar signallers. The infrasound positive control consisted of sine wave tracks with frequencies from 1-8 Hz averaging 4 Hz, because infrasonic signals from the peacock displays recorded in 2009, 2010 and 2011 were determined to fall within that frequency range. All sine waves were produced with a sine wave generator function in Avisoft SASlabPro (Avisoft Bioacoustics, Berlin, Germany). The sine wave tracks were three-second sections of sound separated by eighteen seconds of silence, similar to the durations of sound in the recordings of displaying males gathered in 2010. The infrasound pulse train experimental tracks contained 1-3 seconds of infrasound recorded from displaying males in 2011, separated by eighteen seconds of silence (based on intervals of displays in 2010). The infrasound shiver train, call and wing rotation tracks contained 3 seconds of infrasound recorded from displaying males in 2011, followed by 45 seconds of silence.

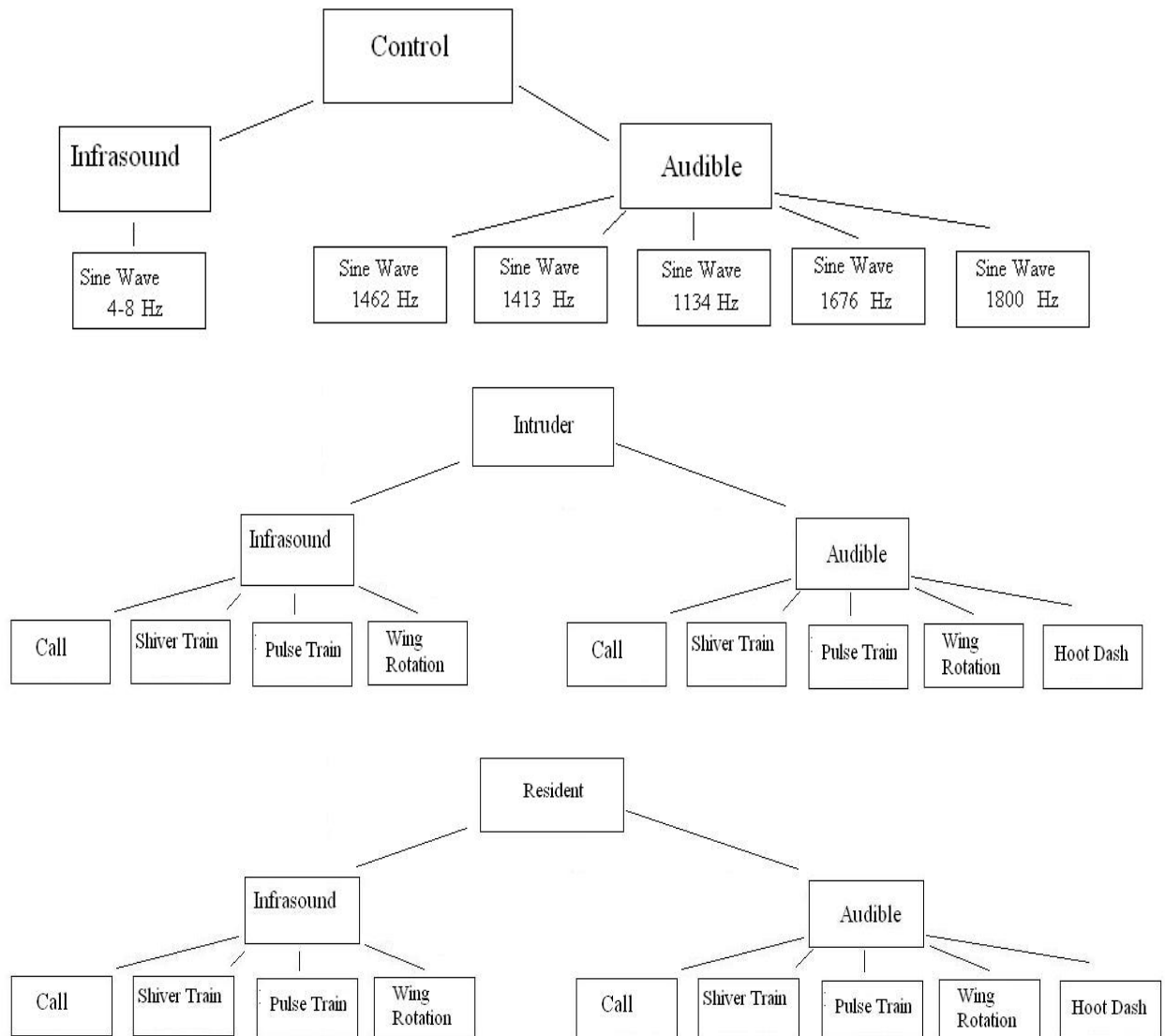
The audible positive control consisted of three-second sections of an audible sine wave at a range of frequencies equalling the bandwidth of the recorded signal (Average frequency (Range ± 100 Hz) Call: 1800 Hz, Shiver train: 1134 Hz, Pulse train: 1413 Hz, Wing Rotation: 1676 Hz, Hoot-Dash: 1462 Hz) separated by 45 seconds of silence (similar to intervals found in the recordings gathered in 2010). The audible experimental

tracks contained three-second sections of audible acoustic displays (> 20Hz, including Hoot-Dash, Call, Shiver Train, Pulse Train and Wing Rotation), separated by 45 seconds of silence (to maintain consistency with the infrasonic playbacks).

Using recordings from a different year can assist in preventing habituation of individuals to calls (Cheney & Seyfarth, 1988). However, seasonal variation in calls may exist and could be conveyed without the researchers' knowledge. As Takahashi and Hasegawa (2008) showed in their study on peacock vocalizations, vocalizations differ between the breeding season and the non-breeding season. To ensure responses are representative of those occurring during breeding, and to avoid introducing extraneous variation owing to seasonal changes in calls, recordings from the breeding season (April-August 2010; May 2011) were used. Additional samples of signalling and recordings of infrasound were collected in May of 2011 for playbacks.

For each playback trial, the playback equipment was set up in a location near (<20 m) the peafowl lek sites. The infrasound playback system included a TRW-17 subwoofer (infrasound trials; Frequency Response 1 – 30 Hz, Eminent Technology Inc., FL, U.S.A) connected to a custom-built amplifier provided by Eminent Technology Inc. for use with the subwoofer, in turn connected to a DAQ-6062E PC Card A/D converter (National Instruments, TX, U.S.A.), allowing the playback of signals with Avisoft's Recorder software (Avisoft Bioacoustics, Berlin, Germany) on a ruggedized Getac M220 laptop (Getac USA, CA, U.S.A.). Visual display characteristics were recorded with a SONY HDR-XR100 camcorder (SONY, Tokyo, Japan) mounted on a tripod. The subwoofer was installed in the back door opening of a cube van (opening 1.22 X 2.13 m),

Figure 1: Playback Scenario Flow Chart in Three Parts: Control, Intruder and Resident



surrounded by 3/4" plywood attached to the interior of the door, with a circular hole allowing the blades of the rotary subwoofer to rotate freely. The van served as a resonance chamber, which absorbed the sound pressure back-wave, ensuring propagation of the low-frequency signal. For audible playback, a Genexxa Pro LX5 speaker (Frequency Response 85 Hz - 25 kHz, InterTan Canada Ltd., Barrie, ON, Canada), powered by a SONY XM-2020 audio amplifier (SONY Electronics Inc., Oradell, NJ, U.S.A.) were connected to the DAQ-6062E PC Card A/D converter (National

Instruments, TX, U.S.A.), allowing the playback of signals with Avisoft's Recorder software on the Getac M220 laptop (Getac USA, CA, U.S.A.). To maintain a consistent visual appearance for both infrasonic and audible playbacks, the speaker was placed in the same cube van just behind the subwoofer. All playback tracks were calibrated to play at 80-100 dB sound pressure level (SPL) at 4m with a GenRad 1988-9700 Precision Sound Level Meter (IET Labs INC, NY, U.S.A.), which exceeded the ambient levels of noise (squirrels, birds, conversations were 60-75 dB SPL at 4m).

The infrasound playbacks were completed from 28 June - 13 July 2011, as these dates were prior to peafowl moult and are the approximate 'middle' of the breeding season. Audible playbacks followed from 19 July - 11 August 2011. Infrasonic playbacks were completed first to ensure that the novel infrasonic playbacks were completed within the breeding season. For each playback session, the peafowl were video recorded for 8 minutes after set up of the playback unit for habituation to the equipment, and to establish their baseline, pre-playback behaviour.

Each experimental track and control track was played at each lek site (a total of 7 sites) determined from field notes and GPS coordinates obtained in 2010 and 2011 (Appendix C). Between sessions, the playback equipment was moved at least 50 m, to avoid interactions between trials at lek sites. I performed playbacks at 7 accessible lek sites, and did not repeat playbacks at any lek site within a 1-hour period (longer when possible). This decreased the probability of habituation by males that have a lek in their territory, but allowed for recording of responses of females who travel and males which may not be associated to a lek site (floater males: as described in Petrie et al., 1991). Playbacks were conducted only when a male was present at the site, and was present for

at least one instance of the acoustic signal. If the peafowl left the area during the period before playback, recorded for 'baseline' behaviour levels, and did not return within the following experimental section, the playback was marked as incomplete and was repeated from the start on a later date.

Playback Data Coding

Behaviours were coded for all video recorded individuals as: displaying (male train open), train shiver (the display in which the peacock vibrated the entire train, starting from the central upper tail coverts and spreading towards the outer coverts in the train), train pulse (the male vibrates the rectrices from the body outwards, which in turn vibrates the elongated train), wing rotation (audible and visible movement of or gyration of the wings in a vertical plane), standing (peafowl on ground, feet touching ground but body not), perching (peafowl on fence, vegetation, or building), preening, walking or running, flying, scratching (peafowl scratches self with feet), eating, calling (any type of vocalization except the hoot dash), allopreening (preening of another peafowl, or being preened by another peafowl), hoot-dashing (the sound and action associated with attempted copulation, see Appendix A: Hoot Call), laying down (the body of the peafowl touches the ground or perch), dustbathing (peafowl toss dirt or pebbles on the feathers while laying down), shaking feathers (done while not displaying), alert (the neck of the peafowl is fully stretched - there are no visible bends in the neck of the peafowl), toward (the peafowl orients his/her head in the direction of the playback unit, using the beak as reference, within 80-100°), and other (any behaviour not encapsulated in the above definitions). In many cases, peafowl engage in more than one behaviour at a time, thus, video recordings were necessary. After 8 minutes of pre-playback recording (to

determine baseline behaviours), the playback started, with either a control or experimental track (selected randomly via random number selection, keeping at least one hour between playbacks at lek sites). The responses of all peafowl on video were recorded, with recordings biased towards recording territory-holding males. Once the playback was complete, I recorded the peafowl's behaviour for another 8 minutes, noting the same behaviours listed above to determine if there was a residual response to acoustic signals by peafowl. The identity of each peafowl, their sex, and their breeding status (adult, moulting, juvenile) were also recorded, where known. Behaviours were coded by reviewing video recordings, as time spent per behaviour. All the information was summarized in a spreadsheet, though because some peafowl could leave the area, or go out of frame on the video recording, to compare recordings, the behaviours were recalculated as a proportion (time spent conducting each behaviour / total time visible). These proportions allowed for comparison between individuals from various playbacks, and allowed for determination of whether audible sound and/or infrasound (and the associated displays) are used as communication signals for peafowl.

I used Mann Whitney-U tests to compare behavioural responses between sexes, between territory holders and floater males, and between resident and intruder playbacks. I rejected the null hypothesis at $\alpha=0.05$ for all tests. Kruskal-Wallis tests were used to compare adult, juvenile, and moulting males' behaviours. Finally, I used Wilcoxon Signed-Rank tests to compare behaviour before playbacks, during playbacks and after playbacks. These non-parametric tests were used due to small sample sizes (Audible: $n = 9$ to 31 , Infrasound: $n = 15$ to 38), which resulted in data that did not conform to a normal distribution. To compare changes of behaviours between the 'prior to' and 'during'

playback sections, and the ‘during’ and ‘post’ playback sections, I subtracted the earlier proportion from the later proportion, yielding a ‘change-in-behaviour’ proportion. I then compared the changes of males to females, of territory holders to floater males, from individuals exposed to resident's signals to individuals exposed to intruder's signals, from individuals and males exposed to experimental and to control tracks, and compared changes from adult males to juvenile males to moulting males. The analysis of the changes in proportions used the same tests (Mann Whitney-U, Wilcoxon Signed-Rank, and Kruskal-Wallis tests) as above for the different comparative groups.

Paternity Analysis

Paternity analysis (Hale et al., 2009; Hanotte et al., 2002) of young was intended to test whether certain male signaling attributes are correlated with male mating success. However, the APZ peafowl population crashed in 2011 (perhaps due to predation, disruption through construction, and/or other possible factors), and only two broods survived (one of which was abandoned by the female, and maternity was unknown). Since such a small sample (three individuals sired by as few as one male), would not provide any insight into the mating choices of females and mating success of the males, this study did not focus on paternity analysis. Instead, female and male behavioural responses to acoustic signals were the focus of this study.

III: RECORDING RESULTS **Recording Data 2009 and 2010**

Four of the seven audible breeding calls (Ka, Keow, Hoot-call, and Eon 2) described in Takahashi and Hasegawa (2008) were observed in 2009 and 2010 as verified through spectrographic analysis (Appendix A for spectrograph examples). Takahashi and

Hasegawa (2008) stated that calls containing more than five notes were infrequently recorded (10.5% of male repetitive calls). Contrary to that assertion 22.7% of all of the calls in 2009 (25.7% in 2010), and 45.5% of the male repetitive calls recorded from the Assiniboine Park Zoo population in the three-day period had more than five notes in 2009 (47.3% in 2010).

Infrasound was detected with audible calls (52% of all calls in 2009, 62.4% of all calls in 2010). Part of the mating display of the peacock called the ‘hoot-dash’ involves both a call and train-based acoustic signal (Petrie et al., 1992). Since it was impossible to determine if the infrasound was associated with the call or the train movement, ‘hoot-dashes’ were excluded and infrasound association with audible calls was calculated again. 33% of audible calls in 2009 were associated with infrasound when ‘hoot-dashes’ were excluded, (63.8% in 2010). Infrasound was correlated with the performance of three display behaviours: pulse train, shiver train, and wing rotations (Table 2). Sixty percent of the shiver train displays in 2009 included infrasound (only 45% in 2010); 57% of the pulse train displays in 2009 were accompanied by infrasound (48% in 2010); and 35% of wing rotation displays in 2009 included infrasound (60% in 2010).

Table 2 summarizes the levels of infrasound across the three display types: pulse train, shiver train, and wing rotation. Displays recorded visually but not acoustically were excluded (such as those at the very beginning or end of video recordings), as the presence or absence of infrasound within these displays cannot be known. Infrasound presence was associated with pulse train and shiver train displays, infrasound was less correlated with wing rotation as the absence of infrasound was more common than presence. Our null hypothesis is that infrasound intensity (absent or at background sound pressure level, low

>10 dB but < 20 dB above background level, pronounced or > 20 dB above background levels) would be independent of display type. I used a Fisher's exact test on the results presented in Table 2 to test for the independence of infrasound level from display type. Display type did not influence infrasound intensity (Table 2; $p = 0.174$, Fisher's exact test).

Table 2: Infrasound Intensity Versus Display Type

Infrasound	Pulse Train		Shiver Train		Wing Rotation	
Year	2009	2010	2009	2010	2009	2010
No Infrasound (0-10 dB) above background (0)	13	233	9	48	8	8
Some Infrasound (10-20 dB) above background (1)	16	95	5	11	3	6
Pronounced Infrasound (>20 dB) above background (2)	39	120	21	29	6	6

A chi-square goodness-of-fit test was also applied to test for the equivalence of infrasound presence across the three display types in 2009, using row 3 of Table 2. My null hypothesis was that pronounced infrasound would be evenly distributed over the three display types. Pronounced infrasound, however, was not evenly distributed across display types: infrasound was detected more often than expected in pulse train displays and less frequently than expected with wing rotation in 2009 (Table 2, row 3; $\chi^2 = 24.817$, $df = 2$, $p < 0.001$).

Our null hypothesis is that infrasound intensity (absent or at background sound pressure level, low > 10 dB but < 20 dB above background level, pronounced or > 20 dB above background levels) would be independent of display type. I used a contingency table analysis on the 2010 results presented in Table 2 to test for the independence of infrasound level from display type (Table 2; $\chi^2 = 90.5588$, $df = 4$, $p < 0.0001$).

Among display types, there is some variation in infrasonic frequencies; wing rotation frequencies are spread between 5 and 14 Hz, whereas shiver train and pulse train have frequencies from 4 - 8 Hz (Figures 2 and 3). Train pulsing has a second pronounced frequency peak from 12 - 14 Hz. Peacock calls (in blue in Figure 2 and Figure 3) appear to peak at 6 - 8 Hz, but infrasound is present from 1 - 20 Hz. As in previous behavioural studies, experimental manipulation was required to determine if peafowl perceive these frequencies, and whether peafowl perceive the signals from all the displays or only a select group, and whether peafowl respond differentially to different display types (Loyau et al., 2007; Lieser et al., 2006; Partan & Marler, 2005). Analysis of the frequency of maximum power in the infrasonic signal (Figure 2, 2009 and Figure 3, 2010) shows that the infrasonic signal is around 4-6 Hz with harmonics at higher frequencies. Responses of both female and male peafowl to these signals were observed to determine if the signal is intersexual, potentially serving as an indicator of male quality and used in female choice, or as an intrasexual signal used in territorial interactions among males.

While viewing video recordings of the peacocks displaying, it appeared that peacocks were more likely to perform some displays when females were near (< 5 m) and other displays when females were far (> 5 m) from the male. I thus tested whether male display elements were contingent on the presence of peahens by testing for the

independence of display components from the maximum distance to the nearest female (Table 3).

This analysis (Table 3) suggests peacocks are more likely to pulse the train when females are close, and more likely to call or shiver train when females are far away.

Table 3: Approximate Distance of Nearest Female from Male Versus Display Type

Distance	Pulse Train	Shiver Train	Wing Rotation	Calls
0 - 1 m	1	1	0	2
1 - 2 m	47	6	5	2
2 - 3 m	25	4	1	0
3 - 4 m	2	3	0	2
4 - 5 m	6	9	2	4
5 - 30 m	1	16	4	6
> 30 m	1	8	0	0

If wing rotation is not dependent on the distance of the female to the displaying male, then our null hypothesis is that the display would be equally distributed among maximum distance categories. A Kolmogorov-Smirnov Test was applied to determine the independence of wing rotation display from female distance (Column “Wing Rotation”, 0 - 1 m to 5 - 30 m, Table 4). Calls and displays exhibited while females were more than 30

Figure 2: Frequency of Maximum Power (Infrasound; Hz) Percentages per Behaviour 2009

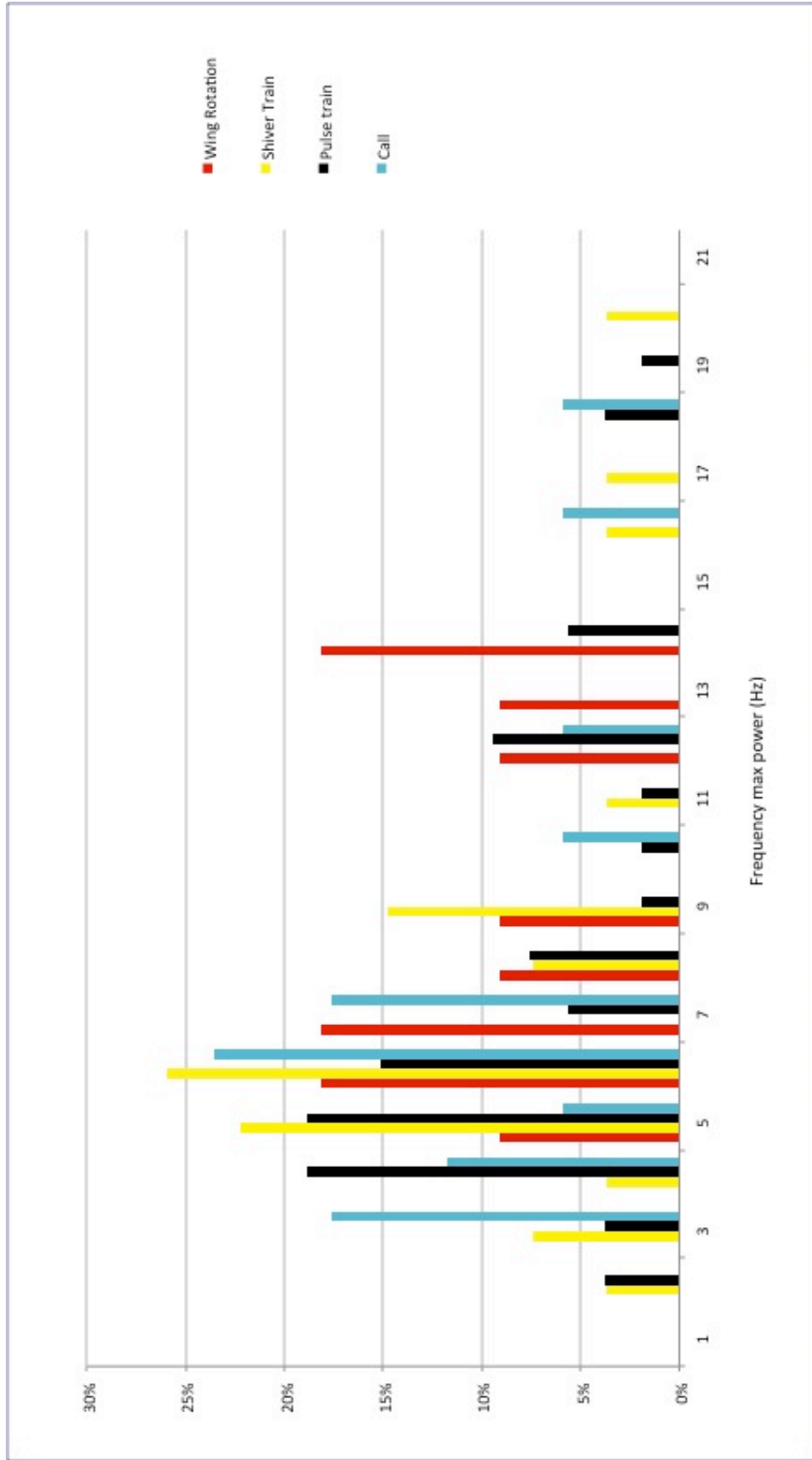
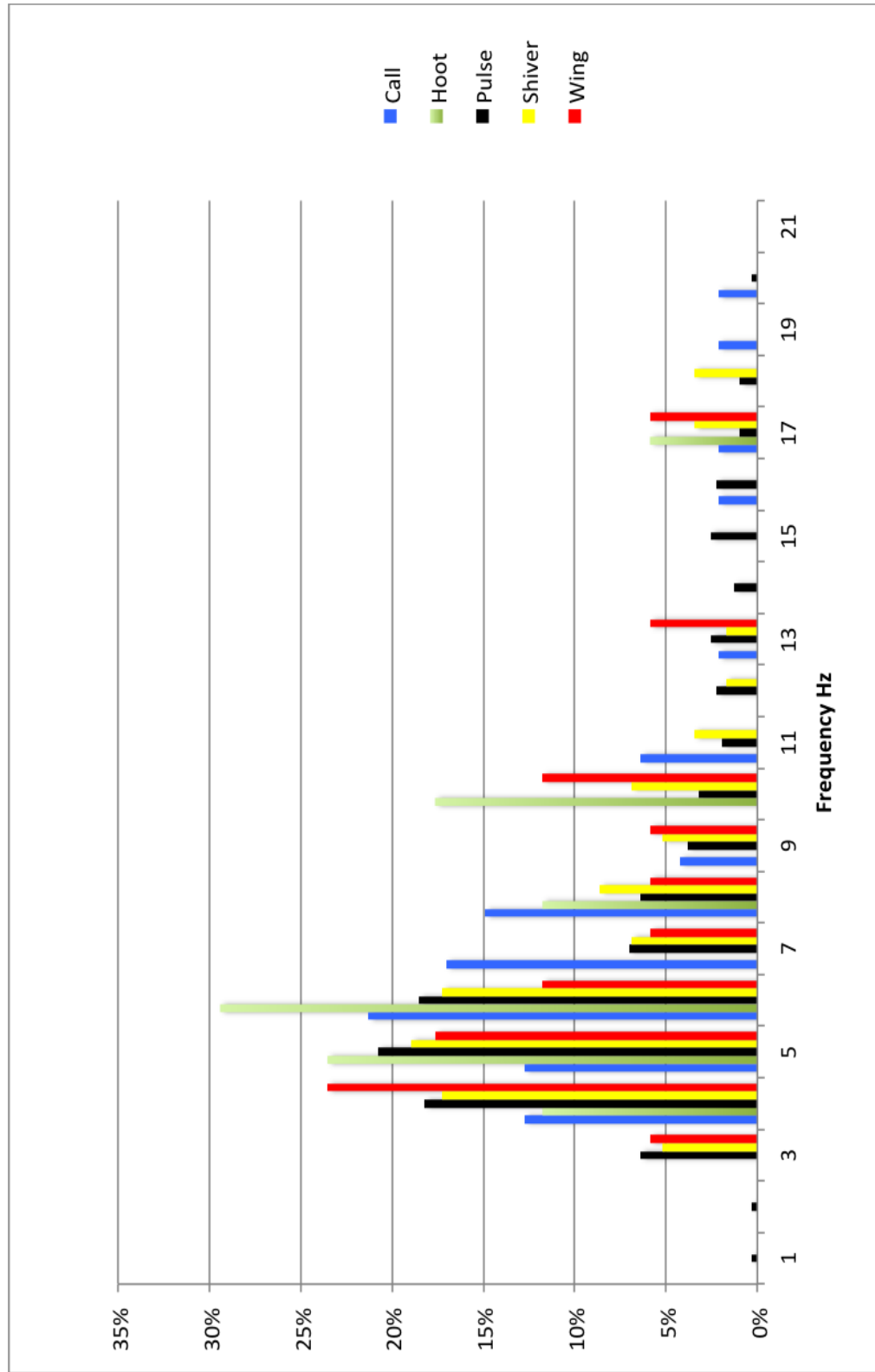


Figure 3: Frequency of Maximum Power (Infrasound; Hz) Percentages per Behaviour 2010



metres away were not included, as females were considered ‘not present’ as defined above. The male’s wing rotation display was independent of female distance (Table 3; $D = 0.16$, $p = > 0.5$). Applying this same test, pulse train displays were dependent on the distance to the female, (Table 3; $n = 82$, $D = 0.39$, $p < 0.01$), with more pulses when the females were close by (Table 3). The shiver train display depended on female distance ($n = 39$, $D = 0.31$, $p < 0.01$); peacocks tended to shiver the train when females were relatively far away (Table 3). The peacock’s calls did not depend on female distance (Table 3; $n = 16$, $D = 0.291$, $0.2 < p < 0.10$). When these data were plotted as percentage of displays versus female distance, it reinforced the fact that males pulsed when females were near and performed other displays at further distances (Figure 4). In 2010, data were re-analysed as a continuous variable, with proportions of display type versus female distance in metres. From this analysis, it was apparent that males tended to pulse their train or complete hoot-dashes at or less than 3 m, performed wing rotation displays at about 3m, and tended to call or shiver between 5-15 m (all distances ± 1 m; Figure 5).

I predicted that peacocks might use buildings and concrete structures to direct and amplify infrasonic signals. The peacock may use the radiating structure to absorb the back wave of the signal and increase sound pressure level (dB) in front of the structure. A contingency table was applied to test the dependence of display characteristics on peacock orientation. Our null hypothesis was that orientation relative to the closest structure would be independent of display type. Peacocks oriented their displays perpendicularly to concrete bunkers and buildings more often than other orientations (Table 4; $\chi^2 = 17.829$, $p = 0.0067$).

Figure 4: Behaviour Proportions at Female Distance (m) in 2009

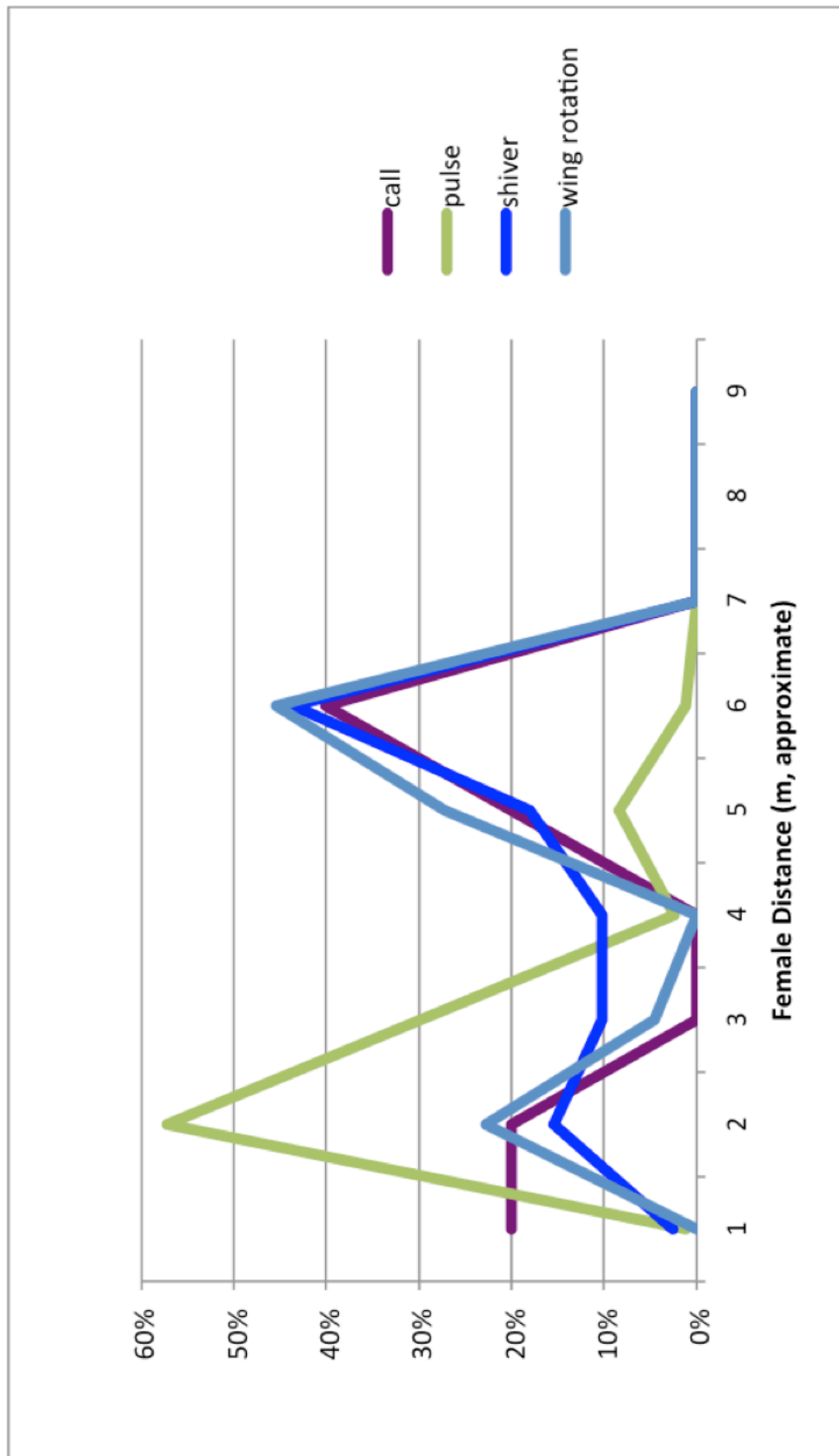


Figure 5: Behaviour Proportions at Female Distance (m) in 2010

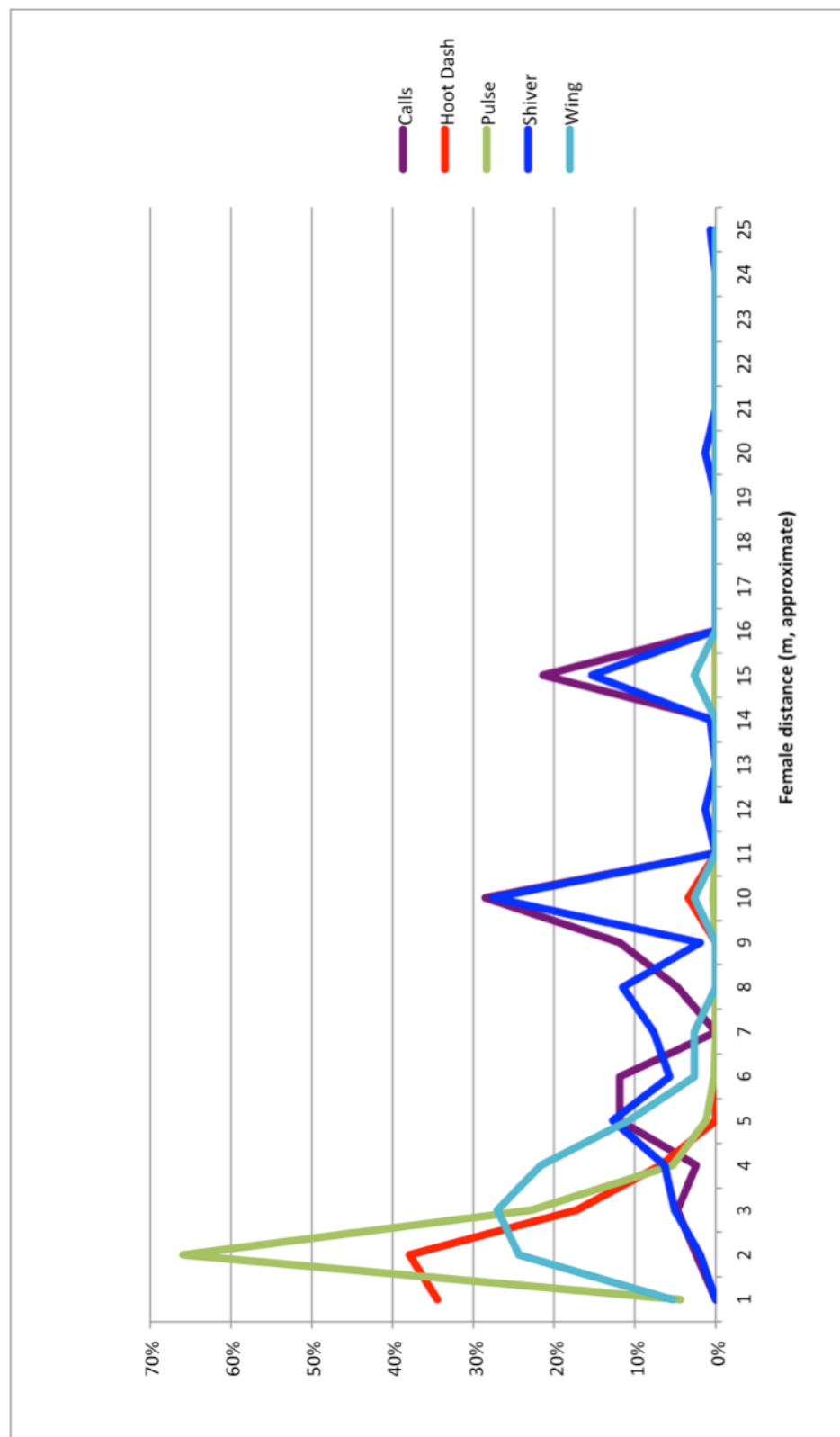


Table 4: Orientation of Displaying Male Versus Display Type 2009

Orientation	Pulse Train	Shiver Train	Wing Rotation	Calls
Towards Structure	18	10	5	4
Perpendicular	42	6	3	0
Away from Structure	12	7	1	0

Many of these 2009 data points (44%), however were from a single peacock (number six); (with the remaining 56% more evenly distributed over 4 peacocks). More examples were obtained in 2010, to address this question again with a larger sample of independent observations. Considered separately, only pulse train was associated with orientation relative to the most proximate man-made structure (Table 6; $\chi^2 = 66.603$, $p < 0.001$); males tended to pulse their train with their head oriented away from buildings. No trends were evident for other display types and orientation. Data from 2011 revealed that peacocks were most often not near a structure of any sort when displaying or calling (Table 7). The ‘both’ category was added for instances in which a structure can be within 2 m of the front and back of the peacock at the same time.

Table 5: Orientation of Displaying Male Versus Display Type 2010

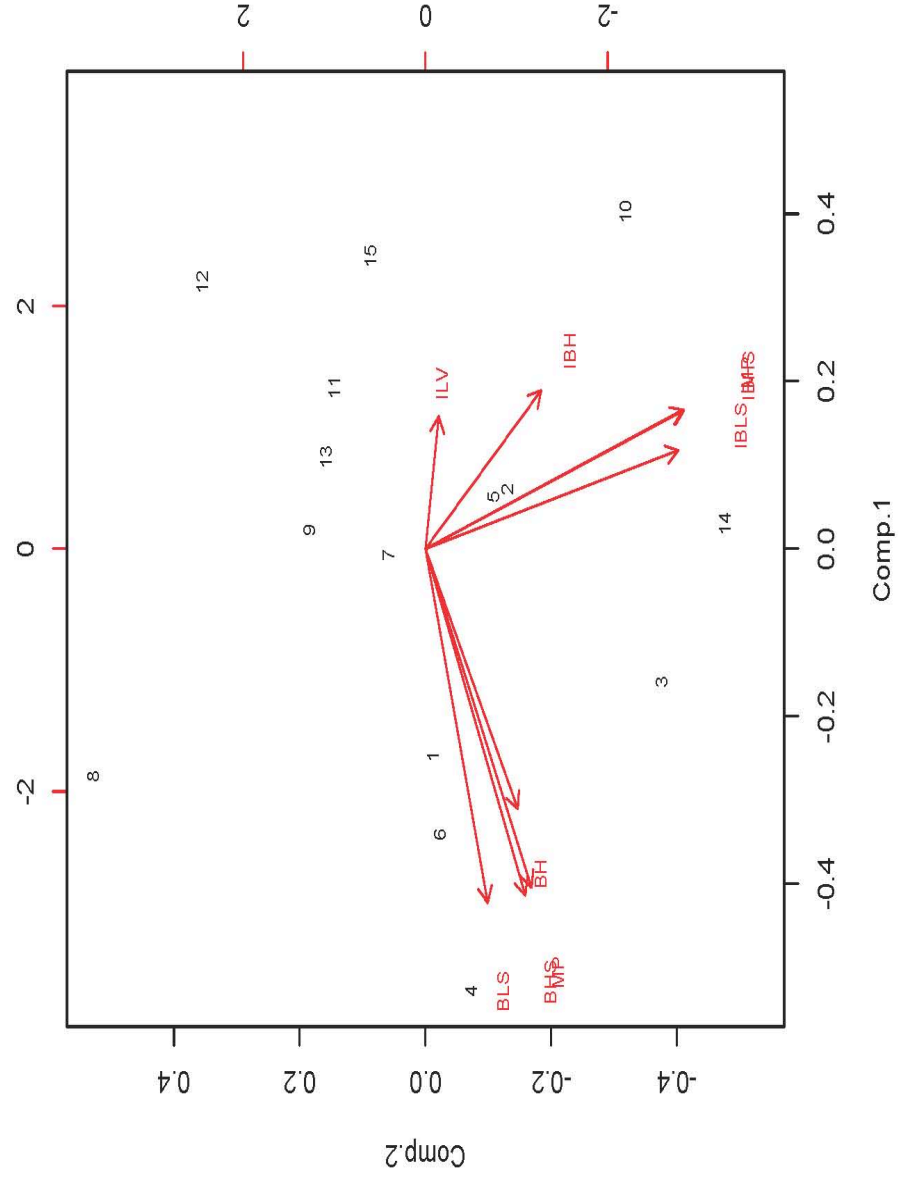
Orientation	Pulse Train	Shiver Train	Wing Rotation	Calls
Towards Structure	30	20	8	3
Perpendicular	64	17	5	4
Away from Structure	123	21	5	9

Table 6: Orientation of Displaying Male Versus Display Type 2011

Orientation	Pulse Train	Shiver Train	Hoot Dash	Wing Rotation	Calls
Towards Structure	19	18	0	6	1
Away from Structure	114	17	2	3	6
Both	10	3	1	2	0
Perpendicular	64	17	3	5	1
None	394	114	25	21	41

I used the recording data from 2010 (as it was the most extensive data set) to test whether certain display behaviours differed from each other based on acoustic properties subjected to principal components and discriminant analyses (Figure 6). I used the average in both infrasound and audible ranges for each behaviour type for each individual male of: the frequency of maximum power for both audible sound and infrasound (Arrows: Audible MP, Infrasound IMP, respectively), the frequency of maximum power's bandwidth maximum (Arrows: Audible BHS, Infrasound IBHS), the frequency of maximum power's bandwidth minimum (Arrows: Audible BLS, Infrasound IBLS), the overall signal bandwidth maximum (Arrows: Audible BH, Infrasound IBH), and the level of infrasound (0, 1, 2) above background levels (Arrow: ILV). Axis 1 accounts for approximately 41% of the variance, whereas component 2 accounts for approximately 34% of the variance. The signal bandwidth minimum was always close to zero, and was excluded from analysis as it did not aid in separation of any display behaviours.

Figure 6: Principal Components Analysis of Infrasonic and Audible Components of Pulse Train Displays (points 1-8) and Shiver Train Displays (points 9-15)



When considering both audible and infrasonic variables, peacock signal attributes tended to have lower frequencies for shiver train displays, and higher frequencies for pulse train displays (Multiple Discriminant Analysis, Figure 6; $\chi^2 = 8.32$, $df = 3$, $p = 0.0398$). Infrasonic components alone were not sufficient to separate the two display types when analysed, which may be due to a limited sample of infrasonic frequencies (0-20 Hz) (Figure 7). Component axis 1 for Figure 7 accounts for approximately 63% of the variance, while component axis 2 accounts for approximately 28% of the variance.

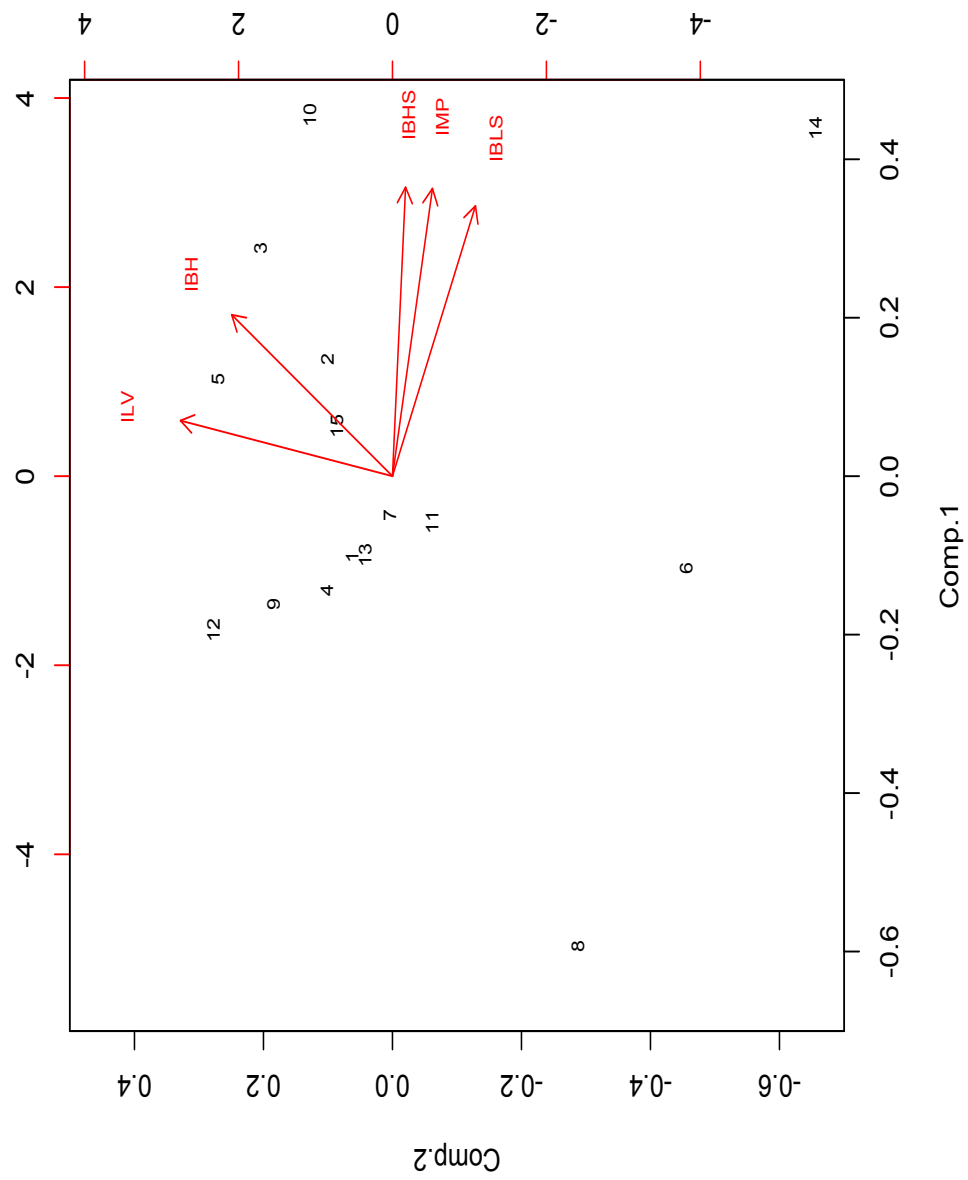
IV: PLAYBACK RESULTS

INFRASOUND

Baseline Tests

To determine if different groups (males versus females, resident signals versus intruder signals, adult versus juvenile versus moulting males, territorial versus floater males) differed in their behaviour prior to playback, during playback, or in the post playback period (referred to as PRE, DUR and POST, respectively), I used Mann-Whitney-U tests or Kruskal-Wallis tests as outlined in the Methods section.

Figure 7: Principal Components Analysis of Infrasonic Components of Pulse Train Displays (points 1-8), and Shiver Train Displays (points 9-15)



Males Versus Females

Pre-playback

Prior to playback (Table 7), males oriented towards the subwoofer more often than females for the following playbacks: wing rotation (Mann Whitney-U test, $U_{25} = 13.5$, $Z = -3.065$, $p = 0.0022$), shiver train (Mann Whitney-U test $U_{34} = 73.5$, $Z = -2.208$, $p = 0.0273$), and call (Mann Whitney-U test, $U_{37} = 99$, $Z = -2.088$, $p = 0.0368$). For pulse train and positive control, males and females did not orient differently. Males and females were not significantly more or less alert prior to the playback.

Females were never observed calling prior to, during, or after playbacks. The difference between the lack of calling by females, and presence of calling by males was significant for wing rotation (Mann Whitney-U test, $U_{25} = 28$, $Z = -2.477$, $p = 0.0133$), and shiver train playbacks (Mann Whitney U-test, $U_{34} = 84$, $Z = -2.443$, $p = 0.0146$). Females and males differed in walking/running prior to playback for wing rotation (Mann Whitney-U test, $U_{25} = 10$, $Z = -3.315$, $p = 0.0009$).

Table 7: Prior to Playback (Infrasound) Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Wing Rotation	Males	Towards	0.276 \pm 0.032
Wing Rotation	Females	Towards	0.078 \pm 0.034
Shiver Train	Males	Towards	0.321 \pm 0.059
Shiver Train	Females	Towards	0.141 \pm 0.046
Call	Males	Towards	0.265 \pm 0.037
Call	Females	Towards	0.148 \pm 0.032
Wing Rotation	Males	Calling	0.009 \pm 0.001
Wing Rotation	Females	Calling	0 \pm 0
Shiver Train	Males	Calling	0.005 \pm 0.0003
Shiver Train	Females	Calling	0 \pm 0
Wing Rotation	Males	Walking/Running	0.107 \pm 0.039
Wing Rotation	Females	Walking/Running	0.003 \pm 0.003

During Playback

Males again oriented towards the subwoofer more often than females during playbacks (Table 8) for the following playbacks: wing rotation (Mann Whitney-U test, $U_{25} = 12$, $Z = -3.151$, $p = 0.0016$) and shiver train (Mann Whitney-U test, $U_{34} = 75$, $Z = -2.198$, $p = 0.0279$). No other significant differences were detected for orientation. Males were significantly more alert than females during playbacks (Table 8) for wing rotations (Mann Whitney-U test: $U_{25} = 38.5$, $Z = -1.979$, $p = 0.0478$) and calls (Mann Whitney-U test: $U_{37} = 97.5$, $Z = -2.587$, $p = 0.0097$). Females were never observed calling during playbacks (Table 8). The difference between males and females was significant with respect to calling for wing rotation playback (Mann Whitney-U test: $U_{25} = 28$, $Z = -2.475$, $p = 0.0133$), shiver train playbacks (Mann Whitney-U test: $U_{35} = 72$, $Z = -2.786$, $p = 0.0053$), and call playbacks (Mann Whitney-U test, $U_{37} = 98$, $Z = -2.735$, $p = 0.0062$). Females and males walked and ran at similar proportions during playback.

Table 8: During Playback (Infrasound), Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Wing Rotation	Males	Towards	0.341 \pm 0.052
Wing Rotation	Females	Towards	0.060 \pm 0.045
Shiver Train	Males	Towards	0.253 \pm 0.040
Shiver Train	Females	Towards	0.107 \pm 0.041
Wing Rotation	Males	Alert	0.068 \pm 0.038
Wing Rotation	Females	Alert	0.0 \pm 0.0
Call	Males	Alert	0.032 \pm 0.012
Call	Females	Alert	0.001 \pm 0.001
Wing Rotation	Males	Calling	0.016 \pm 0.001
Wing Rotation	Females	Calling	0 \pm 0
Shiver Train	Males	Calling	0.012 \pm 0.001
Shiver Train	Females	Calling	0 \pm 0
Call	Males	Calling	0.013 \pm 0.001
Call	Females	Calling	0 \pm 0

Post-playback

Males faced the subwoofer more than females after playback during pulse train playback (Mann Whitney-U test: $U_{20} = 7.5$, $Z = 2.0156$, $p = 0.0438$), and during the positive control (Mann Whitney-U test: $U_{14} = 4.5$, $Z = -2.0125$, $p = 0.0442$). Furthermore, males were alert more often than females after playback for the wing rotation playback (Mann Whitney-U test, $U_{25} = 35$, $Z = -2.145$, $p = 0.032$). Males called more than females after playback for the wing rotation (Mann Whitney-U test: $U_{25} = 38.5$, $Z = -1.9793$, $p = 0.0478$), and shiver train playbacks (Mann Whitney-U test: $U_{34} = 84$, $Z = 2.4425$, $p = 0.0146$). Males walked more than females after playback for the infrasound positive control (Mann Whitney-U test, $U_{14} = 4.5$, $Z = -2.0125$, $p = 0.0442$).

Table 9: Post Playback (Infrasound), Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Pulse Train	Males	Towards	0.180 \pm 0.011
Pulse Train	Females	Towards	0 \pm 0
Wing Rotation	Males	Alert	0.060 \pm 0.006
Wing Rotation	Females	Alert	0 \pm 0
Wing Rotation	Males	Calling	0.007 \pm 0.001
Wing Rotation	Females	Calling	0 \pm 0
Shiver Train	Males	Calling	0.008 \pm 0.001
Shiver Train	Females	Calling	0 \pm 0
Control	Males	Walking/Running	0.210 \pm 0.013
Control	Females	Walking/Running	0 \pm 0

Residents Versus Intruders

To test whether peafowl responded differently to resident signals or intruder signals, experimental tracks were identified as such, and responses were compared using Mann Whitney-U tests.

Pre-playback

Individuals behaved differentially prior to the playback (Table 10) of a resident's or intruder's call (Mann Whitney-U test: $U_{37} = 111.5$, $Z = -2.015$, $p = 0.044$); individuals faced the playback unit more when calls from residents were to be broadcast. Individuals did not behave differentially, however, in terms of alertness, calling, walking or running prior to playback of resident versus intruder signals of any sort (i.e. pulse train, shiver train, wing rotation, or positive control).

Table 10: Prior to Playback (Infrasound Call Playback), Residents Versus Intruders Towards Orientation Behaviour Proportions

Group	Mean \pm SE
Resident Signals	0.272 \pm 0.009
Intruder Signals	0.171 \pm 0.008

During Playback

Individuals did not respond differently during playback to residents' or intruders' signals in terms of their orientation, alertness, or calling. Individuals walked and ran more during the infrasonic shiver train playbacks when signals were given by intruding as opposed to resident males (Table 11, Mann Whitney-U test: $U_{34} = 81$, $Z = -2.306$, $p = 0.0211$).

Table 11: During Playback (Infrasound Shiver Train Playback), Residents Versus Intruders Walking and Running Behaviour Proportions

Group	Mean \pm SE
Resident Signals	0.158 \pm 0.012
Intruder Signals	0.317 \pm 0.019

Post-playback

Individuals did not respond differently after playback to residents versus intruders in terms of orientation, or calling. Individuals were alert more often, however, after residents' sounds for infrasonic call playbacks, (Table 12, Mann Whitney-U test: $U_{37} = 133$, $Z = -2.3602$, $p = 0.0183$). Additionally, individuals walked or ran more often after intruders' than residents' infrasonic call playbacks (Table 12, Mann Whitney-U test, $U_{37} = 100$, $Z = -2.3731$, $p = 0.0176$).

Table 12: Post Playback (Infrasound Call Playback), Residents Versus Intruders Behaviour Proportions

Group	Behaviour	Mean \pm SE
Resident Signals	Alert	0.070 \pm 0.011
Intruder Signals	Alert	0 \pm 0
Resident Signals	Walking/Running	0.137 \pm 0.012
Intruder Signals	Walking/Running	0.271 \pm 0.010

Adult, Juvenile, and Moulting Males

Pre-playback

Adult, juvenile, and moulting males did not show differential orientation, and were similar in their orientation, alertness, and calling rates prior to playback of calls, pulse train, wing rotation, or positive controls (Table 13). Juveniles walked and ran more than adults prior to infrasonic shiver train playbacks (Mann Whitney-U test: $U_{21} = 9$, $Z = -2.314$, $p = 0.0207$).

Table 13: Prior to Playback (Infrasound Shiver Train Playback), Adult, Juvenile, and Moulting Males Walking and Running Behaviour Proportions

Group	Mean \pm SE
Adult Males	0.179 \pm 0.014
Juvenile Males	0.632 \pm 0.106

During Playback

Adult, juveniles, and moulting males did not differ in any measured response during playback.

Post-playback

Adult, juveniles, and moulting males did not differ in any measured response after playback.

Territory-Holding Males Versus Floater Males

Pre-playback

Territory holders oriented towards the subwoofer more than floaters prior to playback (Table 14) of infrasound produced in the context of pulse trains (Mann Whitney-U test: $U_{16} = 13.5$, $Z = -2.099$, $p = 0.0358$). Territory holders were also alert more often than floaters prior to playbacks of shiver trains (Mann Whitney-U test: $U_{20} = 25$, $Z = -2.468$, $p = 0.0081$). Territory holders called more than floaters prior to playback for infrasonic wing rotation playback (Mann Whitney-U test: $U_{14} = 5$, $Z = -2.587$, $p = 0.0097$), and infrasonic shiver train playbacks (Mann Whitney-U test: $U_{20} = 29$, $Z = -2.097$, $p = 0.0360$).

Table 14: Prior to Playback (Infrasound), Territory Holders and Floater Males Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Pulse Train	Territory Holders	Towards	0.359 \pm 0.021
Pulse Train	Floater Males	Towards	0.220 \pm 0.017
Shiver Train	Territory Holders	Alert	0.037 \pm 0.004
Shiver Train	Floater Males	Alert	0 \pm 0
Wing Rotation	Territory Holders	Calling	0.014 \pm 0.001
Wing Rotation	Floater Males	Calling	0 \pm 0
Shiver Train	Territory Holders	Calling	0.006 \pm 0.001
Shiver Train	Floater Males	Calling	0.003 \pm 0.001

During Playback

Floater males walked and ran more than territory holders (Table 15) during infrasonic call playbacks (Mann Whitney-U test: $U_{37} = 25.5$, $Z = -2.084$, $p = 0.0372$), and shiver train playbacks (Mann Whitney-U test: $U_{20} = 25$, $Z = -2.129$, $p = 0.0332$). During playback, territory holders faced the subwoofer more than floaters during infrasonic call playbacks (Mann Whitney-U test, $U_{20} = 21$, $Z = -2.395$, $p = 0.0166$), and shiver train playbacks (Mann Whitney-U test, $U_{34} = 27$, $Z = -1.972$, $p = 0.0486$). Territory holders were not more or less alert than floaters during playback and did not differ in terms of time devoted to walking or running, though territory holders called more than floaters during infrasonic wing rotation (Mann Whitney-U test: $U_{14} = 5$, $Z = -2.582$, $p = 0.0098$), shiver train (Mann Whitney-U test: $U_{20} = 20.5$, $Z = -2.692$, $p = 0.0071$), and pulse train playbacks (Mann Whitney-U test: $U_{16} = 17$, $Z = -1.967$, $p = 0.0492$).

Table 15: During Playback (Infrasound), Territory Holders and Floater Males Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Call	Territory Holders	Walking/Running	0.191 \pm 0.022
Call	Floater Males	Walking/Running	0.353 \pm 0.034
Shiver Train	Territory Holders	Walking/Running	0.131 \pm 0.015
Shiver Train	Floater Males	Walking/Running	0.344 \pm 0.024
Call	Territory Holders	Towards	0.448 \pm 0.020
Call	Floater Males	Towards	0.213 \pm 0.017
Shiver Train	Territory Holders	Towards	0.349 \pm 0.019
Shiver Train	Floater Males	Towards	0.150 \pm 0.012
Wing Rotation	Territory Holders	Calling	0.024 \pm 0.002
Wing Rotation	Floater Males	Calling	0 \pm 0
Shiver Train	Territory Holders	Calling	0.017 \pm 0.002
Shiver Train	Floater Males	Calling	0.002 \pm 0.001
Pulse Train	Territory Holders	Calling	0.055 \pm 0.007
Pulse Train	Floater Males	Calling	0.005 \pm 0.002

Post-playback

Territory holders faced the subwoofer more often than floaters after infrasonic shiver train (Mann Whitney-U test: $U_{20} = 4$, $Z = 3.6597$, $p = 0.0003$), and pulse train (Mann Whitney-U test: $U_{16} = 15$, $Z = 1.9762$, $p = 0.0481$) playbacks (Table 16). Territory holders spent a greater proportion of their time alert after playback than floaters for infrasonic wing rotation (Mann Whitney-U test, $U_{14} = 5$, $Z = 2.582$, $p = 0.0098$), and shiver train playbacks (Mann Whitney-U test, $U_{20} = 24$, $Z = 2.4991$, $p = 0.0125$).

Territory holders called more often than floaters subsequent to playbacks of infrasound associated with infrasonic wing rotation (Mann Whitney-U test: $U_{14} = 7.5$, $Z = 2.3247$, $p = 0.0201$), and shiver train displays (Mann Whitney-U test: $U_{20} = 23.5$, $Z = 2.4581$, $p = 0.014$). Territory holders walked and ran more than floaters after playback of infrasound

derived from shiver train displays (Mann Whitney-U test, $U_{20} = 22.5$, $Z = 2.3545$, $p = 0.0185$).

Table 16: Post Playback (Infrasound), Territory Holders and Floater Males Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Shiver Train	Territory Holders	Towards	0.357 \pm 0.017
Shiver Train	Floater Males	Towards	0.036 \pm 0.007
Pulse Train	Territory Holders	Towards	0.270 \pm 0.021
Pulse Train	Floater Males	Towards	0.074 \pm 0.012
Wing Rotation	Territory Holders	Alert	0.112 \pm 0.015
Wing Rotation	Floater Males	Alert	0 \pm 0
Shiver Train	Territory Holders	Alert	0.070 \pm 0.009
Shiver Train	Floater Males	Alert	0.003 \pm 0.001
Wing Rotation	Territory Holders	Calling	0.011 \pm 0.001
Wing Rotation	Floater Males	Calling	0 \pm 0
Shiver Train	Territory Holders	Calling	0.014 \pm 0.002
Shiver Train	Floater Males	Calling	0.004 \pm 0.001
Shiver Train	Territory Holders	Walking/Running	0.206 \pm 0.012
Shiver Train	Floater Males	Walking/Running	0.075 \pm 0.016

Behaviour Changes Between Sections (PRE, DUR, and POST) and Groups

To test whether there were changes in behaviour of individuals between the PRE versus DUR, and DUR versus POST playback periods, I used Wilcoxon Signed-Rank tests (including tied values). To investigate specific groups of individuals (males and females; individuals exposed to residents' and intruders' signals; territory holders and floater males; and adult, juvenile, and moulting males), and their changes in behaviour, I subtracted the PRE values from DUR values, and DUR values from POST values (giving a change in proportions, wherein a positive value indicates an increase in that behaviour, and a negative value indicates a decrease in that behaviour).

Pre-playback Versus During Playback

Peafowl respond to infrasound by calling. This is significant (at $\alpha = 0.05$) for shiver train playback (Wilcoxon Signed-Rank test: $T_{34} = 195.21$, $Z = -1.962$, $p = 0.0498$), along with the positive control playback (Wilcoxon Signed-Rank test: $T_{14} = 21.25$, $Z = -2.201$, $p = 0.0277$). Males also appeared to call in response to pulse train, wing rotation, and call infrasound playbacks, but those contrasts fell short of statistical significance (Wilcoxon Signed-Rank tests: $T_{20} = 67.11$, $Z = -1.682$, $p = 0.0926$; $T_{26} = 104.47$, $Z = -1.804$, $p = 0.0712$; and $T_{37} = 237.83$, $Z = -1.924$, $p = 0.0543$ respectively). There were no apparent changes between PRE and DUR in orientation, recorded as ‘away’ or ‘towards’ with ‘towards’ defined as the head or beak facing within ± 45 degrees of the playback device in any of the playbacks. When peafowl were preening or eating, they were also recorded as facing ‘away’. Only infrasonic pulse train playbacks caused a change in peafowl alertness between PRE and DUR, which increased from prior to playback to during playback (Wilcoxon Signed-Rank test: $T_{20} = 41.27$, $Z = -2.580$, $p = 0.0099$). Infrasonic wing playbacks elicited a change in peafowl movement (walking and running), which increased from prior to playback to during playback (Wilcoxon Signed-Rank test: $T_{25} = 82.11$, $Z = -2.372$, $p = 0.0177$).

During Playback Versus Post-playback

Orientation towards the subwoofer decreased after playback for all playback types, and significantly decreased between the playback and post-playback periods of infrasonic pulse train (Wilcoxon Signed-Rank test: $T_{20} = 30.97$, $Z = -2.938$, $p = 0.0033$) and infrasonic call playbacks (Wilcoxon Signed-Rank test: $T_{37} = 196.11$, $Z = -2.529$, $p =$

0.0114). Alertness significantly decreased between during and after infrasonic pulse train (Wilcoxon Signed-Rank test: $T_{20} = 57.47$, $Z = -2.017$, $p = 0.0437$) and positive control playbacks (Wilcoxon Signed-Rank test: $T_{14} = 25.49$, $Z = -1.960$, $p = 0.0499$). Calling decreased from DUR to POST in all instances, significantly decreasing for wing playback (Wilcoxon Signed-Rank test: $T_{25} = 66.87$, $Z = -2.759$, $p = 0.0058$), and pulse train playback (Wilcoxon Signed-Rank test: $T_{20} = 45.62$, $Z = -2.429$, $p = 0.0152$).

Males and Females

Pre-playback to During Playback

Males and females did not differ in change in response from prior to playback to during playback via orientation towards the subwoofer, alertness, or walking and running. Males called more during infrasonic call playbacks than prior to those playbacks (Table 17; Mann Whitney-U test: $U_{37} = 112$, $Z = 2.055$, $p = 0.0398$); whereas females did not call before or during playbacks.

Table 17: Prior to During (Infrasound Call Playback) Males and Females Changes in Calling Behaviour Proportions

Group	Mean \pm SE
Males	0.011 \pm 0.001
Females	0 \pm 0

During Playback to Post-playback

Males and females did not differ in their change in response from DUR to POST via orientation towards the subwoofer or alertness. Males increased calling in response

from DUR to POST in the infrasonic wing rotation playback (Table 19; Mann Whitney-U test: $U_{25} = 35$, $Z = -2.0259$, $p = 0.0428$), however, females did not call.

For the playback to post-playback period subsequent to infrasonic wing rotation playbacks (Table 18; Mann Whitney-U test: $U_{25} = 31$, $Z = 2.0536$, $p = 0.0400$), males decreased locomotion after playback, whereas females increased locomotory behaviour.

Table 18: During to Post (Infrasound Wing Rotation Playback) Males and Females Changes in Behaviour Proportions

Group	Behaviour	Mean \pm SE
Males	Calling	0.009 \pm 0.001
Females	Calling	0 \pm 0
Males	Walking/Running	-0.061 \pm 0.019
Females	Walking/Running	0.152 \pm 0.028

Positive Controls and Experimental Tracks

Pre-playback to During Playback

There were no differences between controls and experimental playbacks for any behaviour between the pre-playback and playback periods for infrasonic wing rotation, shiver train, pulse train, or call.

During Playback to Post-playback

Similarly, no differences were detected from DUR to POST between controls or experimental playbacks in any of the behaviours for infrasonic wing rotation. For infrasonic shiver train playbacks, alertness differed between control and experiment for all individuals for DUR to POST (Table 19; Mann Whitney-U test: $U_{49} = 166$, $Z = -$

2.1917, $p = 0.0284$). There were no differences between controls and experimental playbacks in any of the behaviours from DUR to POST for infrasound pulse train, or call.

Table 19: During to Post (Infrasound Shiver Train Playback), Controls and Experimentals Changes in Alert Behaviour Proportions

Group	Mean \pm SE
Control	-0.059 \pm 0.008
Experiment	0.004 \pm 0.002

Residents and Intruders

Pre-playback to During Playback

Individuals differed in response to residents' signals versus intruders' signals from PRE to DUR (Table 20) with regard to orientation towards the subwoofer in response to infrasonic calls (Mann Whitney-U test: $U_{37} = 101$, $Z = 2.330$, $p = 0.0198$); intruder-signal playbacks resulted in individuals increasing the proportion of time spent looking towards the playback unit more than resident-produced signals. Individuals increased alertness from PRE to DUR for residents' signals more than intruders' signals (which showed a decrease in alertness) for infrasonic wing rotation (Mann Whitney-U test: $U_{25} = 47$, $Z = 1.9857$, $p = 0.0471$).

Individuals called more in response to residents and intruders from PRE to DUR in response to infrasonic pulse train playback (Mann Whitney-U test: $U_{20} = 25$, $Z = -2.112$, $p = 0.0347$). No change in behaviour from PRE to DUR via walking and running was detected for resident versus intruder playbacks.

Table 20: Prior to During (Infrasound), Residents' and Intruders' Signals Changes in Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Call	Resident Signals	Towards	-0.012 \pm 0.010
Call	Intruder Signals	Towards	0.086 \pm 0.006
Wing Rotation	Resident Signals	Alert	0.019 \pm 0.004
Wing Rotation	Intruder Signals	Alert	-0.016 \pm 0.004
Pulse Train	Resident Signals	Calling	0.006 \pm 0.002
Pulse Train	Intruder Signals	Calling	0.038 \pm 0.008

During Playback to Post-playback

Further, changes in response from DUR to POST were not evident in contrasting those changes for resident versus intruder playbacks.

Territory Holders Versus Floater Males

Pre-playback to During Playback

Territory holders and floaters differed in change in response from PRE to DUR for orientation during infrasonic shiver train playbacks (Table 21; Mann Whitney-U test: $U_{20} = 19$, $Z = 2.572$, $p = 0.0101$); territory holders increased, while floaters decreased the amount of time facing the playback unit. Territory holders and floaters also differed in change in response from PRE to DUR for walking and running in response to infrasonic pulse train playbacks (Table 21; Mann Whitney-U test: $U_{16} = 14$, $Z = 2.021$, $p = 0.0433$); floaters increased walking and running more than territory holders from PRE to DUR.

Table 21: Prior to During (Infrasound) Territory Holders and Floater Males Changes in Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Shiver Train	Territory Holders	Towards	0.103 \pm 0.022
Shiver Train	Floater Males	Towards	-0.289 \pm 0.039
Pulse Train	Territory Holders	Walking/Running	-0.171 \pm 0.031
Pulse Train	Floater Males	Walking/Running	0.029 \pm 0.005

During Playback to Post-playback

Territory holders increased walking and running from DUR to POST, while floaters decreased their walking and running during the same period in response to infrasonic shiver train playbacks (Table 22; Mann Whitney-U test: $U_{20} = 19.5$, $Z = 2.501$, $p = 0.0124$). Territory holders did not differ from floaters in terms of changes in orientation, alertness or calling from DUR to POST.

Table 22: During to Post (Infrasound Shiver Train Playbacks) Territory Holders and Floater Males Changes in Walking and Running Behaviour Proportions

Group	Mean \pm SE
Territory Holders	0.014 \pm 0.016
Floater Males	-0.081 \pm 0.051

In summary, Table 23 outlines the positive (increases in behaviour) and negative (decreases in behaviour) changes for the five infrasonic playback types. For the changes from prior to during playback, alertness and calling proportions increased for all playback types. Once playbacks were over, calling decreased for all playback types, however, alertness only decreased after playback (POST-DUR) for pulse train, wing rotation, and the positive control. Alertness increased steadily for the “POST-DUR” (i.e. from during playback to post playback) period for call and shiver train playbacks. Walking and

running increased from prior to playback to during playback for all types of playback except pulse train. Overall, individuals decreased walking and running behaviours after all playbacks. Responses of orientation towards the subwoofer were mixed among the playback types; increasing from prior to during playback for call and wing rotation, and decreasing for all others. Despite this variation, orientation towards the subwoofer decreased after playback for all playback types.

Table 23: Overall Average Peafowl Changes in Behaviour Proportions From Pre-Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Five Infrasonic Playback Types

	Orientation		Alertness		Calling		Walking/Running	
	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR
Call	+0.037	-0.091	+0.012	+0.015	+0.007	-0.005	+0.014	-0.077
Shiver Train	-0.056	-0.033	+0.011	+0.004	+0.005	-0.002	+0.008	-0.074
Pulse Train	-0.026	-0.126	+0.112	-0.073	+0.018	-0.019	-0.129	-0.022
Wing Rotation	+0.045	-0.016	-0.002	-0.006	+0.005	-0.007	+0.094	-0.003
Positive Control	-0.091	-0.092	+0.040	-0.059	+0.022	-0.020	+0.048	-0.043

We further hypothesized that males use their train to perceive the infrasound, and examined their changes in rate of display. However, Wilcoxon Signed-Rank tests determined that there were no significant differences in changes in display behaviour proportions (i.e. shiver train, pulse train, wing rotation, hoot-dash, and displaying) between PRE and DUR, or DUR and POST for any playbacks. Table 24 shows the average male changes in display. No trends were detected.

Table 24: Overall Average Male Changes in Display Behaviour Proportions From Pre-Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Infrasonic Playbacks

	DUR-PRE	POST-DUR
Calling	-0.021	-0.005
Wing Rotation	-0.046	+0.065
Pulse Train	+0.060	-0.011
Shiver Train	-0.048	-0.019
Control	-0.024	-0.064

AUDIBLE

Baseline tests

As in the infrasound tests, to determine if different groups (males and females; territory holders and floater males; individuals exposed to signals from residents or intruders; and adult, juvenile, and moulting males) differed in their expression of behaviour prior to playback, during playback, or during the post-playback period (referred to as PRE, DUR and POST, respectively), I used Mann Whitney-U tests, or Kruskal-Wallis tests as outlined in the Methods section.

Males Versus Females

Pre-Playback

Prior to playback, males faced the playback unit more than females for trials slated to involve audible components of the shiver train (Table 25; Mann Whitney-U test: $U_{24} = 15$, $Z = -2.383$, $p = 0.0172$). Males and females did not vary in alertness prior to

playback. Females walked and ran more than males prior to playback of audible components of wing rotation displays (Table 25; Mann Whitney-U test: $U_{22} = 19$, $Z = -2.261$, $p = 0.0238$).

Table 25: Pre-playback (Audible) Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Shiver Train	Males	Towards	0.154 \pm 0.027
Shiver Train	Females	Towards	0.044 \pm 0.027
Wing Rotation	Males	Walking/Running	0.012 \pm 0.034
Wing Rotation	Females	Walking/Running	0.416 \pm 0.147

During Playback

Males oriented toward the playback unit more than females during the playback of audible calls (Table 26; Mann Whitney-U test: $U_{28} = 57.5$, $Z = -1.972$, $p = 0.0486$) and called more than females during those playbacks (Table 26; Mann Whitney-U test: $U_{28} = 60$, $Z = -2.477$, $p = 0.0133$). Males and females did not vary in alertness during playback though females walked and ran more than males during playbacks of audible components of wing rotation displays (Table 26; Mann Whitney-U test: $U_{22} = 22.5$, $Z = -2.039$, $p = 0.0415$).

Table 26: During Playback (Audible) Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Call	Males	Towards	0.332 \pm 0.056
Call	Females	Towards	0.198 \pm 0.084
Call	Males	Calling	0.019 \pm 0.008
Call	Females	Calling	0 \pm 0
Wing Rotation	Males	Walking/Running	0.158 \pm 0.066
Wing Rotation	Females	Walking/Running	0.335 \pm 0.072

Post-playback

Females faced the playback unit subsequent to playback more than males for audible positive control wing rotation playbacks (Table 27; Mann Whitney-U test: $U_{16} = 14.5$, $Z = 2.013$, $p = 0.0441$). Males faced the playback unit after playback more than females during audible call (Table 27; Mann Whitney-U test: $U_{28} = 43$, $Z = 2.8138$, $p = 0.0049$), and audible hoot-dash (Table 27; Mann Whitney-U test: $U_{22} = 8$, $Z = 2.5253$, $p = 0.0116$) playbacks. Males and females did not differ in alertness or calling after playback. Males and females also differed in walking and running after playback for audible call playbacks with males locomoting more than females (Table 27; Mann Whitney-U test: $U_{28} = 42$, $Z = 3.1328$, $p = 0.0017$).

Table 27: Post Playback (Audible) Males and Females Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Positive Control	Males	Towards	0.048 \pm 0.006
Positive Control	Females	Towards	0.198 \pm 0.029
Call	Males	Towards	0.186 \pm 0.057
Call	Females	Towards	0.022 \pm 0.15
Hoot-Dash	Males	Towards	0.109 \pm 0.023
Hoot-Dash	Females	Towards	0 \pm 0
Call	Males	Walking/Running	0.156 \pm 0.050
Call	Females	Walking/Running	0 \pm 0

Residents and Intruders

Pre-playback

Individuals expressed more walking and running prior to playback slated to involve resident sounds than intruder sounds for audible components of wing rotation displays (Table 28; Mann Whitney-U test: $U_{22} = 31$, $Z = -2.174$, $p = 0.0297$). Individuals

also exhibited more walking and running prior to playback to intruder sounds than resident sounds for audible components of shiver train displays (Table 28; Mann Whitney-U test: $U_{24} = 32.5$, $Z = -2.48$, $p = 0.0132$). Apart from these locomotory differences, there were no differences in behaviour prior to resident versus intruder playbacks prior in terms of orientation, alertness or calling.

Table 28: Pre-playback (Audible) Residents and Intruders Walking and Running Behaviour Proportions

Playback Type	Group	Mean \pm SE
Wing Rotation	Resident Signals	0.283 \pm 0.023
Wing Rotation	Intruder Signals	0.095 \pm 0.016
Shiver Train	Resident Signals	0.094 \pm 0.007
Shiver Train	Intruder Signals	0.319 \pm 0.020

During Playback

Individuals responded with more walking and running during playback to resident sounds than intruder sounds for playbacks involving audible wing rotation displays (Table 29; Mann Whitney-U test: $U_{22} = 33$, $Z = -2.075$, $p = 0.038$) though no other differences in responses to residents versus intruders were detected during playback in terms of orientation, alertness or calling.

Table 29: During Playback (Audible Wing Rotation Playbacks) Residents and Intruders Walking and Running Behaviour Proportions

Group	Mean \pm SE
Resident Signals	0.308 \pm 0.024
Intruder Signals	0.092 \pm 0.016

Post-playback

There were no differences in individuals' behaviours after resident and intruder playbacks for any of the recorded behaviours.

Adult, Juvenile, and Moulting Males

Pre-playback and During Playback

There were no significant differences between these types of males' behaviours prior to or during playback (Table 30), except the one marked instance (Control Pulse) in which adults called, but moulting males and juvenile males did not.

Table 30: Summary of Kruskal-Wallis Tests, for Adult, Juvenile, and Moulting Males, H values, $df=2$, where * indicates significance at $\alpha = 0.05$.

	Towards		Alert		Call		Walking/ Running	
	PRE	DUR	PRE	DUR	PRE	DUR	PRE	DUR
Wing Rotation	2.653	0.828	2.643	3.814	5.416	3.814	1.913	3.044
Control Wing	2.287	1.615	1.000	1.000	4.000	0.413	4.034	1.118
Shiver Train	0.800	2.938	1.222	1.222	2.573	4.074	2.064	5.248
Control Shiver Train	-	-	-	-	-	-	-	-
Pulse Train	2.717	0.004	2.429	3.852	1.097	1.349	0.506	0.164
Control Pulse Train	1.783	1.800	2.357	-	-	7.000*	2.121	1.61
Call	0.366	3.573	0.700	2.858	1.488	0.110	2.794	0.403
Control Call	-	-	-	-	-	-	-	-
Hoot Dash	0.101	4.711	1.134	5.902	4.113	5.863	0.323	1.060
Control Hoot-Dash	2.286	2.571	0.000	1.333	0.000	1.333	1.217	0.327

Post-playback

Individual males differed significantly in their orientation after call playback between adults, moulting males and juveniles; adults faced the playback unit the most, followed by juveniles, then moulting males (Table 31; Kruskal-Wallis test: $H_{16} = 7.845$, $p = 0.020$).

Table 31: Post Playback (Audible Call Playback) Adult, Juvenile, and Moulting Males Towards Orientation Behaviour Proportions

Group	Mean \pm SE
Adult Males	0.294 \pm 0.025
Juvenile Males	0.071 \pm 0.032
Moulting Males	0.002 \pm 0.001

Territory Holders Versus Floater Males

Pre-playback

Territory holders called more than floaters prior to trials that were to involve audible components of wing rotation (Table 32; Mann Whitney-U test: $U_{13} = 8$, $Z = -2.587$, $p = 0.0097$). Territory holders also walked more than floaters prior to those playbacks (Table 32; Mann Whitney-U test: $U_{13} = 9$, $Z = -2.016$, $p = 0.0438$).

Table 32: Pre-playback (Audible Wing Rotation Playback) Territory Holders and Floater Males Behaviour Proportions

Group	Behaviour	Mean \pm SE
Territory Holders	Calling	0.009 \pm 0.004
Floater Males	Calling	0 \pm 0
Territory Holders	Walking/Running	0.121 \pm 0.035
Floater Males	Walking/Running	0.059 \pm 0.047

During Playback

Territory holders were alert for a greater proportion of time than floaters during audible pulse train (Table 33; Mann Whitney-U test: $U_{22} = 46$, $Z = -2.065$, $p = 0.0389$), and hoot-dash playbacks (Mann Whitney-U test: $U_{16} = 9$, $Z = -2.679$, $p = 0.0074$).

Further, territory holders called more than floaters during audible hoot-dash playback (Table 33; Mann Whitney-U test: $U_{16} = 16$, $Z = -2.008$, $p = 0.0447$).

Table 33: During Playback (Audible) Territory Holders and Floater Males Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Pulse Train	Territory Holders	Alert	0.020 \pm 0.004
Pulse Train	Floater Males	Alert	0 \pm 0
Hoot-Dash	Territory Holders	Alert	0.105 \pm 0.011
Hoot-Dash	Floater Males	Alert	0.003 \pm 0.001
Hoot-Dash	Territory Holders	Calling	0.010 \pm 0.001
Hoot-Dash	Floater Males	Calling	0.002 \pm 0.001

Post-playback

Territory holders walked and ran more than floaters after audible wing rotation playbacks (Table 34; Mann Whitney-U test: $U_{13} = 8$, $Z = 2.5873$, $p = 0.0097$).

Table 34: Post-playback (Audible Wing Rotation Playback) Territory Holders and Floater Males Walking and Running Behaviour Proportions

Group	Mean \pm SE
Territory Holders	0.268 \pm 0.043
Floater Males	0 \pm 0

Changes in Responses Between Groups

We used Wilcoxon Signed-Rank tests again to compare the PRE and DUR and DUR and POST sections of the playbacks.

Pre-playback to During Playback

Individuals did not differ in orientation between PRE and DUR playback for any of the audible playback types. Individuals showed increased alertness (Table 35) in response to the playback of audible calls (Wilcoxon Signed-Rank test: $T_{28} = 126.86$, $Z = -1.96$, $p = 0.0499$), and audible hoot-dashes (Wilcoxon Signed-Rank test: $T_{22} = 50.31$, $Z = -2.667$, $p = 0.0076$). Individuals also called more frequently during playback (Table 35) than prior to playback for audible pulse (Wilcoxon Signed-Rank test: $T_{30} = 126.81$, $Z = -2.375$, $p = 0.0176$), audible call (Wilcoxon Signed-Rank test: $T_{28} = 108.08$, $Z = -2.366$, $p = 0.018$), and audible hoot-dashes (Wilcoxon Signed-Rank test: $T_{22} = 69.12$, $Z = -2.095$, $p = 0.0362$). Individuals also walked or ran more during playback than prior to playback in response to audible calls (Table 35; Wilcoxon Signed-Rank test: $T_{28} = 80.98$, $Z = -2.952$, $p = 0.0032$).

Table 35: PRE to DUR (Audible) Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Call	PRE	Alert	0.002 \pm 0.002
Call	DUR	Alert	0.016 \pm 0.007
Hoot-Dash	PRE	Alert	0.003 \pm 0.003
Hoot-Dash	DUR	Alert	0.046 \pm 0.017
Pulse Train	PRE	Calling	0.001 \pm 0.0003
Pulse Train	DUR	Calling	0.007 \pm 0.003
Call	PRE	Calling	0.002 \pm 0.002
Call	DUR	Calling	0.011 \pm 0.005
Hoot-Dash	PRE	Calling	0.002 \pm 0.001
Hoot-Dash	DUR	Calling	0.005 \pm 0.002
Call	PRE	Walking/Running	0.155 \pm 0.034
Call	DUR	Walking/Running	0.345 \pm 0.062

During Playback to Post-playback

Individuals decreased their orientation towards the speaker after the playback of audible calls (Table 36; Wilcoxon Signed-Rank test: $T_{28} = 67.75$, $Z = -3.238$, $p = 0.0012$), and subsequent to the playback of audible hoot-dashes (Table 36; Wilcoxon Signed-Rank test: $T_{22} = 29.01$, $Z = -3.315$, $p = 0.0009$). Individuals decreased their alertness after the playback of audible hoot-dashes (Table 36; Wilcoxon Signed-Rank test: $T_{22} = 67.05$, $Z = -2.158$, $p = 0.0309$) and decreased their proportion of calling after the playback of audible pulse train (Table 36; Wilcoxon Signed-Rank test: $T_{30} = 127.26$, $Z = -2.366$, $p = 0.018$). Calling decreased or maintained the same proportionate representation as it did prior to playback, but never increased after playback. Individuals decreased their proportion of walking and running after playback of audible pulse trains (Table 36; Wilcoxon Signed-Rank test: $T_{30} = 84.81$, $Z = -3.198$, $p = 0.0014$), and audible calls (Table 36; Wilcoxon Signed-Rank test: $T_{28} = 39.5$, $Z = -3.849$, $p = 0.0001$).

Table 36: DUR to POST (Audible) Behaviour Proportions

Playback Type	Group	Behaviour	Mean \pm SE
Call	DUR	Towards	0.277 \pm 0.039
Call	POST	Towards	0.118 \pm 0.037
Hoot-Dash	DUR	Towards	0.234 \pm 0.030
Hoot-Dash	POST	Towards	0.091 \pm 0.030
Hoot-Dash	DUR	Alert	0.046 \pm 0.17
Hoot-Dash	POST	Alert	0.008 \pm 0.003
Pulse Train	DUR	Calling	0.007 \pm 0.003
Pulse Train	POST	Calling	0.001 \pm 0.001
Pulse Train	DUR	Walking/Running	0.171 \pm 0.048
Pulse Train	POST	Walking/Running	0.047 \pm 0.015
Call	DUR	Walking/Running	0.035 \pm 0.062
Call	POST	Walking/Running	0.092 \pm 0.032

Because groups differed in baseline behaviour, to further evaluate responses, we subtracted the proportion of each behaviour prior playback from that during playback (DUR-PRE), and during playback from post playback (POST-DUR). Thus, a positive value represents an increase in the proportionate expression of the behaviour in question from one playback period to the next, while negative values indicate a reduction in the proportionate expression of that behaviour. By comparing the changes in behaviour, we can best compare the varied response of groups to audible signals.

Table 37 provides a summary of the overall changes of behaviours of peafowl for the ten playback types. The largest proportionate increases were in walking and running, especially for call and hoot playbacks. These values were used in the tests that follow, and are presented here for visual comparison.

Table 37: Overall Average Peafowl Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls).

	Orientation		Alertness		Calling		Walking/Running	
	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR
Call	+0.072	-0.159	+0.014	-0.009	+0.009	-0.003	+0.190	-0.253
Shiver Train	+0.022	+0.031	-0.003	0.000	-0.001	+0.004	+0.053	+0.021
Pulse Train	-0.009	-0.057	+0.007	+0.015	+0.006	-0.006	-0.026	-0.124
Wing Rotation	+0.003	-0.001	+0.002	-0.004	+0.003	-0.001	+0.011	-0.071
Hoot Dash	+0.006	-0.144	+0.043	-0.039	+0.003	-0.003	+0.080	-0.040
Call Control	+0.099	-0.054	+0.005	0.000	+0.005	-0.004	+0.040	-0.054
Shiver Control	-0.037	-0.071	+0.007	-0.013	+0.007	-0.009	+0.009	-0.011
Pulse Control	+0.013	-0.081	-0.004	0.000	0.000	0.000	+0.018	-0.025
Wing Control	+0.012	-0.025	+0.001	-0.001	+0.002	-0.001	-0.051	-0.043
Hoot Control	+0.032	-0.037	+0.001	+0.018	+0.003	-0.003	+0.046	-0.158

Table 38 focuses on changes in male behaviour only. Males walked and ran four times more for call playback than call control playback. Call playbacks elicited the most obvious responses from males, involving calling, walking/running, and alertness. These values and the associated statistical tests used to compare them are discussed below.

Table 38: Overall Average Male Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls)

	Orientation		Alertness		Calling		Walking/Running	
	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR
Call	+0.128	-0.147	+0.021	-0.012	+0.015	-0.005	+0.204	-0.233
Shiver Train	+0.004	+0.022	-0.004	-0.001	-0.001	0.005	+0.077	+0.004
Pulse Train	+0.023	-0.082	+0.008	+0.020	+0.008	-0.008	-0.030	-0.121
Wing Rotation	+0.004	-0.002	+0.002	-0.005	+0.004	-0.002	+0.044	+0.010
Hoot Dash	+0.023	-0.145	+0.052	-0.047	+0.004	-0.003	+0.084	-0.034
Call Control	+0.107	-0.027	+0.006	0.000	+0.006	-0.005	+0.050	-0.030
Shiver Control	-0.076	-0.098	+0.010	-0.016	+0.009	-0.012	+0.027	-0.014
Pulse Control	-0.017	-0.095	-0.006	0.000	0.000	0.000	+0.013	-0.004
Wing Control	-0.014	-0.078	+0.001	-0.002	+0.003	-0.002	-0.009	-0.044
Hoot Control	+0.033	-0.040	+0.001	+0.009	+0.004	-0.004	+0.040	-0.193

Female change-in-response values were also summarized in tabular format (Table 39), to facilitate visual comparison between and within the sexes. Females also walked and ran more, and were more alert in response to call playback. The significance of these values was assessed using Mann Whitney-U tests and is discussed below.

Table 39: Overall Average Female Changes in Behaviour Proportions From Prior to Playback to During Playback (DUR-PRE), and From During Playback to After Playback (POST-DUR) for Ten Audible Playback Types (Experimental and Controls)

	Orientation		Alertness		Calling		Walking/Running	
	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR	DUR-PRE	POST-DUR
Call	-0.006	-0.176	+0.006	-0.006	0.000	0.000	+0.169	-0.282
Shiver Train	+0.094	+0.070	0.000	0.000	0.000	0.000	-0.044	+0.091
Pulse Train	-0.117	+0.027	0.000	0.000	0.000	0.000	-0.014	-0.136
Wing Rotation	0.000	0.000	0.000	0.000	0.000	0.000	-0.081	-0.300
Hoot Dash	-0.079	-0.135	0.000	0.000	0.000	0.000	+0.059	-0.066
Call Control	+0.075	-0.135	0.000	0.000	0.000	0.000	+0.010	-0.126
Shiver Control	+0.099	+0.024	0.000	0.000	0.000	0.000	-0.051	0.000
Pulse Control	+0.060	-0.058	0.000	0.000	0.000	0.000	+0.027	-0.059
Wing Control	+0.049	+0.051	0.000	0.000	0.000	0.000	-0.111	-0.042
Hoot Control	+0.028	-0.031	0.000	+0.040	0.000	0.000	+0.062	-0.076

Males Versus Females

Pre-playback to During Playback

Males increased calling from PRE to DUR significantly more than females for audible call playbacks (Table 40; Mann Whitney-U test: $U_{28} = 60$, $Z = -2.4769$, $p = 0.0133$).

Table 40: PRE to DUR (Audible Call Playback) Males and Females Calling Behaviour Proportion Changes

Group	Mean \pm SE
Males	0.015 \pm 0.002
Females	0 \pm 0

During Playback to Post-playback

Males changed in walking and running positively from DUR to POST for audible wing rotation playbacks, and significantly differed from females for the same playback (Table 41; Mann Whitney-U test: $U_{22} = 8$, $Z = -3.0751$, $p = 0.0021$); females decreased their proportion of locomotory behaviour.

Table 41: DUR to POST (Audible Wing Rotation Playback) Males and Females Walking and Running Behaviour Proportion Changes

Group	Mean \pm SE
Males	0.010 \pm 0.010
Females	-0.300 \pm 0.030

Positive Controls Versus Experimental Playbacks

Pre-playback to During Playback

There were no significant differences between controls and experimentals for changes in behaviour for all individuals or males only from PRE to DUR. Females, however, differed in their changes in behaviour via orientation from PRE to DUR for audible pulse playbacks and control pulse playbacks (Table 42; Mann Whitney-U test: $U_{11} = 2$, $Z = 2.3589$, $p = 0.0183$); females increased orientation towards the playback unit for the control pulse train playback, while decreasing orientation for the experimental playback of the same type.

Table 42: PRE to DUR (Audible Pulse Train) Controls Versus Experimentals Towards Orientation Behaviour Proportion Changes

Group	Mean \pm SE
Control - females	0.060 \pm 0.014
Experimental - females	-0.117 \pm 0.024

During Playback to Post-playback

Individuals decreased their orientation toward the playback unit after playback, however, more so in control than experimental trials for audible wing rotation playbacks (Table 43; Mann Whitney-U test: $U_{40} = 97$, $Z = -2.8517$, $p = 0.0043$). Males also decreased their orientation towards the playback unit from DUR to POST more in control than experimental trials, for audible wing rotation playbacks (Table 43; Mann Whitney-U test: $U_{27} = 2$, $Z = -3.3551$, $p = 0.0008$). Finally, individuals increased calling subsequent to the playback of audible shiver train components more than in controls (which decreased in calling proportion) for audible shiver train (Table 43; Mann Whitney-U test: $U_{34} = 77$, $Z = 1.9608$, $p = 0.0499$).

Males increased their calling after playback of audible shiver train components more than controls (which decreased; Table 43; Mann Whitney-U test: $U_{27} = 42.5$, $Z = 1.9742$, $p = 0.0484$). Males also increased alertness after playback more than controls in trials involving audible pulse train display components (Table 43; Mann Whitney-U test: $U_{32} = 63$, $Z = -1.985$, $p = 0.0471$). Females decreased walking and running more subsequent to playbacks of audible wing rotation components than to positive controls (Table 43; Mann Whitney-U test: $U_{12} = 4$, $Z = 2.442$, $p = 0.0146$). There were no other

significant differences between experimentals and controls for PRE to DUR or DUR to POST for either all individuals or females or males only.

Table 43: DUR to POST (Audible) Controls Versus Experimentals Behaviour Proportion Changes

Playback Type	Group	Behaviour	Mean \pm SE
Wing Rotation	Control	Towards	-0.025 \pm 0.011
Wing Rotation	Experimental	Towards	-0.001 \pm 0.001
Wing Rotation	Control - Males	Towards	-0.078 \pm 0.009
Wing Rotation	Experimental - Males	Towards	-0.002 \pm 0.001
Shiver Train	Control	Calling	-0.009 \pm 0.002
Shiver Train	Experimental	Calling	0.004 \pm 0.0004
Shiver Train	Control - Males	Calling	-0.012 \pm 0.003
Shiver Train	Experimental - Males	Calling	0.005 \pm 0.001
Pulse Train	Control - Males	Alert	0 \pm 0
Pulse Train	Experimental - Males	Alert	0.020 \pm 0.005
Wing Rotation	Control - Females	Walking/Running	-0.042 \pm 0.014
Wing Rotation	Experimental - Females	Walking/Running	-0.300 \pm 0.030

Residents Versus Intruders

There were no differential responses from PRE to DUR to playbacks involving signals from residents versus intruders. Individuals differed, however, in the degree of response change from DUR to POST for resident versus intruder playbacks in terms of increased walking and running in response to intruders for audible wing rotation (Table 45; Mann Whitney-U test: $U_{23} = 33$, $Z = 2.0745$, $p = 0.038$). No other differences between responses to residents versus intruders were detected for the period between playback and post-playback.

Table 44: DUR to POST (Audible Wing Rotation Playbacks) Residents Versus Intruders Walking and Running Behaviour Proportion Changes

Group	Mean \pm SE
Residents	-0.173 \pm 0.015
Intruders	0.041 \pm 0.019

Territory Holders Versus Floater Males

Pre-playback to During Playback

Territory holders increased orientation towards the speaker more than floaters from PRE to DUR for audible hoot-dash playbacks (Table 45; Mann Whitney-U test: $U_{17} = 12$, $Z = 2.238$, $p = 0.0252$) and increased alertness from PRE to DUR more than floaters for those playbacks (Table 45; Mann Whitney-U test: $U_{17} = 9$, $Z = -2.679$, $p = 0.0074$). Territory holders increased walking and running more for PRE to DUR than floaters for audible control hoot-dash playbacks (Table 45; Mann Whitney-U test: $U_7 = 0$, $Z = -2.1405$, $p = 0.0323$).

Table 45: PRE to DUR (Audible) Territory Holders Versus Floater Males Behaviour Proportion Changes

Playback Type	Group	Behaviour	Mean \pm SE
Hoot-Dash	Territory Holders	Towards	0.126 \pm 0.018
Hoot-Dash	Floater Males	Towards	-0.132 \pm 0.033
Hoot-Dash	Territory Holders	Alert	0.105 \pm 0.011
Hoot-Dash	Floater Males	Alert	0.003 \pm 0.001
Control Hoot-Dash	Territory Holders	Walking/Running	0.243 \pm 0.082
Control Hoot-Dash	Floater Males	Walking/Running	-0.231 \pm 0.133

During Playback to Post-playback

Territory holders became less alert than floaters after playbacks of audible pulse train (Table 46; Mann Whitney-U test: $U_{23} = 35$, $Z = -2.4083$, $p = 0.016$); no other differences between territory holders and floaters were detected in the change of behaviour between the playback and post-playback period.

Table 46: DUR to POST (Audible Pulse Train Playback) Territory Holders Versus Floater Males Alert Behaviour Proportion Changes

Group	Mean \pm SE
Territory Holders	0.196 \pm 0.004
Floater Males	0.053 \pm 0.012

V: DISCUSSION

Infrasound

It is apparent from my results that infrasound constitutes an integral component of the peacock's tail display (Appendices A and B for spectrograms). Infrasound was detectable most often when males shivered or pulsed their trains - behaviour which involves vibrations of the elongated upper tail coverts and rectrices. Thus, one might expect males and females to respond most strongly to these signals (train pulsing and shivering).

Males responded to all infrasonic signals by calling, with statistically significant increases in calling in response to the pulse train and positive control playbacks. Peacocks thus appear to be responsive to infrasound in general, as homing pigeons are (Kreithen & Quine, 1979), rather than to specific acoustic patterns constituting discrete

signals. Such generalized response, however, may reflect the underlying salience of infrasound as a constituent of natural signals, which act upon pre-existing receiver sensory biases (Basolo, 1990; Ryan, 1990). The generalized response to infrasound could also be attributable to the fact that all the signals (Pulse Train, Shiver Train, Call, Wing Rotation) have intense formant frequencies between 4 and 8 Hz. This limited range may not be distinguishable to peafowl and, thus, they respond to a 4 Hz sine wave as they would to a 4 Hz pulse train.

The similar changes in behaviour of males and females when subjected to infrasound show that all peafowl respond to infrasound. When averaged over all individuals (Table 7 for a summary), changes in alertness were positive (i.e. increasing) from prior to during playback for all playback types except wing rotation playback. Changes in calling behaviour were positive for all playback types, despite inclusion of female values that were consistently zero, as females were never observed calling. Walking and running behaviour increased overall for call, control, shiver train, and wing rotation playbacks. The exception in this case was pulse train playback, which was characterized by a decrease in walking and running behaviour. Overall, peafowl called, walked or ran more, and were more alert when exposed to infrasonic playbacks.

Males showed a greater tendency to orient toward the subwoofer than females in the context of infrasonic playbacks. This may reflect female-biased preening, eating, or dustbathing, and male display biases, which collectively diminish the time that could otherwise be allotted to orienting toward the source of infrasonic stimulation (Walther, 2003). Male-biased orientation to the source of infrasonic stimulation may also indicate that males that maintain territories must be vigilant in protecting their lek site (Storch,

1997; Arcese, 1987), and hence show heightened responsiveness to infrasonic frequencies coincident with those produced in the context of tail displays. The fact that males tended to walk and run more than females prior to playbacks is consistent with heightened male vigilance. After playbacks, males decreased their proportions of walking and running to levels similar to the baseline, or slightly greater than baseline levels. Similarly, males were alert more often during playbacks than females (for two playback types), and maintained levels of alertness greater than those of females after playbacks, which may illustrate the vigilance required by males for territory maintenance (Arcese, 1987).

Both during and after playback, males faced the playback setup more often than females. However, the change in response from the pre-playback to playback periods for males and females were not significantly different. All individuals significantly increased their proportion of time spent orienting towards the subwoofer in response to intruder's call signals over resident's call signals. The only change in behaviour with infrasonic playback that differed between males and females was call response - females did not call at all. Males increased their calling behaviour coincident with the playback of infrasound, calling significantly more in response to pulse train signals from intruder males over resident males. When observed both in the field and during video recordings, males called once the infrasonic signals were played, and would often refrain from calling until another signal was played; illustrated by the drop in male calling proportions after playbacks.

Display Type Selection

In addition to examining differences between male and female response to infrasonic signals, we examined in detail pulse train and shiver train displays, which were associated with infrasonic signals. As shown in the results of a Kolmogorov-Smirnov test of display type and female distance, males performed pulse train displays when females were closer than 5 m and shiver train displays when females were further than 5 m away (Figure 4 and 5). In addition to these findings, the data were supported by the acoustic properties of these two behaviours. Previous peafowl research has focused on the pulse train only (e.g. Dakin & Montgomerie, 2009). The shiver train was on average lower in frequency when measured via a number of acoustic properties than pulse train, and this difference was confirmed with a Multivariate Discriminant Analysis, which tested the differences between the two displays based on a number of acoustic properties. The lower-frequency shiver train, which is used when females are farther away, might be used as a long-distance signal, as lower frequencies attenuate less over long distances. Other animals, such as elephants, use low-frequency vocalizations to communicate to conspecifics that are far away (McComb et al., 2003). As the natural habitat of the peafowl is shrubby (del Hoyo et al., 1994), the low frequencies in the train signals of the males' display may have evolved in this natural habitat.

Resident Signals Versus Intruder Signals

I hypothesized that peafowl might respond differently to residents or intruders, as other birds do (e.g. Alder Flycatcher, *Empidonax alnorum*, Lovell & Lein, 2004; Purple Swamphen, *Porphyrio porphyria*, Clapperton, 1978; White-throated Sparrows, *Zonotrichia albicollis*, Brooks & Falls, 1975), and playback trials were identified as

having signals from only resident males from the site, or only males from other lek sites (intruders). In some cases individuals responded more strongly to residents, and in other cases, more strongly to intruders. For signals with strongly associated infrasonic components (i.e. pulse train and shiver train), pulse train signals from intruders received more calls from males than signals from resident males. Thus, the responses to resident or intruder signals may only be distinguishable by males in signals with pronounced infrasound. Furthermore, differences in responses to individuals may also exist, and may affect male call responses, and could be further examined in future studies.

I hypothesized that adult males, juvenile males, and moulting males, might respond differently based on their potential mating success for that season. Since moulting males are no longer breeding, and juvenile males do not breed, one could logically conclude that they may behave differently in response to infrasound compared to adult breeding males (Komers et al., 1997; Petrie et al., 1991). However, no apparent differences between those males were detected. Due to small samples of certain groups (juveniles $n= 1$ to 4; and moulting males $n= 0$ to 4), in some cases (infrasonic shiver and pulse playbacks) a comparison could not be drawn between the three groups. However, based on the data at hand, adult, juvenile, and moulting males do not behave differently from each other. Furthermore, tests to determine if males displayed (i.e. opened their train) more often during playback showed no difference between prior to, during, and after playback, which not only reinforces the apparent potency of infrasound as a stimulus of considerable relevance to males in general, but also suggests that an intact tail is not necessary to detect and perceive infrasound.

Territory Holders Versus Floater Males

As previously mentioned, I hypothesized that territory-holders invest highly in their lek site, and may act differently than other individuals, as they must remain vigilant for predators and possible intruding males that would benefit from usurping their lek site (as in Capercaillie, *Tetrao urogallus*, Storch, 1997; and Golden-winged sunbirds, *Nectarinia reichenowi*, Gill and Wolf, 1975). To investigate this hypothesis, I compared territory-holding males, and floater males. Territory-holding males were always adult males that held their lek throughout the period when infrasonic playbacks were being conducted. Floater males were adult males or juvenile males. When I compared the baseline behaviours of territory-holders and floaters, territory holders were always more investigative or vigilant (measured by the orientation, calling, and alertness), the exception being walking and running behaviour, however, this may be due to floaters travelling between lek sites. Prior to playback, floaters walked or ran more than territory holders, however, during playback there was no difference between the two groups, and after playback, territory holders walked and ran significantly more than non-holders in one playback type (shiver train playback).

When I analysed the changes in behaviour for territory holders and floaters, there were many differences between them in the changes in behaviour from the pre-playback to playback period, and from the playback to the post-playback period. Territory holders increased the proportion of time they spent facing the playback unit (+0.103), while floaters decreased that (-0.289) for shiver train playbacks. Territory holders decreased walking and running (-0.171) for infrasonic pulse train playbacks, while floaters increased walking and running (+0.029). Again, this is consistent with the suggestion that

territory holders, which must remain at the lek site, are generally more vigilant than floaters (Westcott, 1992). Floaters might walk or run more than territory holders due to the floaters' nomadic nature (Petrie et al., 1991), the potential selective advantage of copulations while following females from site to site, and also, the possibility of being chased by the territory holder. After playbacks were over, territory holders increased walking and running (+0.014), while floaters decreased the proportion of time devoted to such locomotion (-0.081). This difference was unexpected, and further study might elucidate why this change occurred. It is conceivable that subsequent to detecting infrasound within their territory, territory holders may be selected to investigate their territory to ensure the source of the infrasound was no longer present, and floaters might have walked far enough from the territory holder that the territory holder will not actively pursue the floater male (Petrie et al., 1991). However, it is not clear why these changes have occurred, and a more in depth analysis of the relationship of lekking territory holders and floater male behaviours would be required to arrive at an explanation.

After determining that peafowl perceive infrasound, it was hypothesized that males might use their trains to perceive the low-frequency sounds, because presumably, the relatively long tail feathers, held together to form what effectively constitutes a parabolic dish, would be stimulated by low frequency sound. To investigate this possibility, we performed Wilcoxon Signed-Rank tests on the proportions of displaying by males in the PRE and DUR, and DUR and POST sections of the infrasound playbacks. There was no significant increase in the frequency of displaying for any of the playback types. Instead, males were more likely to reduce the amount of time spent displaying during playbacks (Table 24). Only pulse train playbacks caused an increase in male

display behaviours, and that change was not statistically significant. Furthermore, the fact that no difference in the responsiveness of adult, juvenile, or moulting males to infrasound was detected, and that females, like males, changed their behaviour, indicative of their perception of infrasound, renders it unlikely that the male train plays any role in the reception of infrasound.

Homing pigeons (*Columbia livia domestica*) are known to perceive infrasound auditorily (Kreithen & Quine, 1979), whereas other animals may perceive infrasound seismically (e.g. wolf spiders, Uetz et al., 2009). It is unclear whether peafowl perceive infrasound via their middle and inner ear (Kreithen & Quine, 1979), via seismic vibrations (Uetz et al. 2009), or both. However, since all sex and age classes perceive infrasonic signals in some way, we have determined the concave train is not necessary in infrasonic perception (although its shape may have implications in signal production).

Audible Signals

For audible playbacks, males and females also differed in their baseline behaviours. Males oriented toward the playback unit more than females (for call playback, shiver train, hoot dash), and called more than females during call playback. Females walked more than males during playback, but not prior to playback for audible wing rotation playbacks. Males increased walking and running generally during playback, however not as much as females did. Thus, males maintain higher vigilance through orientation and calling (as in the infrasonic playbacks) than females, possibly due to their territorial nature (Olendorf et al., 2004; Westcott, 1992; Payne, 1984).

Similar to the infrasonic playback analysis, while males and females may have differed in their baseline behaviour, we tested for changes in the proportions of their

behaviours to determine if these groups differed significantly in their responses using Wilcoxon Signed-Rank tests, and Mann Whitney-U tests.

For all individuals, peafowl were more alert, during audible call and hoot-dash playbacks (both of which include vocalizations) than prior to playback. In response, individuals called in response to both call and hoot-dash playbacks, as well as audible pulse playbacks. The call and hoot-dash playbacks resulted in responses typical of vigilant peafowl - alertness and calling increased, and stayed the same or decreased after the playbacks, indicating that the peafowl perceive the vocalizations as relevant signals. Males might perceive these signals as indicators of a potential threat; either a predator (Nowicki, 1983) or an intruding male (Westcott, 1992). When calls were broadcast, males increased walking and running behaviour, and were observed circling the playback unit -possibly endeavoring to localize the source (i.e. peafowl) of the vocalizations. Once the playbacks were complete, peafowl decreased their walking and running behaviour (as if they ceased searching for the source of the vocalizations).

For changes in behaviours from prior to during playback, males increased calling rates more than females (who did not call). However, there were no other significant changes in behaviour for males and females. Thus, as revealed by the infrasonic analysis -males and females (Table 17) responded similarly to audible playbacks, except for calling (see Table 23 for a summary of the average changes for all individuals). Both males and females responded to call playback by walking or running more. Males circled the playback unit in response to call playback signals, and sometimes called in response to these audible call playbacks, but the overall change was not significant.

When positive controls and experimental playbacks were compared using Mann Whitney-U tests, the differences between those were not statistically significant. However, visual examination of the results presented in Tables 7, 8 and 9 suggest that the call responses for both males and females exceeded those of the control. However, individuals did not differentiate between the call and control playbacks sufficiently to reach statistical significance. Males in particular increased alertness in response to call and hoot-dash playbacks to a greater degree than in the controls. As hoot-dash playbacks contain a vocal signal, it is likely that these audible vocal signals are important for peafowl. These copulatory vocalizations may be honest signals of male quality (Hauser, 1993). Males in particular might respond to the hoot-dash, as it may indicate female presence.

For audible playbacks, there were no differences in the changes in response from prior to during playbacks for resident or intruder playbacks. There was little variation in responses to intruders' and residents' signals overall, and the differences were often conflicting. While in one playback, individuals might walk more often for intruder playback, in the next, the resident playback would elicit more walking. Thus, I concluded that non-infrasonic components inhibit the peafowl's ability to determine the signaller's status as a resident or intruder. This finding suggests that infrasonic components of certain displays are essential in increasing responses of peafowl to intruders. Without the infrasonic frequencies, peafowl respond at a similar level and do not discriminate between signals from intruders or residents.

Territory Holders and Floaters

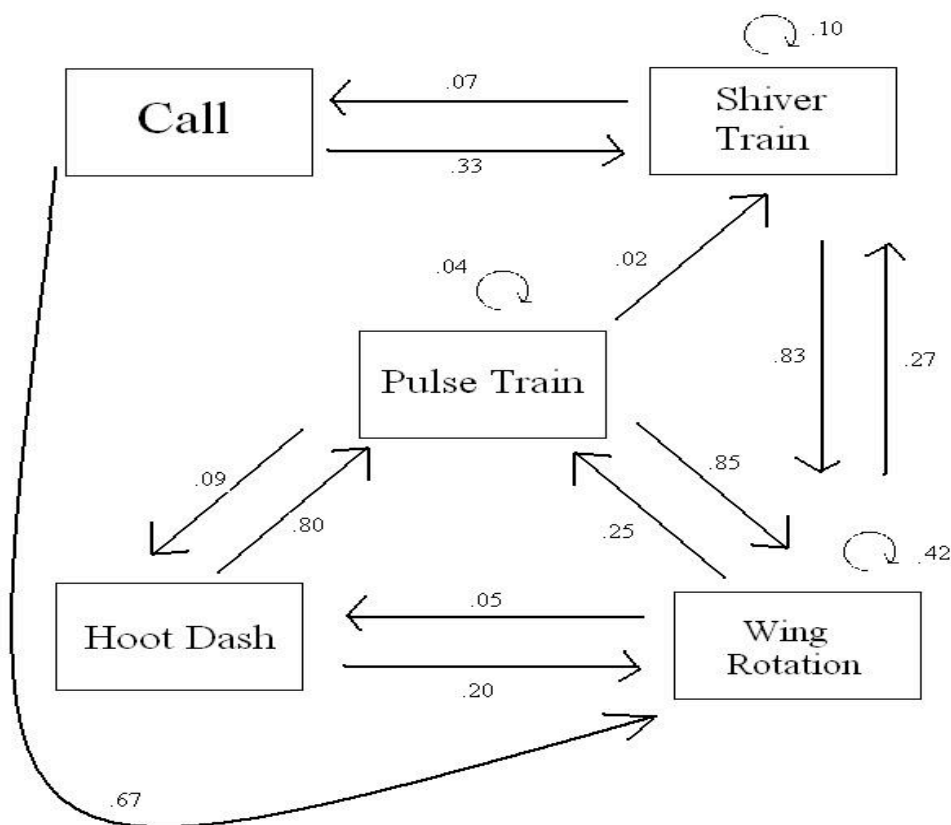
Despite no differences in response to intruders' or residents' signals, territory holders and floaters varied in their behaviours. Prior to playback, territory holders called more and walked or ran more (during what ultimately would be wing rotation playbacks) than floaters. During playbacks, territory holders were alert more often (pulse train and hoot-dash playbacks), and called more than floaters (hoot-dash playbacks). A bias for territory holders to show greater responsiveness during hoot-dash playbacks was expected (Westcott, 1992), as the hoot-dash is associated with an attempted (or successful) copulation. It was expected that territory-holding males would be more likely to respond to the sounds of copulation than floater males might, as successful copulations by floaters compromise the fitness benefit of investing energetically in maintaining a display territory (Arcese, 1987). Subsequent to playback, territory holders again walked more than floaters (wing rotation playback). Territory holders and floaters also varied in their changes in behaviour. Territory holders increased their orientation towards the playback unit, and increased alertness significantly more than floaters during hoot-dash playbacks. This is in accord with the hypothesis that territory holders have a greater interest than floaters in preventing copulations at the lek site (Arcese, 1987). After playback, the only significant difference between territory holders and floaters was in the decrease in alertness by territory holders that was not apparent in floaters (pulse train playback).

Future Directions

While we used an approach of deconstructing the peacock display into component parts, including infrasonic and audible acoustic signals, it is likely that greater insight can

ultimately be gained by taking into account the natural order of signal components within peacock tail displays. I examined all the changes in displays made by males in 2010, and determined the transition probabilities from each behaviour to the next (Figure 8).

Figure 8: Order of Behaviours as Recorded in 2010



Thus, while our playbacks facilitate interpretation of the role infrasound may play in isolation of other signal components, these playbacks did not reflect the natural order of behaviours and their associated signal components in peacock displays and, hence, cannot address how these multi-modal signals function in nature. For example, in the playbacks, pulse train signals were played consecutively, however, in the field, peacocks rarely repeat a pulse train (Figure 8). Instead, they are likely to rotate their wings (85% of the time) after pulsing their train. Future studies could consider the order of behavioural

components, and how that order might influence the message conveyed by the display. As in other species, peacocks might vary the acoustic properties, including the order of sounds to create different messages (Uetz et al., 2009; Blumstein & Armitage, 1997). Furthermore, as discussed in the introduction, multimodal signals (i.e. visual and acoustic) can increase the perception of the signals, and in peafowl, the visual in conjunction with the acoustic might serve as a more potent signal. This potential for signal enhancement, redundancy, and change should be addressed in future studies of peacock displays.

In 2011, the population of peafowl at the Assiniboine Park Zoo did not increase. The five young from two broods provided an insufficient sample to determine mating success through paternity. There are a few potential reasons why this population of peafowl did not breed as successfully as it had in previous years. The Assiniboine Park Zoo was home to a family of wild, free-ranging, red fox (*Vulpes vulpes*) in 2011, which were a new predator for the peafowl. The fox ate or attacked at least 2 adult peafowl, and it is possible that they consumed more that were not observed. Furthermore, Cooper's hawks (*Accipiter cooperii*) were commonly observed at the zoo, and could easily catch peafowl chicks, although the presence of hawks at the zoo was certainly not limited to 2011. Finally, the Assiniboine Park Zoo in 2011 was undergoing major construction, which changed some of the lek sites for males. In so doing, some males that held territories (e.g. C.C male) in 2010 were displaced from their territories by other males that had held lek sites in the areas under construction. In that peafowl respond to infrasound, and these responses may divert the peafowl from completing normal mating behaviours, noise resulting from construction activities could have adversely impacted peafowl mating behaviour in 2011. Noise from industrial activities, and urban environments has previously been shown to affect mating behaviours in other birds

(Habib et al., 2007), as well as affect the acoustic properties of their communication signals (Slabbekoorn & Peet, 2003).

Perhaps most interesting is the variation within individuals. Ranges from all recordings of peacocks overlap, which might lead one to the conclusion that peacocks manipulate their train to produce lower frequency sounds through various behaviours, or that individual variation in physical attributes of the train affect signal production. My findings reveal that males use different behaviours based on female distance (i.e. shiver train when females are far, and pulse train when females are near), but it remains possible that males could fine-tune their behaviours in other ways to the context at hand. This possible individual-level selection of display frequency should be investigated in future studies. In particular, train structure might affect acoustic properties, and may have affects on male and/or female response behaviours. Communication between territory holders and floaters should be studied further to determine how territory holders might advertise their presence to other males, and which signals are most readily perceived. Indeed, my data suggest that the infrasonic components in particular may convey information concerning residents and intruders that is not present in the audible range. As in the ochre-bellied flycatcher (*Mionectes oleaginosa*), males may use acoustic cues to signal their territory, and may lose territory if they are unable to signal adequately (Westcott, 1992; this may occur in peacocks through feather loss, as seen anecdotally in the change of the "C.C" male's territory after feather loss through an encounter with another peacock). Further investigation of territory usurpation events may provide data addressing this intrasexual function of infrasound production and perception.

References

- Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.
- Arcese, P. (1987). Age, intrusion pressure and defence against floaters by territorial male song sparrows. *Animal Behaviour*, *35*, 773-784.
- Barklow, W. E. (2004). Amphibious communication with sound in hippos, *Hippopotamus amphibious*. *Animal Behaviour*, *68*, 1125-1132.
- Basolo, A.L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science*, *250*, 808-810.
- Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *The Quarterly Review of Biology*, *47*, 412-434.
- Blumstein, D.T., & Armitage, K.B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*, 143-171.
- Brooks, R.J., & Falls, J.B. (1975). Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. *Canadian Journal of Zoology*, *53*, 879-888.
- Budde, C., & Klump, G. M. (2003). Vocal repertoire of the black rhino *Diceros bicornis* ssp. And possibilities of individual identification. *Mammalian Biology*, *68*, 42-47.
- Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, *36*, 477-486.
- Clapperton, K. (1987). Individual recognition by voice in the pukeko, *Porphyrio porphyrio melanotus* (Aves: Rallidae). *New Zealand Journal of Zoology*, *14*, 11-18.
- Cronin, H. (1991). *The Ant and the Peacock*. University Press, Cambridge.

- Dakin, R., & Montgomerie, R. (2001). Peahens prefer peacocks displaying more eyespots, but rarely. *Animal Behaviour*, 82, 21-28.
- Dakin, R., & Montgomerie, R. (2009). Peacocks orient their courtship displays towards the sun. *Behavioral Ecology and Sociobiology*, 63, 825-834.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- Del Hoyo, J., Elliott, A., & Sargatal, J. Eds. (1994). *Handbook of the Birds of the World*. Vol. 2 New World Vultures to Guinea-fowl. Lynx Edicions, Barcelona.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Freeman, A., & Hare, J.F. (2011). Infrasound in the flutter-jump display of Capercaillie (*Tetrao urogallus*): Signal or artefact? *Journal of Ornithology*, 152, 815-816.
- Gill, F.B., & Wolf, L.L. (1975). Economics of feeding territoriality in the golden-winged sunbird. *Ecology*, 56, 333-345.
- Habib, L., Bayne, E.M., Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, 44, 176-184.
- Hale, M. L., Verduijn, M. H., Møller, A. P., Wolff, K., & Petrie, M. (2009). Is the peacock's train an honest signal of genetic quality at the major histocompatibility complex? *Journal of Evolutionary Biology*, 22, 1284-1294.

- Hanotte, O., Burford, M. W., & Burke, T. (1992). Multilocus DNA fingerprinting in gallinaceous birds – general approaches and problems. *Heredity*, *68*, 481-494.
- Harper, D. G. C. (2006). Maynard Smith: Amplifying the reasons for signal reliability. *Journal of Theoretical Biology*, *239*, 203-209.
- Hauser, M.D. (1993). Rhesus monkey copulation calls: honest signals for female choice? *Proceedings: Biological Sciences*, *254*, 93-96.
- Hopp, S.J., Owren, M.J., & Evans, C.S. Eds. (1997). *Animal acoustic communication: Sound analysis and research methods*. Springer-Verlag, Berlin.
- Komers, P.E., Pélabon, C., & Stenström, D. (1997). Age at first reproduction in male fallow deer: age-specific versus dominance-specific behaviors. *Behavioral Ecology*, *8*, 456-462.
- Kreithen, M.L., & Quine, D.B. (1979). Infrasound detection by the homing pigeon: A behavioral audiogram. *Journal of Comparative Physiology*, *129*, 1-4.
- Lieser, M., Berthold, P., Manley, G. A. (2006). Infrasound in the flutter jumps of the capercaillie (*Tetrao urogallus*): apparently a physical by-product. *Journal of Ornithology*, *147*, 507-509.
- Lovell, S.F., & Lein, M.R. (2004). Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behavioral Ecology*, *15*, 799-804.
- Loyau, A., Saint-Jalme, M., Cagnaint, C., & Sorci, G. (2005). Multiple sexual advertisements honestly reflect health status in peacocks (*Pavo cristatus*). *Behavioural Ecology and Sociobiology*, *58*, 552-557.

- Loyau, A., Saint-Jalme, M., & Sorci, G. (2005b). Intra- and Intersexual selection for multiple traits in the peacock (*Pavo cristatus*). *Ethology*, *111*, 810-820.
- Loyau, A., Gomez, D., Moureau, B., Théry, M., Hart, N. S., Saint-Jalme, M., Bennet, A. T. D., & Sorci, G. (2007). Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. *Behavioural Ecology*, *18*, 1123-1131.
- Manning, J. T. (1989). Age advertisement and the evolution of the peacock's train. *Journal of Evolutionary Biology*, *2*, 379-384.
- Manning, J. T., & Hartley, M. A. (1991). Symmetry and ornamentation are correlated in the peacock's train. *Animal Behaviour*, *42*, 1020-1021.
- Marchetti, K. (1998). The evolution of multiple traits in the yellow-browed leaf warbler. *Animal Behaviour*, *55*, 361-376.
- McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, *65*, 317-329.
- Møller, A. P., & Petrie, M. (2002). Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behavioural Ecology*, *13*, 248-253.
- Møller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, *32*, 167-176.
- Møller, A. P., Saino, N., Taramino, G., Galeotti, P., & Ferrario, S. (1998). Paternity and multiple signalling: Effects of a secondary sexual character and song on paternity in the barn swallow. *The American Naturalist*, *151*, 236-242.

- Nowicki, S. (1983). Flock-specific recognition of chickadee calls. *Behavioral Ecology and Sociobiology*, *12*, 317-320.
- Olendorf, R., Getty, T., Scribner, K., & Robinson, S.K. (2004). Male red-winged blackbirds distrust unreliable and sexually attractive neighbours. *Proceedings of the Royal Society of London B.*, *271*, 133-1038.
- Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, *166*, 231-245.
- Payne, R.B. (1984). Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithological Monographs no. 33* American Ornithologists' Union, Washington, D.C.
- Payne, K. B., Langbauer, W. R. Jr., & Thomas, E. M. (1986). Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, *18*, 297-301.
- Payne, R., & Webb, D. (1971). Orientation by means of long range acoustic signalling in baleen whales. *Annals of the New York Academy of Sciences*, *188*, 110-141.
- Petrie, M. (1992). Peacocks with low mating success are more likely to suffer predation. *Animal Behaviour*, *44*, 585-586.
- Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, *371*, 598-599.
- Petrie, M., Cotgreave, P., & Pike, T. W. (2009). Variation in the peacock's train shows a genetic component. *Genetica*, *135*, 7-11.
- Petrie, M., Cotgreave, P., & Stewart, I. (1996). Variation in the train morphology of peacocks (*Pavo cristatus*). *Journal of Zoology*, *238*, 365-371.

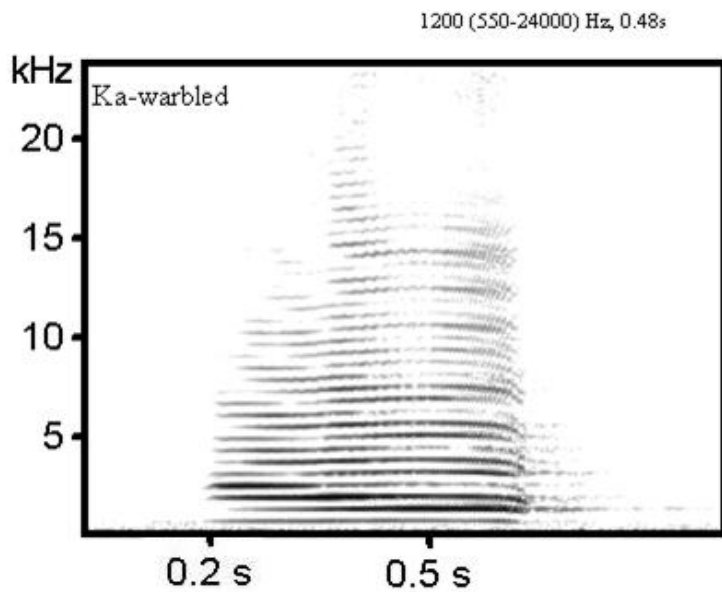
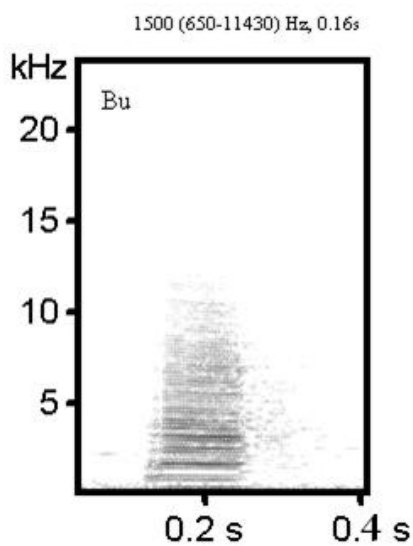
- Petrie, M., Hall, M., Halliday, T., Budgey, H., & Pierpoint, C. (1992). Multiple mating in a lekking bird: Why do peahens mate with more than one male and with the same male more than once? *Behavioral Ecology and Sociobiology*, *31*, 349-358.
- Petrie, M., & Halliday, T. (1994). Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. *Behavioral Ecology and Sociobiology*, *35*, 213-217.
- Petrie, M., Halliday, T., & Sanders, C. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, *41*, 323-331.
- Petrie, M., & Williams, A. (1993). Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society of London B*, *251*, 127-131.
- Ryan, M.J. (1990). Sexual selection, sensory systems, and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, *7*, 158-195.
- Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban areas: great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature*, *424*, 267.
- Storch, I. (1997). Male territoriality, female range use, and spatial organization of capercaillie *Tetrao urogallus* leks. *Wildlife Biology*, *3*, 149-161.
- Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M., & Hasegawa, T. (2008). Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour*, *75*, 1209-1219.
- Takahasi, M., & Hasegawa, T. (2008). Seasonal and diurnal use of eight different call types by Indian peafowl (*Pavo cristatus*). *Journal of Ethology*, *26*, 375-381.

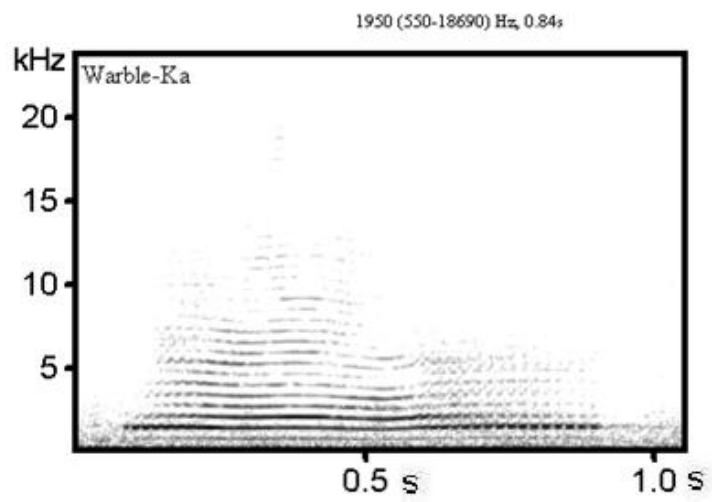
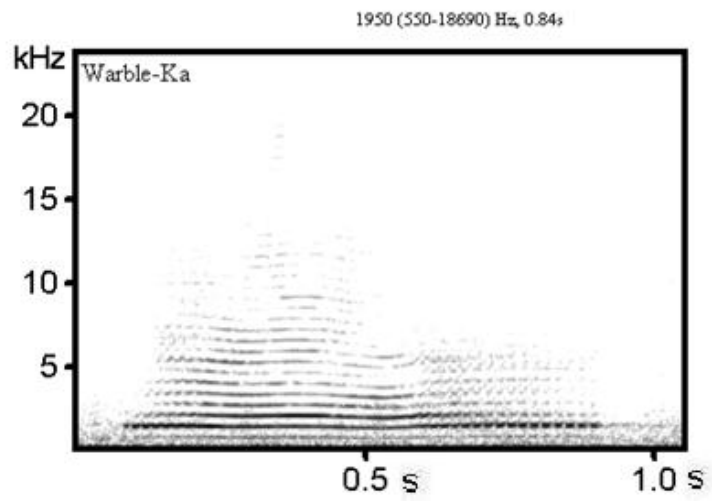
- Uetz, G. W., Roberts, J. A., & Taylor, P. W. (2009). Multimodal communication and mate choice in wolf spiders: Female response to multimodal versus unimodal signals. *Animal Behaviour*, *78*, 299-305.
- Walsh, E., Wang, L.M., Armstrong, D.L., Curro, T., Simmons, L.G., & McGee, J. (2003). Acoustic communication in *Panthera tigris*: A study of tiger vocalization and auditory receptivity. Presented at 145th Acoustical Society of America meeting, Nashville, TN.
- Walther, B.A. (2003). Do peacocks devote maintenance time to their ornamental plumage? Time budgets of male blue peafowl *Pavo cristatus*. *Lundiana*, *4*, 149-154.
- Westcott, D. (1992). Inter- and intra-sexual selection: the role of song in a lek mating system. *Animal Behaviour*, *44*, 695-703.
- Yasmin, S., & Yahya, H. S. A. (1996). Correlates of mating success in Indian Peafowl. *The Auk*, *113*, 490-492.
- Yodlowski, M. L., Kreithen, M. L., & Keeton, W. T. (1977). Detection of atmospheric infrasound by homing pigeons. *Nature*, *265*, 725-726.
- Zahavi, A., & Zahavi, A. (1997). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. New York: Oxford.

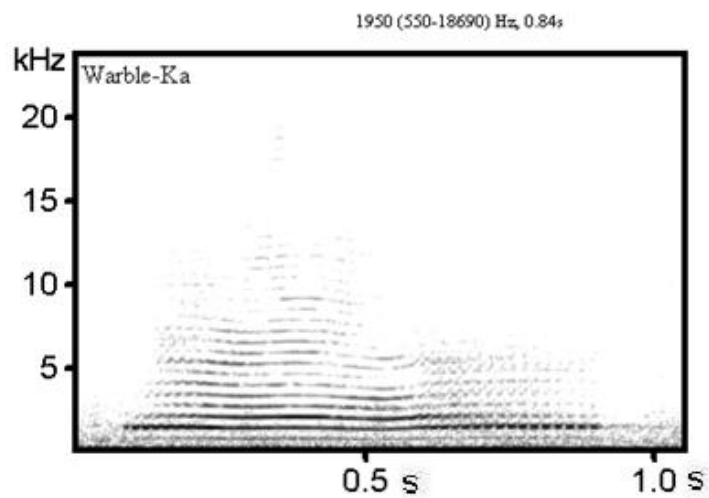
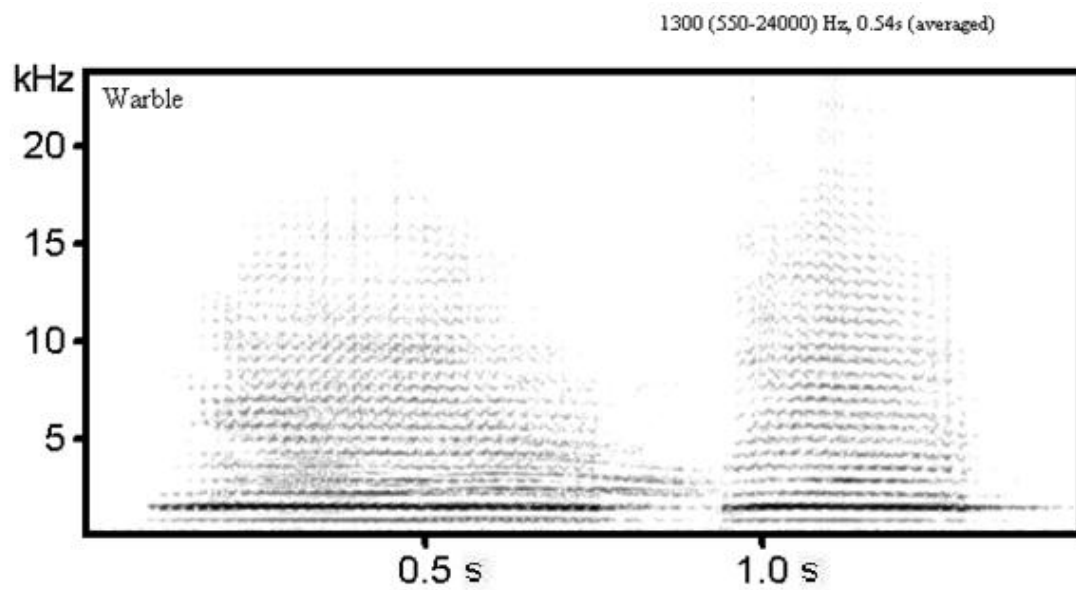
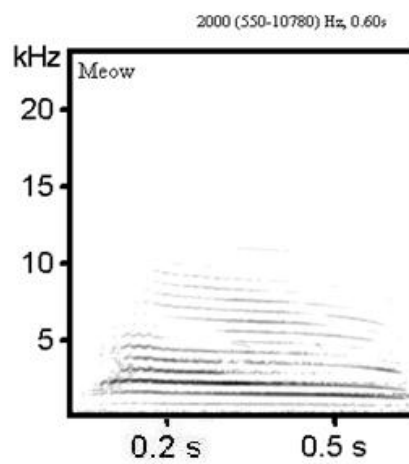
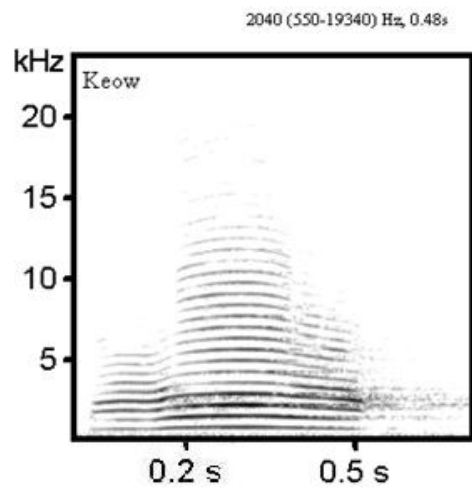
Appendix A: Spectrographs of Displays and Vocalizations

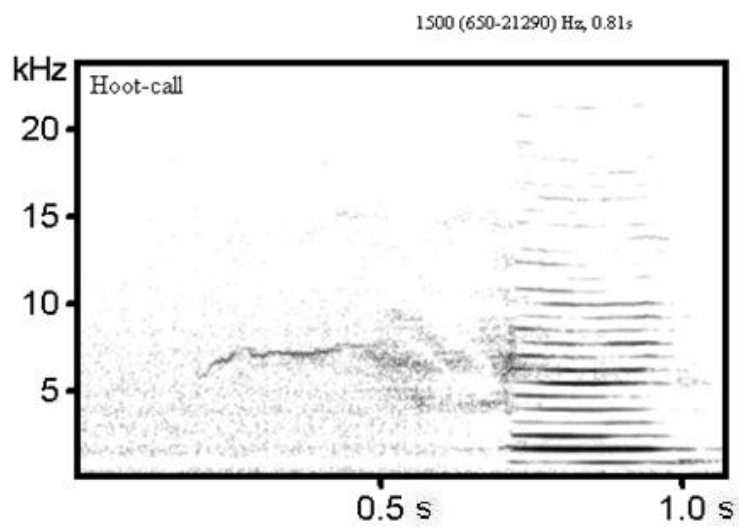
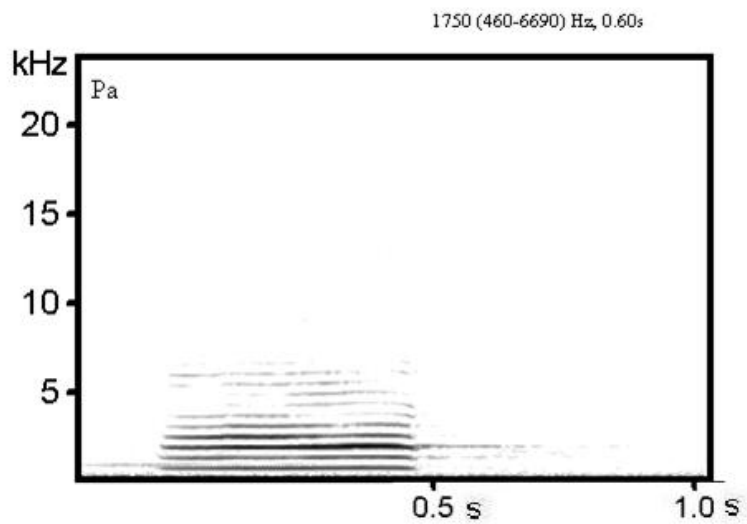
Numbers indicate average formant frequency (range of formant frequencies), average length in seconds

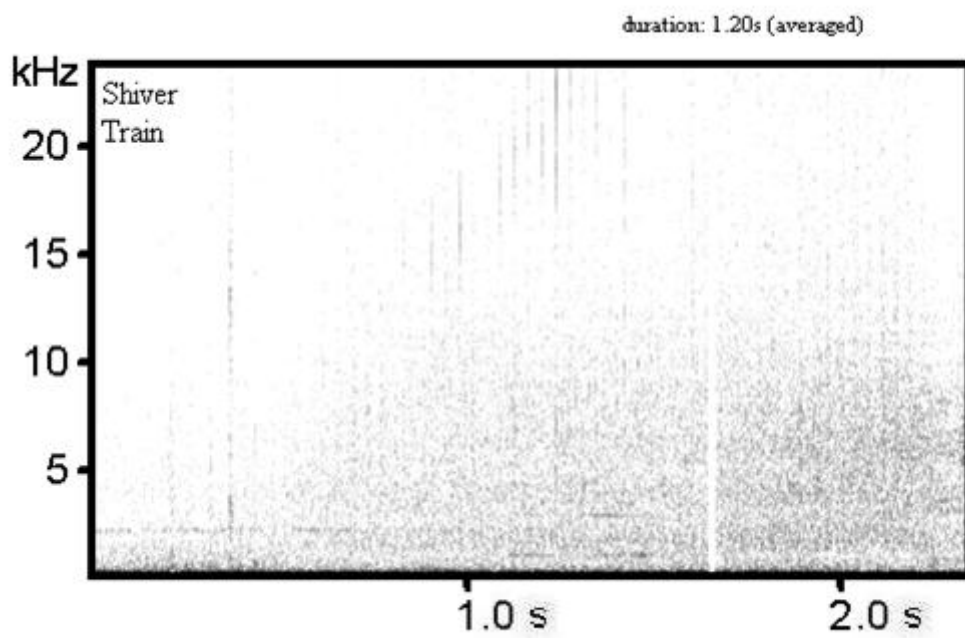
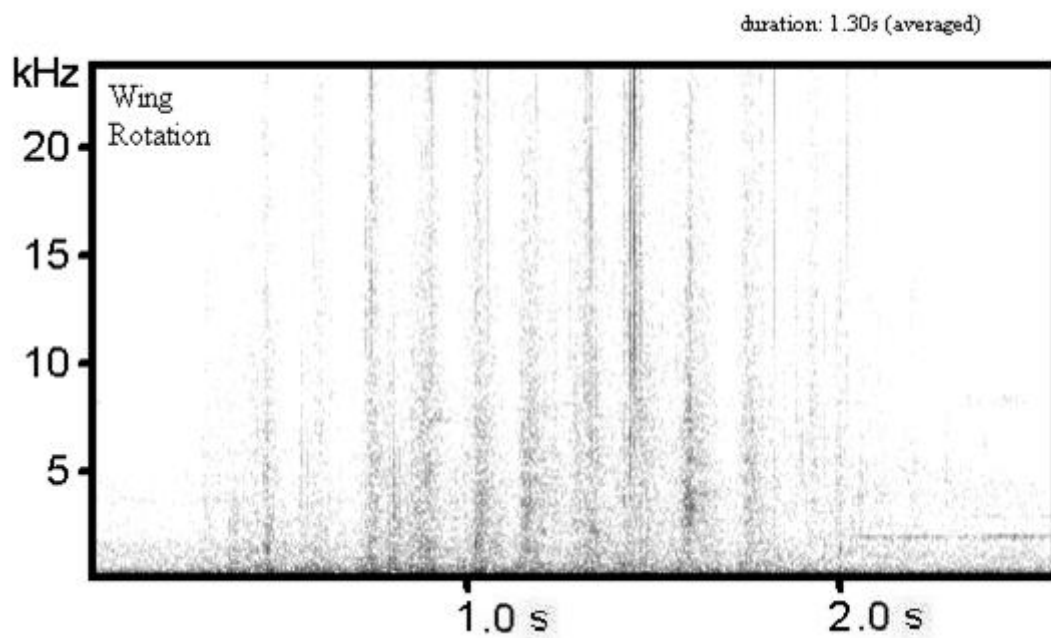
Circled parts indicate sounds other than those from the peafowl

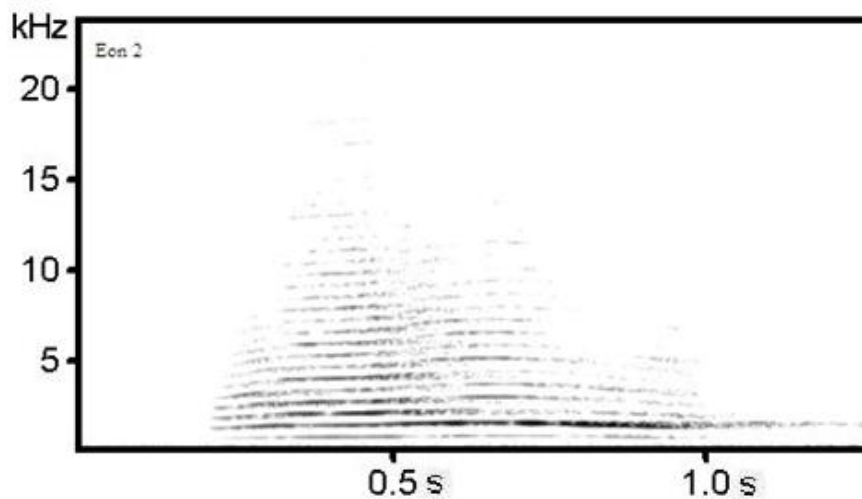
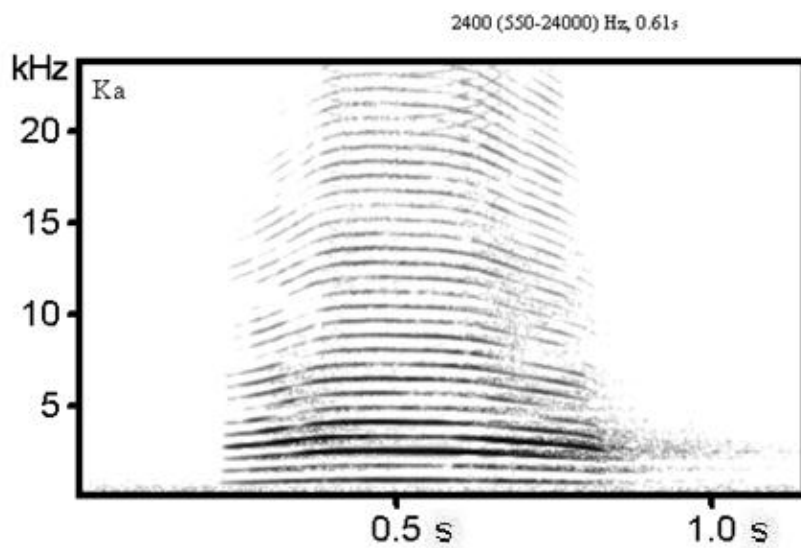
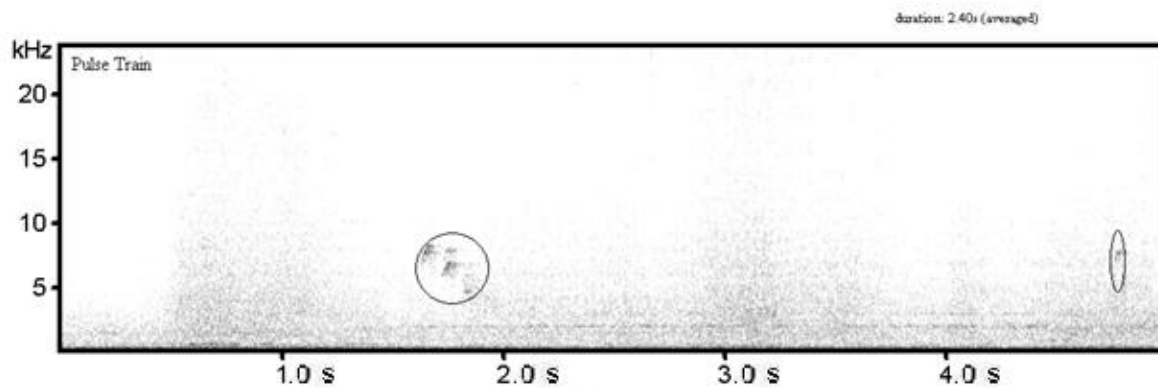








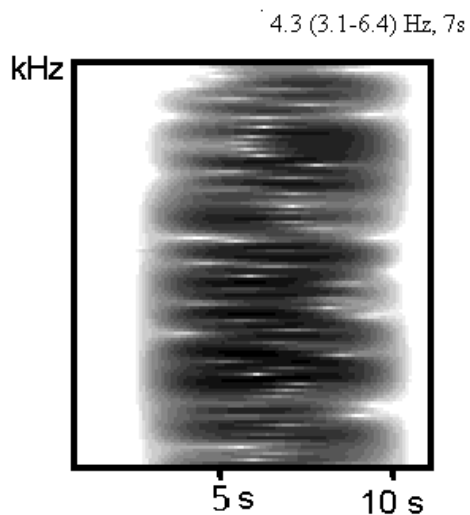




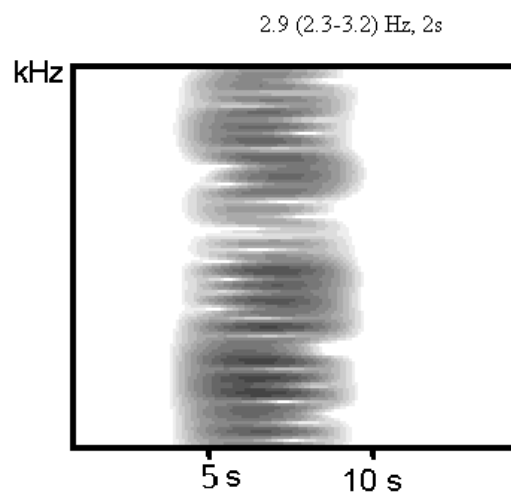
Appendix B: Infrasonic Spectrographs

Numbers indicate average formant frequency (range of formant frequencies), average length in seconds

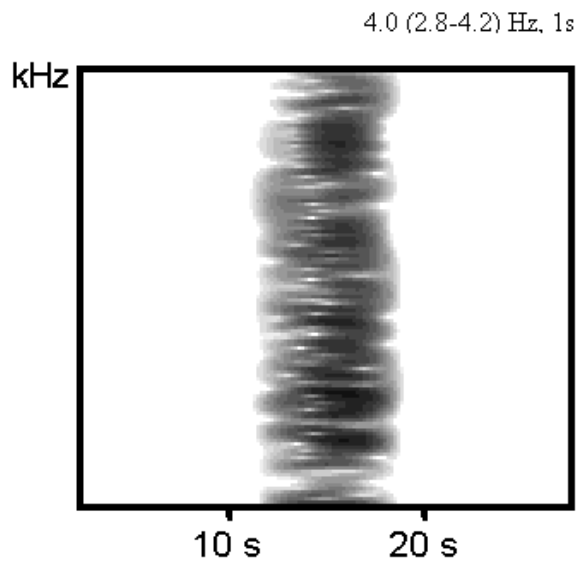
Infrasound Pulse Train



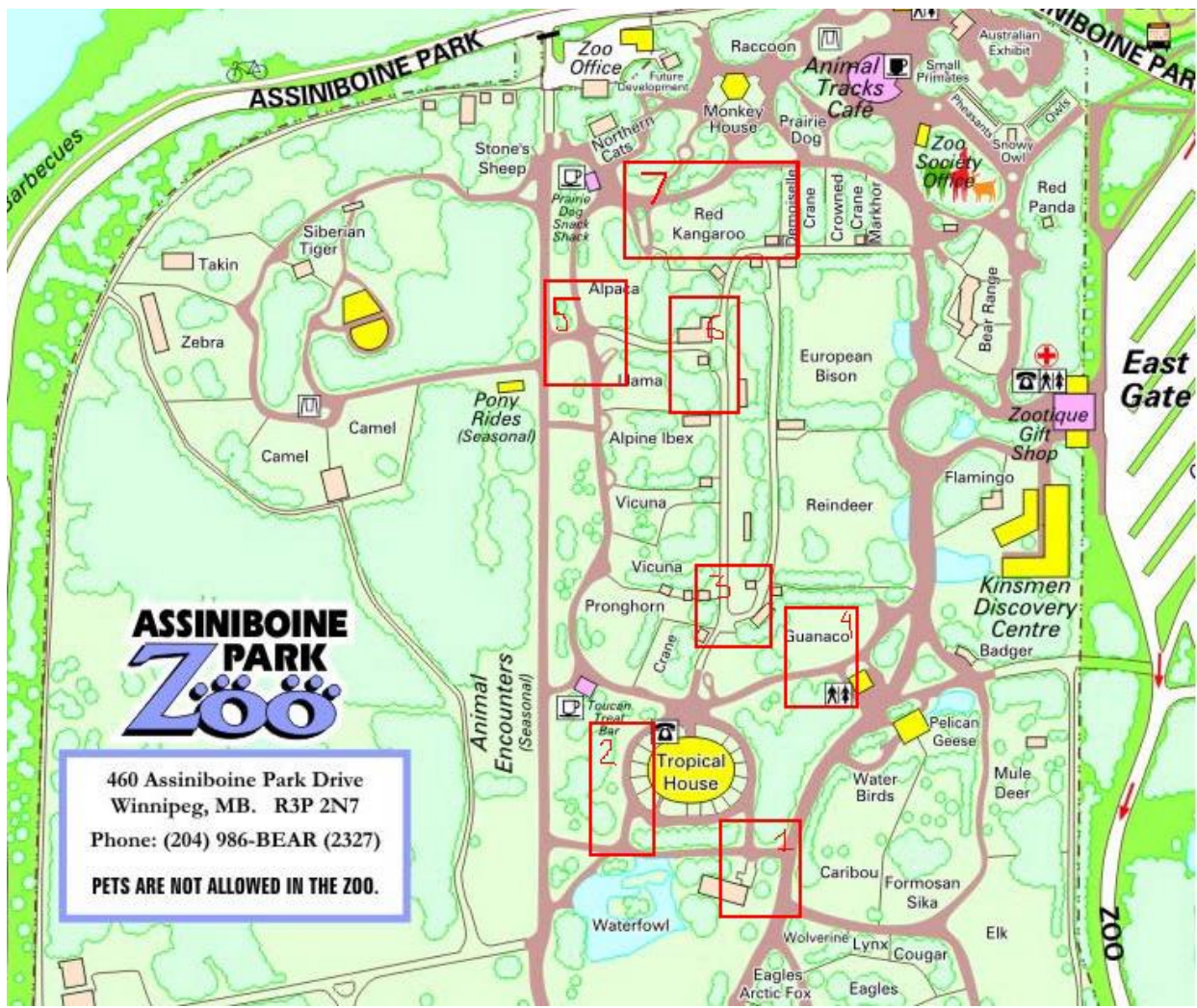
Infrasound Wing Rotation



Infrasound Shiver Train



Appendix C: Map of Lek Sites for Playback (noted with red rectangles, numbered; modified from assiniboineparkzoo.ca)



Appendix D: 2010 Ornamentation Summary

Peacock I.D.	Train Length (m)	Peacock Height (m)	# Eyespots	Eyespot Density (#/m ²)	Symmetry Score
G.R	1.45	1.86	155	46.93	3.5
N.B	1.31	1.55	144	53.35	0.6
N.R	1.27	1.81	143	56.44	0.7
R.N	1.15	1.36	143	68.57	0.5
Y.N	1.27	1.66	152	59.80	12
C.C	1.35	1.65	150	52.54	2
Y.Y	1.33	1.60	136	48.95	18.5
Y.N (BS)	1.21	1.61	152	66.09	1
N.G	1.22	1.46	130	55.60	11