



University of Tennessee, Knoxville
**TRACE: Tennessee Research and Creative
Exchange**

Doctoral Dissertations

Graduate School

12-2017

Investigating the Chickadee *Ethos*.

David L. Book

University of Tennessee, Knoxville, dbook@vols.utk.edu

Follow this and additional works at: https://trace.tennessee.edu/utk_graddiss



Part of the [Psychology Commons](#)

Recommended Citation

Book, David L., "Investigating the Chickadee *Ethos*." PhD diss., University of Tennessee, 2017.
https://trace.tennessee.edu/utk_graddiss/4763

This Dissertation is brought to you for free and open access by the Graduate School at TRACE: Tennessee Research and Creative Exchange. It has been accepted for inclusion in Doctoral Dissertations by an authorized administrator of TRACE: Tennessee Research and Creative Exchange. For more information, please contact trace@utk.edu.

To the Graduate Council:

I am submitting herewith a dissertation written by David L. Book entitled "Investigating the Chickadee *Ethos*." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Todd M. Freeberg, Major Professor

We have read this dissertation and recommend its acceptance:

Matthew A. Cooper, Gordon M. Burghardt, Mary L. Erickson, Garriy Shteynberg

Accepted for the Council:

Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Investigating the Chickadee *Ethos*.

A Dissertation Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

David L. Book

December 2017

Copyright © 2017 by D.L. Book

All rights reserved.

For Cincinnatus and Athena.

Acknowledgements

There were many people who helped make this dissertation possible: My wife, a boundless source of encouragement and an expert in finding missing indefinite articles. My father, the hardest worker I have ever known, who help construct all of the seed houses and who also found an appreciation of the chickadee. My mother, who poured love into my son while I hunted for chickadee emotion. My mentor, Todd Freeberg, who taught me the ways of the chickadee and the modern academy – and who had to endure such an irritably obdurate student. Gordon Burghardt, from who I learned the perspective of the ages – a great wealth of science and philosophy that lay buried beneath the latest trends of thought. From Matt Cooper, I learned of the neuron and her systems, and the arch principle of brain plasticity. Garry Shteynberg, from whom I learned a social science not rooted in headlines, but timeless principles of human attention and interaction. And Molly Erikson, from whom I learned of the meaning carried in the voice above and beyond the mere information.

I would also like to thank: Ron Vanover at the Kentucky Department of Parks and Joyce Bender at Kentucky State Nature Preserves Commission for their help in obtaining research permits. “The Jacks” at Boonesboro State Park for their help in locating research sites. Mr. Gary for allowing me to use his land for research. The Comparative Communications Lab for their feedback on earlier manuscripts. Connie Ogle for bailing me out of multiple self-imposed logistical quagmires. Sylvia Miller, Dean Thompson, and many others at the Graduate Office for helping a first generation college student navigate the process. Thank you all.

Abstract

Morality, as used within this dissertation, is conceptualized as having two distinct components – a shared, norm-based, cultural component and a subjective, character-based, emotion-based component. Using this dual-aspect model of morality, we examine the roots of morality using a comparative, 5th-Aim Ethological framework. This ethological framework was applied to study possible emotional states of the Carolina chickadees. Three experiments are presented which attempt to identify the most likely proximate emotion for the general call of the foraging chickadees. These studies examined food presence, food type and volume, and vocal cues of predator presence. Our data suggest that a homeostatic-related emotion is unlikely to be a significant proximate emotion for the general call of the chickadee in response to food discovery. A modest amount of evidence is also presented which suggests that threat-based motivation is not the dominant proximate emotion for the general call of the Carolina chickadee. In light of these findings, new motivational hypotheses are presented that may explain the subjective motivation elements preceding the chickadee call. We conclude with some scientific and philosophical parallels of our morality model, and some implications for the scientific investigation of morality.

Table of Contents

Chapter 1: Morality in Ethology	1
Overview	1
Philosophical Assumptions	2
Assumption I: The validity of reason as absolute	4
Assumption II: A parsimonious, yet non-reductive, evolutionary framework.....	5
Assumption III: The mind as neither completely distinct from, nor reducible to, matter	6
An Ethological Framework.....	8
Morality Defined Within a 5 th -Aim Ethology.....	11
Twin Origins of the Two Moralities.....	14
A Tension between the Moralities.....	20
Searching for Moral Fundamentals.....	23
Chapter 2: Avian Moral Motivation	26
Avian “Parental and Filial Affections”	27
Avian “Intellectual Powers”	30
Individual Recognition and Image Scoring	32
Social Learning	35
Emotional Signaling.....	36
Animal food signaling: The motivational question.....	38
Two Hypotheses.....	40
The Predator Defense → FEAR Hypothesis	41
The Homeostatic → SEEKING Hypothesis.....	45
Chapter 3: Chickadee Food Discovery and Calling.....	51
Focal Species	51
Call Characteristics	52
Site Locations.....	55
Equipment	55
Habituation Period	58
Preferred Food Type Test	58
Conditions for Experiment 1 (Food Variation).....	58
Conditions for Experiment 2 (Predator Cue).....	59
Recording Durations	60

Experimental Measures.....	60
Results.....	62
Analysis and Interpretation.....	64
Chapter 4: Replications and Revisions	69
Methods.....	70
Focal Species and Vocalizations	70
Site Locations.....	71
Equipment.....	72
Habituation.....	74
Conditions and Recording Procedure	74
Experimental Measures.....	74
Replication Results	75
Discussion.....	77
Revised Motivational Models for General Call.....	80
Chapter 5: Implications and Directions	87
Philosophical and Scientific Parallels.....	92
Some Dangers of Manipulating Morality	94
List of References	99
Chapter 1 References	100
Chapter 2 References	104
Chapter 3 References	110
Chapter 4 References	112
Chapter 5 References	114
Appendices.....	117
Vita.....	128

List of Tables

Table 1.1: Panksepp’s Primary Emotional Systems.....	15
Table 2.1: “Predator Defense” Hypotheses.....	43
Table 3.1: Feeding Site Locations.....	55
Table 3.2: Experimental Conditions for Studies 1 and 2.....	61
Table 4.1: Study 3 Research Sites.....	71
Table 4.2: Experimental Conditions for Study 3.....	75

List of Figures

Figure 1.1: Umwelt and External Stimuli.....	13
Figure 1.2: Genotype, Phenotype, and Proximate Factors Influencing Behavior.....	17
Figure 1.3: Morality (Ethos) and a Morality (Culture) Matrix	19
Figure 1.4: Morality (<i>Culture</i>) Within a Social Network	24
Figure 2.1: Ethos Complexity X Cognitive/Communicative Complexity.....	33
Figure 2.2: FEAR and SEEKING Hypotheses	50
Figure 3.1: General Call Spectrogram.....	53
Figure 3.2: Experimental Apparatus	57
Figure 3.3: Chickadee General Calls.....	63
Figure 3.4: Owl/Goose General Calls.....	64
Figure 4.1: Experimental Apparatus with Rear-mounted Camera.....	72
Figure 4.2: NO SEED and SEED General Calls.....	73
Figure 4.3: A Revision of Hypothesized Motivations.....	82
Figure 5.1: <i>Ethos</i> , Social Complexity and Communicative Complexity.....	91

CHAPTER 1: MORALITY IN ETHOLOGY

A Theoretical Approach and Philosophical Assumptions

“This is my starting point and it could be wrong.”¹

Overview

Moral character is the central motif of this dissertation. To understand the essence of moral character, it is proposed, requires the identification of certain fundamental emotional elements comprising morality. The definition of “morality” has differed, to a minor degree, between cultures, ages, and among the various sciences.² However, these definitions usually possess a common element of a shared set of social norms, or expectations, which govern the behavior of a particular group. Morality, as used within this dissertation, is conceptualized as having two components – a shared, norm-based, cultural component and a subjective, character-based, emotion-based component. The distinction between these two uses of morality will be explained in greater detail later in this chapter.

We begin this dissertation with a brief description of the philosophical assumptions which underlie our framework, methodology, and interpretations. We offer this assumptions as part of a general disclosure concerning our perspective on the science of animal sentience. These philosophical assumptions are followed by a description of the ethological framework we used to conceptualize morality. This framework assumes that evolutionary pressures had a major role in

¹ Wilson, E. O. (1999). *Consilience: The unity of knowledge*. Vintage. p. 263.

² Gert, Bernard and Gert, Joshua, "The Definition of Morality", *The Stanford Encyclopedia of Philosophy* (Spring 2016 Edition), Edward N. Zalta (ed.), URL = <<https://plato.stanford.edu/archives/spr2016/entries/morality-definition/>>.

shaping morality and that both humans and animals possess a capacity for experiential,³ henceforth motivational, states.⁴ These evolutionary pressures and use of subjective capacities, and their respective roles in morality, are also expanded upon below.

Several empirical studies, found in the third and fourth chapters of the dissertation, are part of a comparative (multi-species) approach to identifying some of the fundamental motivational aspects of moral motivation. Our goal in these studies is to try and determine the most probable proximate emotion related to the general call of the chickadee. The rationale for this comparative approach will receive greater treatment in chapter two. The final chapter applies our framework and empirical findings to other models, described some other possibilities to expand our framework of morality, and described some dangers with the scientific study of morality. But before addressing morality as a motivational phenomenon, experienced within multiple species, we should make some other clarifications are required concerning our basic philosophical assumptions.

Philosophical Assumptions

The connection between the various sciences and philosophy is not always apparent due to a common tendency in modern academia to frame science and philosophy as distinct systems of thought. The sciences, being empirical, are assumed by many to hold greater validity than mere contributions of philosophy, which have been perceived as producing unfalsifiable, metaphysical propositions in the past – or even disparaged the empirical study of natural

³ Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press, p. xiii. "...we use the word *animals* to refer to nonhuman beings because always writing 'nonhuman animals' gets tiresome."

⁴ The word motivation is often used to refer to both internal and external forces which shape behavior. Our focus is on the internal, subjective influences and unless otherwise noted, motivation will be used exclusively to refer to subjective experiential states influencing behavior.

phenomena.⁵ As a result, the academic universe is often presented as a collection of the various arts, humanities, and sciences with philosophy left as a field of residuum comprising a set of abstract concepts not yet incorporated into one of the sciences.⁶ This view that philosophy should play a limited role in scientific scholarship may not be universal. Yet it is prominent enough to create problems for researchers when they attempt to explain certain phenomena using a scientific approach.

The central problem in ignoring philosophical questions or subjugating philosophy to the sciences is that many philosophical assumptions which underlie scientific investigation have become implicit rather than explicit. Few modern scientists describe their philosophical assumptions when publishing their findings in scientific journals. There may be several reasons for this omission. A scientist might assume that their assumptions are so widely shared, or irrelevant to their topic of study, that to describe them would be superfluous. Geneticists, studying the role of various gene polymorphisms in the onset of diabetes, perhaps need not state their assumptions on the nature of epistemology in order to publish their findings in an epidemiology journal. Conversely, a scientist may hold assumptions that they believe to be out of the scientific mainstream and to describe them in print would be to invite criticism from departmental peers, journal editors, or grant reviewers on grounds other than the empirical evidence they present. Challenging pervasive, mainstream assumptions has never been an easy task in any discipline.

But whatever the reasons may be for discontinuing the practice of clarifying one's

⁵ For one popular example of this tension see: Damasio, A. (1994). *Descartes' error: Emotion, reason, and the human brain*. Avon Books.

⁶ Wilson, E. O. (1999). *Consilience: The unity of knowledge*. Vintage.

philosophic assumptions, this discontinuance holds certain risks. Implicit assumptions become hidden to a reader and are difficult to contest. The empirical nature of observation can also become confused with the inference-based nature of interpretation under a vague notion of scientific authority.⁷ A form of objectivity that is not grounded in “the spirit of the age” and that is applicable across diverse cultures and time periods can become jeopardized.⁸ For these reasons, some philosophical groundwork seems fitting prior to addressing the ethological framework of morality here employed. An excellent example of this turning ones’ philosophical “cards face up” is provided by E.O. Wilson.⁹ He encourages everyone who studies moral reasoning to suffer the indignity of having their personal beliefs clearly understood.¹⁰ We agree with this practice and follow suit accordingly.

Assumption I: The validity of reason as absolute

Reason, as used in this dissertation, is defined as the capacity for applying logical principles to facts in order to make inferences and to derive valid conclusions. The difference between humans and animals in this capacity is beyond the scope of this dissertation and will not here be addressed. Following a series of studies that revealed a failure of many study participants to properly utilize purely logical reasoning on certain tasks and in certain contexts,¹¹ other academics have called into question the objective validity of the human faculty of reason.^{12 13}

⁷ Ruse, M. (2003) Is evolution a secular religion? *Science* 299.5612 p. 1523-1524.

⁸ Lewis, C. S. (1964). *The discarded image: An introduction to medieval and renaissance literature*. Cambridge University Press.

⁹ Wilson, E. O. (1999). *Consilience: The unity of knowledge*. Vintage. p.263

¹⁰ Ibid.

¹¹ Kahneman, D. (2011). *Thinking, fast and slow*. New York: Farrar, Straus and Giroux.

¹² Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York: Pantheon Books.

¹³ Mercier, H., & Sperber, D. (2011). Why do humans reason? Arguments for an argumentative theory. *Behavioral and Brain Sciences*, 34(2), 57-74.

These skeptics of reason have implied that these empirical examples from social psychology are evidence that humanity may not be in possession of an objective faculty of reason. We disagree with this conclusion. It is important to emphasize here that a failure of research participants to utilize reason in a particular setting is not the same as the questioning the existence of the faculty of reason itself. There may be many contexts in which human reason is biased, limited, or underutilized. However, to abandon objective reason wholesale is to simultaneously abandon the foundation of every system of thought and the ability to create any cogent argument. If the potential for an objective form of reason is on trial, the rules of logic, science, and whatever claims the skeptic of reason might present, will share the verdict. Arguments for the denial of reason are also based upon reason. In short, they are self-refuting.

Assumption II: A parsimonious, yet non-reductive, evolutionary framework

The popular view of evolution often portrays the theory as a scientific monolith.¹⁴ In reality, however, there is a tremendous amount of diverse, and often competing, evolutionary ideas found within biology and evolutionary psychology.¹⁵ We start with Darwin. As will be discussed in chapter two, Darwin predicted cooperation would occur in species that had developed offspring care and certain cognitive capacities.¹⁶ He also wrote extensively on the role of emotion and of transmittable “serviceable habits” that could convey adaptive advantages to individuals. If we take Darwin’s evolutionary theory in general, and as applied to morality, we would describe it as both parsimonious in its assumptions and comprehensive in applications.

But in the wake of *Origin*¹⁷ some authors have attempted to modify Darwin’s theory for

¹⁴ Ruse, M. (2003) Is evolution a secular religion? *Science* 299.5612 p. 1523-1524.

¹⁵ Van der Braak, H. (2013). *Evolutionary Psychology*. Pearson Education Limited.

¹⁶ Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London. p. 28.

¹⁷ Darwin, Charles (2003). *On the Origin of Species by Means of Natural Selection*. Ed. Joseph Carroll.

various other purposes. Spencer attempted to expand upon natural selection to the extent of conceptualizing the theory as a central component of a constant progression of the universe¹⁸ – a type of cosmic developmentalism. Freud adapted evolutionary principles in order to develop his psychoanalytic theory and a model of civilization that pitted the *eros* against a death drive.¹⁹ Dawkin's *The Selfish Gene*,²⁰ in an apparent attempt to increase the parsimony of natural selection as a theory, overemphasized the role of genotype versus Darwin's incorporation of both genetic and non-genetic inheritance of behavioral traits. The theoretical approach utilized in this dissertation is Darwinian in that it assumes a significant role for non-genetic inheritance of behavior and a potential preference for cooperation over competition among conspecifics under some conditions.

Assumption III: The mind as neither completely distinct from, nor reducible to, matter

Within the ancient debate concerning the mind's connection with matter²¹, this dissertation assumes a centrist position – avoiding a reduction of mind to mere matter or a reduction of matter to a mere product of mind. Much of the controversy surrounding mind and body debate may stem from the acceptance of either a Cartesian or Baconian set of first principles. Descartes proposed that the existence of a self as a perceiving agent was the most fundamental axiom of rational thought – summarized in the famous phrase *Cogito ergo sum*.²² He argued that, though his perception may be in error, the existence of an agent to make the error

Peterborough, Ont.: Broadview.

¹⁸ Spencer, Herbert (1876). *First principles of a new system of philosophy*. D. Appleton.

¹⁹ Freud, Sigmund (1961). *Civilization and its Discontents*. W.W. Norton & Company.

²⁰ Dawkins, Richard (1989). *The selfish gene*. Oxford: Oxford University Press.

²¹ Van Oudenhove, L., & Cuypers, S. E. (2010). The philosophical "mind-body problem" and its relevance for the relationship between psychiatry and the neurosciences. *Perspectives in biology and medicine*, 53(4), 545-557.

²² Descartes, René (1968). *Discourse on Method and the Meditations*. Penguin UK.

was more self-evident than any information he could have received through his sensory inputs. Conversely, Bacon, in his *Novum Organum*,²³ argued that all knowledge is derived from experience and proposed a system of knowledge be built based on experience alone – heralding in the modern empirical approach to science.

The theoretical approach developed in this dissertation is neither strictly dualistic, based on subjective philosophical idealism, nor strictly monistic, based upon assumptions from a materialistic philosophical realism. Both extremes are here rejected. Cartesian agency, and an accompanying sentience, is assumed to exist. Evidence supplied from a shared and objective reality, fundamental to Baconian empiricism, is assumed to be valid. Any attempt to reduce experience to the mere product of the agent's mind inevitably leads to solipsism.²⁴ Solipsism, by definition must be incompatible with a scientific method based on a shared reality. Any attempt to reduce mind to the mere product of material mechanisms has a strong potential to minimize or eliminate all subjective phenomena such as sentience, consciousness, or the *Umwelt*²⁵ of living creatures. In a field such as psychology, where the object of study, at least in origin, is the mind, both reductionistic empiricism and solipsistic idealism lead to a dead end in the pursuit of knowledge.

²³ Bacon, Francis (2016). *Novum organum*. Jazzybee Verlag.

²⁴ Solipsism: (a) the theory that the self can be aware of nothing but its own experiences and states; (b) the theory that nothing exists or is exists or is real but the self. Webster, Noah (1966). *Webster's New Twentieth Century Dictionary: Second Edition*, unabridged. Publishers International Press.

²⁵ Umwelt: the world as it is experienced by a particular organism. Von Uexküll, Jakob (1992). A stroll through the worlds of animals and men: A picture book of invisible worlds. *Semiotica*, 89(4), 319-391.

An Ethological Framework

With these philosophic assumptions in mind, we can now turn our attention to the conceptual framework used in this dissertation. Using an ethological approach, the principal goal is to identify the fundamental motivations that compose a moral character. Ethology was originally defined in a broad sense as the study of character. But the focus of Ethology has changed substantially from its etymological roots. Ethology, in origin, is the combination of *ethos*, meaning “custom” or “character” and *logos*, meaning “reason” or “logic.” Thus ethology was defined as 1) a depicting of character, 2) a treatise on morality, or 3) the science of applied ethics.²⁶ But as evolutionary theory became more prominent within biology and other sciences, a new, expanded definition of ethology was required which focused on questions of animal behavior and incorporated research from multiple fields – including biology, psychology, physiology, and ecology.²⁷ This expansion was largely provided by early ethologists and formalized by Niko Tinbergen in his four aims of Ethology.^{28 29} Tinbergen described four categories of questions that should be applied concerning the behavior of animals. Two of these questions involved the biological origins of the behavior. Why a behavior was adaptive within its present natural context, and why a behavior originally evolved (and being careful not to assume these questions are identical) are the evolutionary ultimate questions of behavior. The other two center on are proximate questions focused on either the development of a behavior across the lifespan of the organism or the immediately causal factors that lead to the display of the behavior

²⁶ Webster, Noah (1966). *Webster's New Twentieth Century Dictionary: Second Edition*, unabridged. Publishers International Press.

²⁷ Burghardt GM. (1977) The ontogeny of communication. In: Sebeok TA, editor. *How Animals Communicate*. Bloomington, Ind, USA: Indiana University Press; pp. 67–93

²⁸ Tinbergen, Niko (1963). On aims and methods of ethology. *Ethology*, 20(4), 410-433.

– such as the smell of food initiating salivation.

Tinbergen's four aims have been tremendously beneficial to the field of ethology in helping expand the understanding of many behaviors, including some aspects of morality. However, for researchers who do not assume that mind can be reduced to matter, as described above, or those who conceptualize the mind as an emergent property or interactional force, there is a missing aim of ethology. Based on these premises, the subjective, motivational elements that initiate behavior do not fit effortlessly within one of Tinbergen's four aims. Subjective motivations are neither observable behavior nor are they stimuli. They therefore cannot be easily conceptualized as merely part of an evolutionary history, an adaptive advantage, a stage in a growth process, or as proximate stimuli – although emotion has a connection to all of these types of aims. Motivations, that is emotions, are, by nature, intangible phenomena that cannot be directly observed or measured. Their existence can only be inferred by other forms of empirical evidence.

For this reason this dissertation applies a 5th-Aim ethological approach to the study of moral character. Using the 5th-Aim, a researcher attempts to discover the subjective experiences, or the *Umwelt*, of animals that correspond to behavior.³⁰ An animal may begin to salivate at the smell of food, but between the objective, external presence of the food and the objective, external behavior of salivation lies the internal experience of the animal. Just as a human can experience hunger sensations at the sight of food, animals are assumed by 5th-Aim ethologists to experience something akin hunger as well. The important point to emphasize here is that animals are thought

³⁰ Burghardt, G.M. (1997). "Amending Tinbergen: A fifth aim for ethology". In R.W. Mitchell; N. S. Thompson; H. L. Miles. *Anthropomorphism, anecdotes and animals*. Albany: State University of New York Press.

to be able to experience sensations analogous to human hunger, not necessarily the identical experience of human hunger. Assuming that an animal thinks or feels much like humans might think or feel in a particular context is an uncritical form of anthropomorphism. What a 5th-Aim ethologist utilizes when investigating animal experience is a critical form of anthropomorphism. With critical anthropomorphism, a researcher uses their own subjective experience, along with multiple other lines of evidence, such as the results of experiments or behavioral patterns described in ethograms, in order to approximate the subjective state experienced in animals.³¹

Panksepp's psycho-neuro-ethological triangulation approach to neuroscience holds many parallels with critical anthropomorphism.³² Panksepp argues that animal sentience can be inferred by simultaneously examining three forms of evidence. Neurological homologues of human motivation, such as certain neurochemical regulators, provide initial evidence that a similar motivational system exists in other species. If there is additional ethological evidence, such as a probable shared evolutionary history to the behavior, the probability of animal sentience increases. Evidence from psychological experiments can also be used to increase the likelihood that animals possess some form of sentience. If these animals also display similar patterns to humans within parallel operant learning contexts, such as seeking the same rewards and avoiding the same punishers, the probability for, and the ability to distinguish between, an animal's subjective state increases. Since the chief goal of this dissertation is to discover the some of the emotional rudiments of morality, an approach based upon critical anthropomorphism and psycho-neuro-ethological triangulation is warranted. For purposes of brevity, this multi-

³¹ Burghardt, Gordon M. (1985). Animal awareness: Current perceptions and historical perspective. *American Psychologist*, 40(8), 905.

³² Panksepp, Jaak (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and cognition*, 14(1), 30-80.

evidential method will be summarized as a “5th-Aim moral ethology.” This approach is essentially the exploration of the moral *Umwelt* of the animal. We turn now to the definition of morality as used within this framework.

Morality Defined Within a 5th-Aim Ethology

Morality is seldom used in conjunction with animal behavior. Historically, humans have been the only species assumed in mainstream biology and psychology to possess the type of sentience capable of knowing or adhering to a moral standard.³³ But as non-human animals have increasingly demonstrated motivational and cognitive capacities once thought reserved for humans,³⁴ the assumption of human uniqueness in moral conduct has come under dispute. Bekoff and Pierce have argued that morality should be a term added to the ethological lexicon.³⁵ However, their use of morality is largely based upon the target species’ social norms and expectations. Morality, for Bekoff and Pierce, is shared within a group. But using the 5th-Aim ethological approach necessitates a distinction between this norm-based definition of morality and the affective elements of that compose morality. In order to distinguish between these two rival conceptions of morality, the shorthand Morality (*Ethos*) will be used to indicate the individual’s subjectively-experienced moral character, whereas Morality (*Culture*) will be used to designate the shared, socially-constructed, components of morality. And while Morality (*Ethos*) and Morality (*Culture*) are significantly interrelated concepts, and both are necessary for understanding morality in general, each has unique properties. Thus, it is crucial to maintain the ability to differentiate between the two phenomena.

³³ Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press.

³⁴ de Waal, Frans (2016). *Are we smart enough to know how smart animals are?* WW Norton & Company.

³⁵ Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press.

In order to differentiate between these two concepts of morality, some examples from human and animal moral experiences might prove helpful as a starting point. Morality (*Ethos*) comprises the subjective feeling of injustice when one is cheated out of an expected reward. A similar aversion to inequity, sometimes displayed in the form of angry protests, has also been observed in capuchin monkeys. These monkeys will often cease exchanging tokens for a lesser reward, such as a cucumber chip, if a neighboring conspecific receives a greater reward, like a grape, for the same task.³⁶ Morality (*Culture*) specifically defines the rules of justice within the context of society, and the framework for correcting specific injustices, often through a third-party punishment system.³⁷ Morality (*Ethos*) is also composed of the subjective compulsion, experienced via empathic concern or in association with pair-bonding, to help the victims of malice or unforeseeable accidents. Rhesus monkeys, for example, resist pulling levers that result in pain for conspecifics.³⁸ Rats proactively pull levers that relieve distress in conspecifics.^{39 40} Morality (*Culture*) describes expectations for which parties are most responsible for the care of victims and the nature of that care. These expectations may be related to a role, such as that of parent, or embedded within a species' hierarchical structure – such as grooming behavior in primates. In short, the focus of Morality (*Ethos*) is in satisfying of the subjective social emotions and intuitions found in healthy social organisms. Morality (*Culture*) is the shared norms and expectations for satisfying these social motivations and moral precepts. The relationship between

³⁶ Brosnan, Sarah F., and Frans BM De Waal (2003). Monkeys reject unequal pay. *Nature*, 425(6955), 297-299.

³⁷ Jensen, Keith (2010). Punishment and spite, the dark side of cooperation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1553), 2635-2650.

³⁸ Masserman, J. H., Wechkin, S. & Terris, W. (1964) "Altruistic" behavior in rhesus monkeys. *American Journal of Psychiatry*, 121:584-585.

³⁹ Rice, George E., and Priscilla Gainer (1962). 'Altruism' in the albino rat. *Journal of comparative and physiological psychology*, 55(1), 123.

⁴⁰ Bartal, I. B. A., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, 334(6061), 1427-1430.

Morality (Ethos) and Morality (Culture) for the individual, using Von Uexküll’s model of the *Umwelt*, is depicted in **Figure 1.1**.

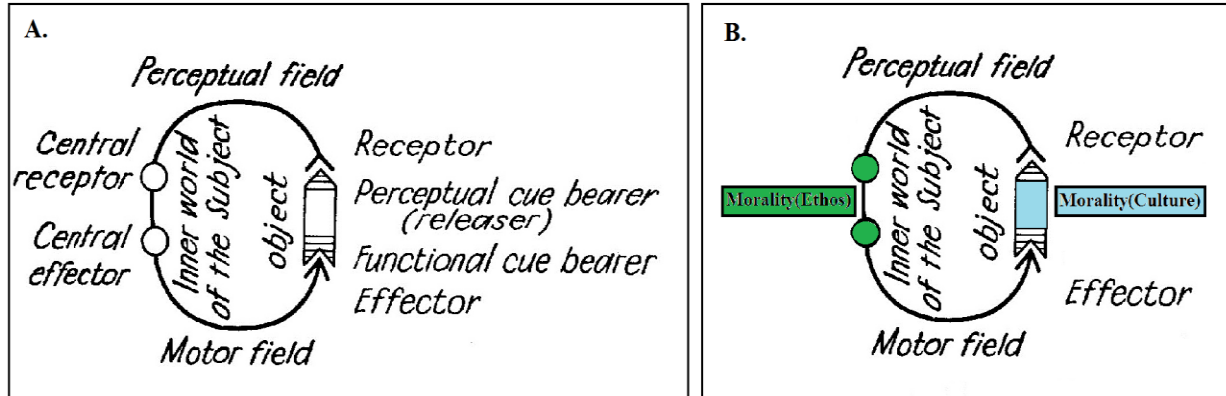


Figure 1.1: (A.) Von Uexküll’s original conceptualization of the *Umwelt* versus in relationship to external stimuli.⁴¹ (B.) The relationship of Morality (Ethos) and Morality (cultural) within Von Uexküll’s model.

The set of social emotions which will receive the greatest attention in the dissertation are related to pair-bonding. Pair-bonding, especially the bond between parent and offspring, and mate pairs, is ubiquitous within most social species. Pair-bonding, as a component of Morality (*Ethos*) has been proposed as the biological foundation of all cooperation-based moral systems.⁴² As the attachment between parent and offspring became generalized to mates, kin, and other conspecifics, a robust degree of altruism became possible.⁴³ Panksepp, who has extensively examined the emotional networks of social mammals, has proposed seven distinct primary neural systems which provide the emotional drive to form lasting social bonds. Four of these systems directly pertain to the hypotheses described in chapters two through four deserve to be

⁴¹ von Uexküll, Jakob (1992). A stroll through the worlds of animals and men: A picture book of invisible worlds. *Semiotica*, 89(4), 319-391.

⁴² Singer, P. (2011). *The expanding circle: Ethics, evolution, and moral progress*. Princeton University Press.

⁴³ Preston, Stephanie D. (2013). The origins of altruism in offspring care. *Psychological bulletin*, 139(6), 1305.

highlighted here. A list of all Panksepp's proposed systems is shown in **Table 1.1**.

The SEEKING system is connected to general motivation and appetitive behavior. It is largely governed by the neurotransmitter dopamine extending to and from the ventral tegmental area (VTA) and nucleus accumbens (NA). The CARE system, which is partially modulated by the neuropeptide of oxytocin (OT) and vasopressin (VP) in mammals, promotes the “mother love” of caregiving. The GRIEF/PANIC system, largely modulated by OT, prolactin, and endogenous opioids, promotes the negative affect when these pair bonds are lost or threatened. The FEAR system, largely modulated by the HPA and select nuclei in the amygdala, promote freezing and hiding in response to a perceived threat. As applied to the morality system described above, an individual may experience either high or low degrees of the “mother love,” CARE-elicited emotions as part of their Morality (Ethos). But the expectations for social bond-related behavior within a group would be contained in the Morality (Culture). For any given individual, these two types of morality may be congruent or incongruent to any given context.

Twin Origins of the Two Moralities

The evolutionary relationship between these two types of morality is unavoidably complex. In some ways a moral *ethos* can be viewed as a result of Natural Selection in that the motivational networks underlying the *ethos* are assumed to have evolved *via* biological mutation or genetic recombination in interaction with a developmental process, variation between individuals, and a subsequent selection based upon their adaptive advantage. However, Morality (Ethos) is not solely biological. In order to better explain the position Morality (Ethos) holds in

Table 1.1: Panksepp’s primary emotional systems and their key neural mechanism (excluding the more recently proposed SELF system).

SYSTEM	KEY BRAIN AREA	KEY NEUROTRANSMITTERS
SEEKING	Nucleus accumbens - VTA, Mesolimbic mesocortical outputs, lateral hypothalamus – PAG,	DA, glutamate, other neuropeptides, opioids, neurotensin
RAGE	Medial amygdala to BNST, Medial and perifornical hypothalamus to dorsal PAG	Substance P, Ach, Glutamate
FEAR	Central and lateral amygdala to medial hypothalamus and dorsal PAG	Glutamate, many neuropeptides, DBI, CRF, CCK, alpha-MSH, NPY
LUST	Corticomedial amygdala, BNST, Preoptic and ventromedial hypothalamus, lateral and ventral PAG	Steroids, vasopressin, oxytocin, DBI, CRF, CCK alpha-HSH, NPY
CARE	Anterior cingulate, BNST, Preoptic area, VTA, PAG	Oxytocin, Prolactin, DA, Opioids
PANIC	Anterior Cingulate, BNST, Preoptic area, Dorsomedial thalamus, Dorsal PAG	Opioids, Oxytocin, Prolactin, CRF, glutamate
PLAY	Dorsomedial diencephalon, parafascicular area, ventral PAG	Opioids, glutamate, ACH, any agent evoking negative emotion reduces play

respect to Morality (Culture) within an evolutionary framework, we must begin with a basic model of a moral phenotype.

Within the old debate concerning *Nature* versus *Nurture*, most Ethologists now agree that organisms are actually a complex interaction between the forces of “Nature,” (biological), and “Nurture,” (experiential or psychological), forces. To view any person as a collection of mere biological mechanisms, without regard to the experiences of the person, or as a mere collection of experiences, without regard to any biological mechanisms or processes, can only lead to a distorted view of humans or other animals. In order to sufficiently describe an individual’s *ethos*, we must view humans as an interaction between both biological and psychological influences. In biology, the product of this interaction between inherited mechanisms and experiential factors is called a phenotype. And this phenotype typically exhibits a certain array of phenotypic behavior, including communicatory acts, that are influenced by these biological mechanisms and learning experiences. This, hopefully uncontroversial, model of human phenotype is summarized in

Figure 1.2.

Since Morality (*Ethos*) has its essence derived from both its neural circuitry and own experiences, it is significantly influenced by natural selection and cultural transmission.⁴⁴ Given the complexity of a gene, and the potential variation in experiences, when the principle of dual origin is applied to any species, a great deal of variation is possible. On one hand, gene polymorphisms, epigenetics, *in utero* nutritional availability, hormone exposure, and the presence or absence of teratogens could have significant consequences for the neural circuitry underlying

⁴⁴ Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

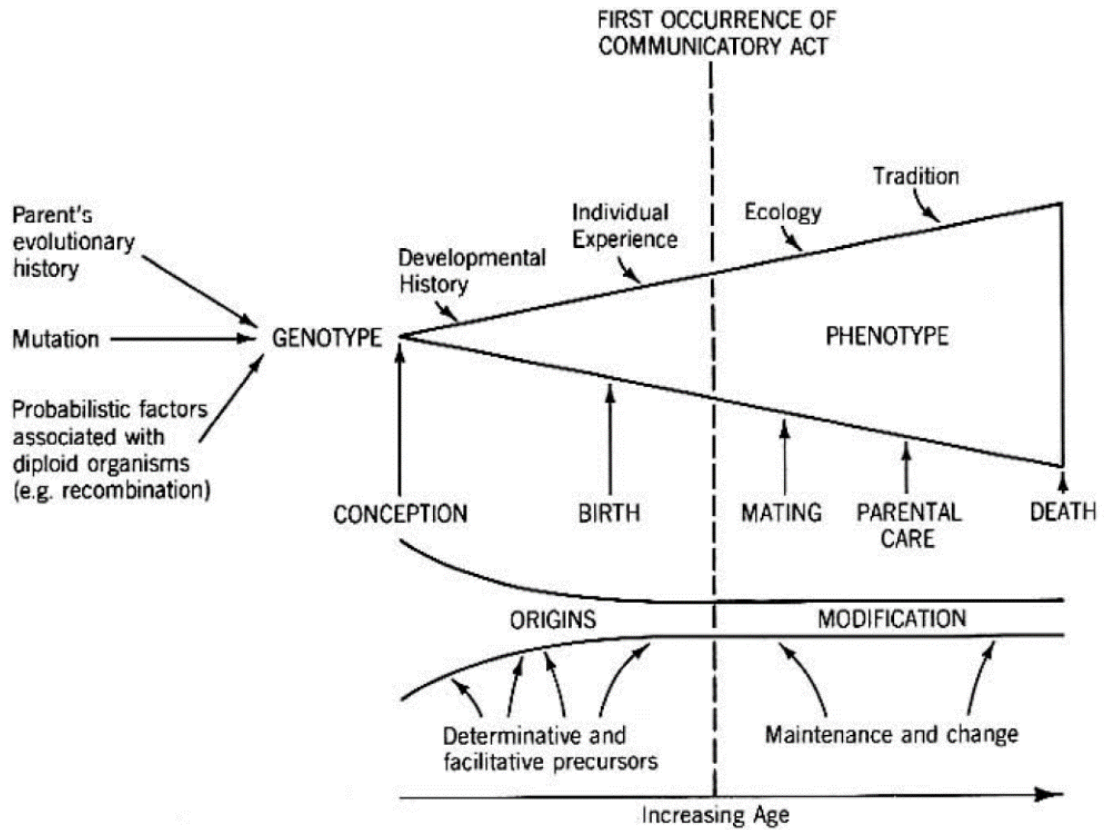


Figure 1.2: A depiction of the relationship between genotype, phenotype, and proximate factors influencing behavior— with a focus on communication.⁴⁵

⁴⁵ Burghardt GM. (1977) The ontogeny of communication. In: Sebeok TA, editor. *How Animals Communicate*. Bloomington, Ind, USA: Indiana University Press; pp. 67–93

the moral sentiments of a given phenotype. Just as with individual animals one phenotype may be more biologically prone for displays of empathy or less sensitive to detecting injustice than another.⁴⁶

Conversely, the nature of offspring care, the norms of Morality (Culture), and many other motivational factors could have a significant impact on how the moral precepts are expressed, applied, and the relative importance assigned to each motivation in a particular context. An organism's biological predisposition toward sympathy or sensitivity to injustice may receive significant approval (reward) or censure (punishment) from their social environment and subsequently decrease or increase the innate strength of these sentiments. Thus, Morality (*Ethos*) is driven both by the biological forces of natural selection and genetic drift as well as the transmission of the rules or norms found in Morality (*Culture*). Or, more succinctly, Morality (*Ethos*) is the "motivational bridge" between the neurology and the subjective experience of an individual. It comprises the deepest social emotions found within a species. Morality (*Culture*) is the shared moral norms of a group. An extension of the Von Uexküll *Umwelt* model to incorporate multiple, interacting individuals is depicted in **Figure 1.3**.

Often the norms and expectations of the Morality (Culture) are often communicated through cues and signals between individuals. The use of cues and signals to communicate moral expectations to conspecifics will receive greater attention in the next chapter. However, at this point it is important to point out that the morality-related signals sent or received by the individual can be used for variety of purposes. They can be used to indicate cooperative or

⁴⁶ Richerson, P., Baldini, R., Bell, A. V., Demps, K., Frost, K., Hillis, V., & Ross, C. (2016). Cultural group selection follows Darwin's classic syllogism for the operation of selection. *Behavioral and Brain Sciences*, 39.

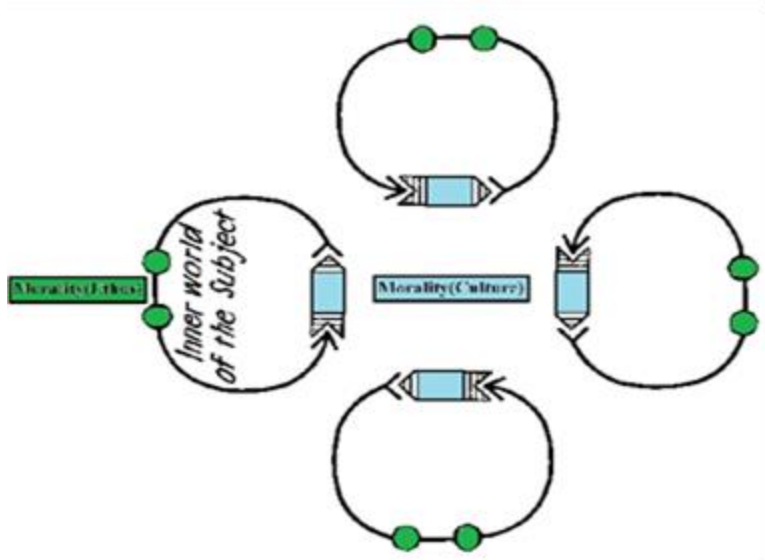


Figure 1.3: Interacting Morality (Ethos) forming a Morality (Culture) Matrix.

hostile intentions. A dog may bare its teeth at a stranger or use a play bow to initiate play with a litter mate. These signals may be honest signaling or deceptions. The signals may be effected by social roles or place on a dominance hierarchy. There is a tremendous amount of potential for diversity in moral-related communication⁴⁷ which is required in order to maintain even a relatively simple Morality (*Culture*) system.

Many possibilities arise when a focus is placed upon behavioral interactions between moral phenotypes. There may be only one optimal Morality (*Ethos*) for all members of a species, or there may be a diverse set of interacting moral characters that are the most advantageous. Moral phenotypes that are advantageous under one set of conditions, such as resource scarcity, might not be advantageous other conditions, such as resource abundance. Despite these possibilities, the Morality (*Ethos*) of the individual remains the foundation of cultural morality. And this *ethos* is greatly influenced both by the forces of natural selection and cultural selection. An *ethos* in early development would be heavily influenced by the Morality (*Culture*) surrounding it. Then, as the organism develops, it would, in most cases, increasingly influence the shared Morality (*Culture*) of which it was part.

A Tension between the Moralities

The separation of morality into two components, *ethos* and culture, raises an important paradox concerning natural selection: Is it the *ethos*-based morality that is selected for or against in nature and the culture-based morality that is derivative, or vice versa? The answer to this

⁴⁷ Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a paradigm perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

paradox has been addressed by the Wilson & Wilson in multilevel selection theory.^{48 49} One of the central components of multi-level selection is that certain traits can evolve in an individual despite being locally disadvantageous to the organism. This can occur when advantages of membership in a group outweigh the fitness burden of the locally disadvantageous traits to the individual over the long term. When this type of selection of multiple traits is successful, a “superorganism” can form. Wilson and Wilson point out that evolutionary biology has many examples of superorganism emergence.⁵⁰ They argue that many multicellular organisms are a product of cooperative single cells. Many genetic and developmental phenomena such as “chromosomes, the rules of meiosis, a cell stage in the life cycle, the early sequestration of the germ line, and programmed death of cell lineages” are examples of superorganism principles suppressing the primacy of the individual elements that constitute an organism.⁵¹

These multi-level selection principles, applied to morality, suggest that morally-related emotion in one’s *ethos* can be locally disadvantageous to an individual, at least in some instances, as long as there are greater advantages to the individual as a member within the larger group. Thus, an organism can theoretically possess a moral *ethos* which contains elements that conflict with individual fitness advantages, provided that they are compensated for by the fitness advantages of Morality (*Culture*). However, it is probable that the relatively rapid process of cultural transmission would promote much greater variability in any particular generation in moral behavior than the (typically) much slower process of natural selection. With respect to

⁴⁸ Sober, E., & Wilson, D. S. (1999). *Unto others: The evolution and psychology of unselfish behavior* (No. 218). Harvard University Press

⁴⁹ Wilson, David Sloan, and Edward O. Wilson (2007). Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology*, 82(4), 327-348.

⁵⁰ Ibid.

⁵¹ Ibid.

natural selection, we would anticipate selection for moral flexibility in response to a changing Morality (*Culture*). This type of phenotypic flexibility was previously predicted in what is known as the Baldwin Effect.^{52 53}As applied to morality, we would anticipate flexibility in response to a dynamic morality (*Culture*) to be more advantageous than a rigid and unchanging *ethos* incapable of adapting to the rapid changes of culture.

The group can be defined in numerous ways. We assume that families, tribes, communities, corporations, organizations, and nations all compose types of societies that may provide advantages to an individual. And we would expect that differences between these groups would draw upon the Morality (*Ethos*) in different ways. One's own family, supported by all the impetus of kin selection and inclusive fitness,⁵⁴ would likely result in an increased demand on many of the individual's moral sentiments compared to a more tangential relationship. When dealing with individuals from an out-group, or where the advantages of group membership are small, we would expect smaller demands on the locally disadvantageous moral motivations. These various expectations, found in the form of rules, laws, policies, and etiquette of humans, form the vast and complex set of moral behavior and expectations notated as Morality (*Culture*). And though no human groups meet the criteria of interconnectedness of a "superorganism," prehistoric tribes or a nuclear family would be much closer to this superorganism state, than, say, a nation.

Two important features of morality require emphasis. First, the group-level, Morality

⁵² Baldwin, J. Mark (1896). A new factor in evolution. *The American Naturalist*, 30(354), 441-451.

⁵³ Badyaev, A. V. (2009). Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364(1520), 1125-1141.

⁵⁴ Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of theoretical biology*, 7(1), 17-52.

(*Culture*) is based upon the individual Morality (*Ethos*); much like organs are comprised of sets of cells, systems compose sets of organs, and organisms compose sets of systems. Each individual *Ethos*, as mentioned earlier, may vary in some respects. However, the *ethos* of each individual composing a group cannot be incompatible to each other without diminishing, or eliminating, the overall group fitness – just as an organism’s glands cannot produce massive amounts of substances that are unfilterable and toxic to their central nervous system and remain viable.

The second important feature of Morality (*Culture*) is competition. Groups and their Morality (*Culture*) can exist in a network which is in competition for various types of resources with other groups as depicted in **Figure 1.4**. Thus, a Morality (*Culture*) which is composed of incompatible, inter-competing, and segregated set of Morality (*Ethos*) phenotypes are less likely to successfully compete against Morality (*Culture*) composed of a compatible, cooperating, and integrated set of Morality (*Ethos*) phenotypes. We thus arrive at the arch-principle of multilevel selection theory: individual altruism “wins” between groups, individual selfishness “wins” within the group. So which came first, the *ethos* or the culture? The answer from a Multi-level Selection perspective is that they evolved as sometimes cooperating, at other times competing, twins.

Searching for Moral Fundamentals

This complex picture of Morality (*Culture*) becomes much more complicated as we move from the individual and their *ethos* and the Morality (*Culture*) of their group membership, into a model incorporating multiple group memberships. It is here that humans and animals differ significantly. Humans are often simultaneously members of many groups. Many of these groups exist by voluntary membership, such as a modern place of employment, while membership

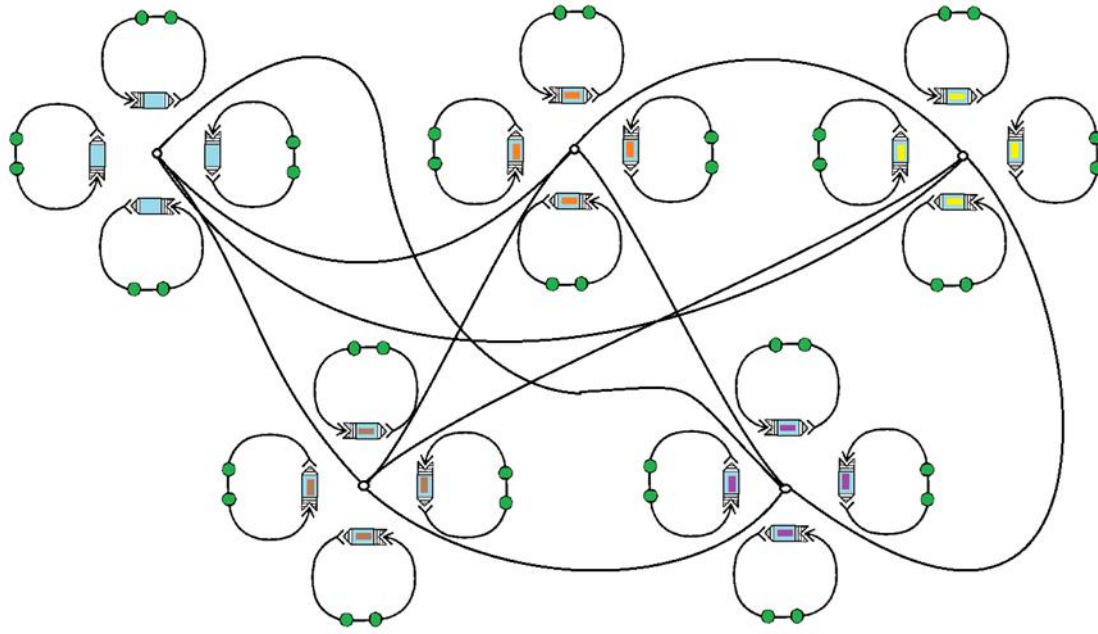


Figure 1.4: As simplified version of the exponential complexity that can occur as various groups of Morality (*Culture*) interact within a social network.

in other groups is not a product of choice, such as the biological family. As the number of these group memberships increase they can create interlocking, possibly competing, layers of Morality (*Culture*), which presents substantial challenges in the study of human morality. Humans are quite unique in the type, complexity of, and number of, groups in which they are members. Compared to humans most other species, as far as we can observe, possess membership in few other groups. They might be part of a mate pair, a family, or a flock or band. Few other species have frequent contact with other groups, or those outside their flock or band, which result in sustained, coordinated, and cooperative behavior. This may be due to the cognitive limitations of these various species or a more a fundamental set of biological constraints of nature. But whatever the reasons may be for the complexity of human social systems, the search for fundamental set moral motivations would be greatly enhanced by the examination of the moral motivations experienced by animals living in a simpler social context, in short — a comparative species approach to morality.

CHAPTER 2: AVIAN MORAL MOTIVATION

Rationale and Hypothesis Generation

“The following proposition seems to me in a high degree probable—namely, that any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well, or nearly as well developed, as in man. For, firstly, the social instincts lead an animal to take pleasure in the society of its fellows, to feel a certain amount of sympathy with them, and to perform various services for them.”⁵⁵

Darwin argued that any animal species would inevitably develop a moral conscience once that species had obtained certain social and intellectual prerequisites via natural selection. He emphasized parental and affiliation-based social instincts and certain “intellectual powers” as the foundation for this moral conscience.⁵⁶ Thus, according to Darwin, one would not expect to find expressions of sympathy, helping behavior, or the pleasure in affiliating others, in completely solitary animals – or in animals that did not care for their own offspring. The care of offspring then, according to Darwin, is central to the probable evolutionary path of morality. Applying Darwin’s argument to the two types of morality presented in chapter one, we would expect that morality has a basis in parental and filial affections, or what we would call offspring care, in the Morality (*ethos*) and some intellectual powers that allow for the moral interaction of culture.

⁵⁵ Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London.

⁵⁶ *Ibid.*

Avian “Parental and Filial Affections”

Many avian species appear to possess these “well-marked” parental instincts, which Darwin suggested were fundamental to prosocial motivation. Many birds care for their offspring,⁵⁷ indicating they possess these strong parental and filial instincts. Female chickens, which also use food-related calls, show physiological changes—like an increased heart rate—and vocalize more when their chicks are distressed.⁵⁸ This suggests that chickens possess a rudimentary capacity to detect distress in others and that this perceived distressed state alters their own affective state—a behavior that fits within Darwin’s statement of “a certain amount of sympathy.” And these “affections” do not appear isolated to offspring. The heartrate of geese elevated when their mate enters a fight.⁵⁹ Social monogamy is more common in birds than mammals.⁶⁰ This widespread monogamy suggests that there is a greater percentage of birds than mammals that have extended these strong pair bonds beyond their offspring to their mates. And beyond Darwin, these findings are consistent with several models that propose that altruistic behavior evolved as an extension of parental care and pair bonding.^{61 62}

Carolina chickadees have also been shown to invest a significant amount of time into the care of their mates and offspring. Male chickadees have been observed feeding their mates just

⁵⁷ Royle, N. J., A. F. Russell, and A. J. Wilson (2014). The Evolution of Flexible Parenting. *Science*, 345(6198), 776–81.

⁵⁸ Edgar, J. L., J. C. Lowe, E. S. Paul, and C. J. Nicol (2011). Avian Maternal Response to Chick Distress. *Proceedings of the Royal Society of London B: Biological Sciences*, 22;278 (1721):3129-34.

⁵⁹ de Waal, F. B. (2013). *The bonobo and the atheist: In search of humanism among the primates*. WW Norton & Company.

⁶⁰ Mock, Douglas W., and Masahiro Fujioka (1990). Monogamy and Long-Term Pair Bonding in Vertebrates. *Trends in Ecology & Evolution*, 5(2), 39–43.

⁶¹ de Waal, Frans BM (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy. *Annu. Rev. Psychol.* 59: 279–300

⁶² Donaldson, Z. R., and L. J. Young. 2008. Oxytocin, Vasopressin, and the Neurogenetics of Sociality. *Science*, 322(5903), 900–904. doi:10.1126/science.1158668; Preston, Stephanie D. (2013). *The Origins of Altruism in Offspring Care*.

prior to copulation and continue to return to the nest during the incubation period (at a rate of 2.2 visits per hour) to provide food for their mate.^{63 64} Female chickadees invest the majority of their time (approximately 77.2% of daylight hours) attending to their active nests.⁶⁵ Parental care by both parents continues throughout incubation and hatchling phases. Both the female and the hatchlings may be fed exclusively by the male in the first few days after the hatching process begins. This offspring care extends past the fledging period as parents escort the fledged birds to the edge, or out of, their territory. During this period, vocalizations from both parents are common.^{66 67}

In the previous chapter we described moral character, or Morality (*Ethos*), as a set of subjectively experienced moral motivations. Using Darwin's proposition that "parental and filial affections" form the basis for helping, sympathy, and presumably other positive forms of moral behavior, we can begin to develop this model with the first potential motivational prerequisite of a moral *ethos*, or character. This rudimentary moral emotion, using Darwin's words, is affection. The examples of chickadee parental and mate care-giving provide evidence that Carolina chickadees meet the basic motivational criterion of affection. Using the Panksepp model of social emotions, this type of affection best fits within his description of the CARE system. The CARE system is described as the source of nurturance, or in the vernacular, "mother love."

However, it is important to note that Panksepp's emotional model is focused on emotional commonalities within mammalian, not avian, species. An avian species, such as a

⁶³ Brewer, R. (1961). Comparative notes on the life history of the Carolina Chickadee. *The Wilson Bulletin*, 348-373.

⁶⁴ Odum, E. P. (1942). Annual cycle of the black-capped chickadee: 3. *The Auk*, 59(4), 499-531.

⁶⁵ Brewer, R. (1961). Comparative notes on the life history of the Carolina Chickadee. *The Wilson Bulletin*, 348-373.

⁶⁶ Ibid.

⁶⁷ Clemmons, J., & Howitz, J. L. (1990). Development of early vocalizations and the chick-a-dee call in the black-capped chickadee, *Parus atricapillus*. *Ethology*, 86(3), 203-223.

Carolina chickadee, can provide some examples of similarity between their CARE system and the CARE system common amongst mammals. Some of these similarities, such as the parental investment highlighted above, or the neurological similarities summarized below, suggest a similar functional and motivational capacity for CARE. However, there are also likely to be many examples in which these systems differ, at least, in mechanism. For this reason it is important to emphasize that the CARE system of the chickadee, abbreviated as CARE-chickadee, is essentially a homeologue,⁶⁸ not necessarily a homologue, of the mammalian CARE system. The goal here is to identify motivational correlates, not to assume interchangeable subjective experiences between avian and mammalian species.

One of the chief obstacles in comparing these Pankseppian emotional systems is that—relative to what is known about mammalian motivational neurology—much less is known about their avian homeologues. Avian brains have many unique neurological features in comparison to many mammalian brains, such differences as overall brain size, grey to white matter ratios, and the nature of seasonal endocrine changes. However, there is also some evidence that avian brains possess areas analogous to a human cortex.⁶⁹ The avian homologues of oxytocin and vasopressin, mesotocin and vasotocin, may modulate affiliative behavior in birds in ways similar to mammals.⁷⁰ Thus, while the neuroanatomy of avian social motivation remains significantly less developed than the neuroanatomy of mammalian social motivation, from the evidence that does exist, there appear to be at least some parallels between a mammalian and an avian social

⁶⁸ From the Greek *homeo* meaning “similar.” Homeologue is used here to denote a similar subjective experience whereas homologue, is usually focused on similarities in structure due to common ancestry.

⁶⁹ Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., & Wild, M. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology*, 473(3), 377-414.

⁷⁰ Goodson, J. L., Schrock, S. E., Klatt, J. D., Kabelik, D., & Kingsbury, M. A. (2009). Mesotocin and nonapeptide receptors promote estrildid flocking behavior. *Science*, 325(5942), 862-866.

motivation for Darwin's parental and filial affections. It should be emphasized that the differences between the neural correlates of the CARE system also suggest some difference in the CARE-related emotion experienced by birds and mammals. However, these systems can also be assumed to have a least one important commonality. Any CARE-based emotion, whether avian or mammalian, by definition must have a positive emotional valence that can become associated with another organism. Without this positive affect, and an object for this positive affect, a CARE-based emotion would lose its functional purpose. It would cease to describe a CARE system.

Despite the issues that surround comparative neuroanatomy and the many possibilities for divergence in subjective experience, from a 5th-Aim perspective it is a relatively safe assumption that Carolina chickadees possess a strong capacity for experiencing positive emotion in connection to their mates and offspring. As a result of this motivational capacity, both male and female chickadees can invest significantly into helping behavior. Given the presence of these extensive and costly parental investments, objections to the idea that Carolina chickadees are capable of exhibiting some form of morality system is likely to be based more on a lack of what Darwin referred as the "intellectual powers" than any deficiency in the "parental and filial instincts".

Avian "Intellectual Powers"

What are the "intellectual powers," or cognitive capacities, which combine with these filial instincts to create what Darwin called a "moral conscience"? Darwin held that these capacities should be, at least in some ways, humanlike. The inclusion of humans as the standard for morality-generating intellectual capacity begs at least one important question. Which of

mankind's intellectual powers was Darwin speaking to? The capacity to learn, to detect the motivations of others, to solve complex problems using abstract symbol-based reasoning, or to formulate the probabilities of future events? All of the capacities are examples of "intellectual powers" possessed by at least some humans. Which of these, if any, is the foundation of this moral conscience? It is unlikely that Darwin believed all of these particular human capabilities were required. If this were true, it would reduce Darwin's proposition to an empty tautology. We would be forced to read Darwin to mean that any being with all of humanities' instincts and intellectual characteristics would probably behave much like a human. This is true, of course, but not worth writing.

This motivational model used in this dissertation assumes another possibility. If we remove humans as the standard of intellectual comparison, and take a comparative cognition approach, we can envision a continuum of cognitive capacities playing an important role in the moral *ethos* of a species or individual. If we start by incorporating this continuum, we need not assume that the cognitive "prerequisites" for morality require complex perspective-taking capacities such as a Theory of the Mind (ToM).⁷¹ Higher-order intelligence can promote a "common good" morality or self-interest.⁷² And as de Waal has observed, conceptualizing morality as the exclusive or primary domain of higher-order cognition is a post-Kantian idea.⁷³ Simply framed, the model used in this dissertation views the Morality (*Ethos*) and Morality

⁷¹ Theory of the Mind: the ability to attribute mental states—beliefs, intents, desires, pretending, knowledge, etc.—to oneself and others and to understand that others have beliefs, desires, intentions, and perspectives that are different from one's own.

⁷² Byrne, R., & Whiten, A. (1989). Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford science publications.

⁷³ de Waal, F. (2009). *The age of empathy*. New York: Harmony.

(*Culture*) both as existing on a continuum of complexity.⁷⁴ The more complexity in the emotional system possessed by the individual or a species, the greater the potential for complexity within the corresponding Morality (*Ethos*). The more complex the cognitive and communicative capacity is in the individual or species, the greater the potential for complexity in the combined Morality (*Culture*). This relationship between cognitive and communicative complexity, moral motivation, and the potential for Morality (*Culture*) complexity is illustrated in **Figure 2.1**. The connection between cognitive and communicative capacity is outlined below. However, first we examine a few fundamental “intellectual powers” that may underlie a rudimentary morality.

Individual Recognition and Image Scoring

One of the most important cognitive requirements we might assume to exist in a species with a moral system is the ability to discriminate between conspecifics. The ability of a chickadee, or any other species, to distinguish between males and females has obvious fitness advantages, at least during the mating season. The ability to distinguish flock mates from rival groups also has obvious fitness advantages in some domains such as food recruitment. Many bird species have been shown to distinguish between genetically-related individuals and non-related individuals. This suggests the possibility of a kin selection evolutionary driver for this ability to discriminate between conspecifics. Black-capped chickadees (*Poecile atricapillus*) possess the ability to discriminate between conspecifics using only auditory cues. Many parid species, including chickadees, also have well-established dominance hierarchies which suggest the ability

⁷⁴ Complexity is defined here as being composed of additional components or possible states as opposed to few components or possible states.

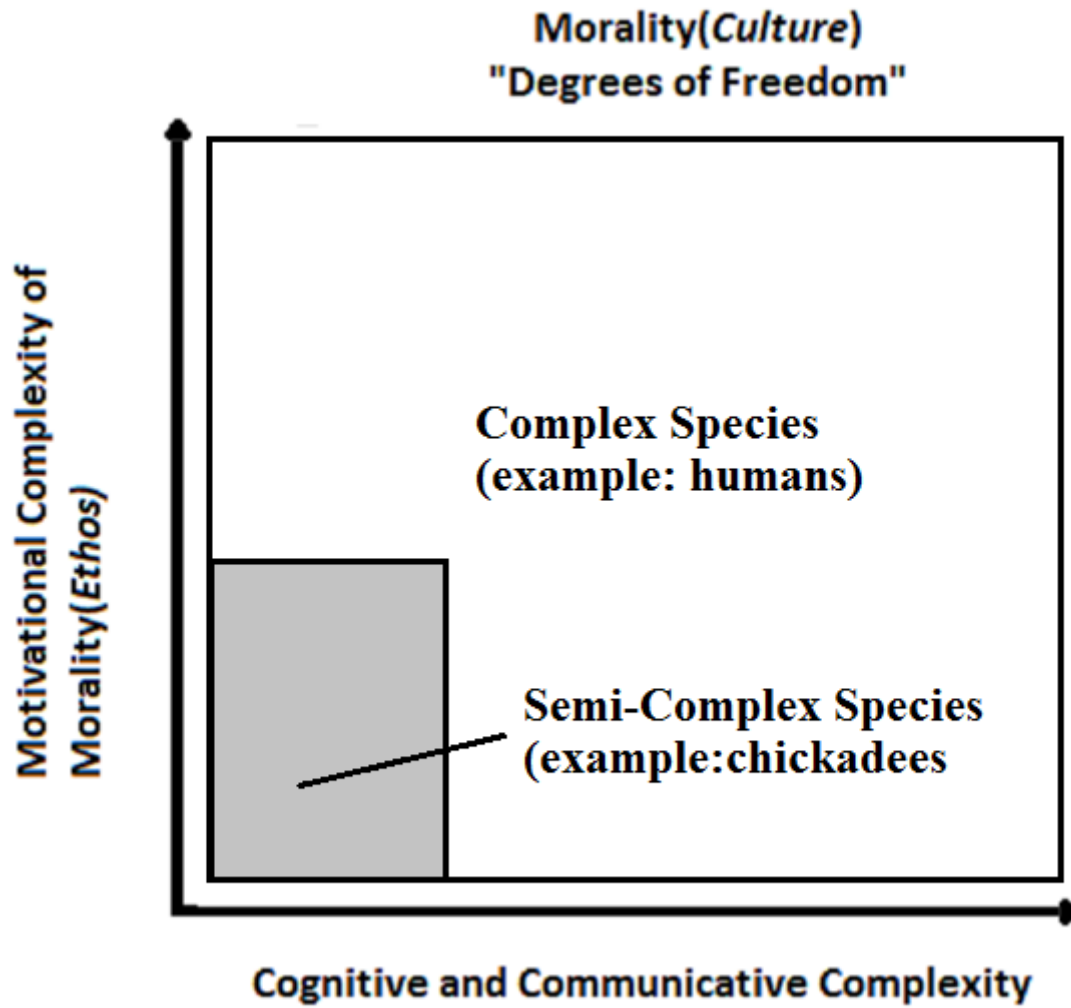


Figure 2.1: The complexity of a moral system can be summarized as a product of *Ethos* complexity X Cognitive/Communicative complexity.

to recognize and store information for conspecifics. Thus, many avian species, including chickadees, appear to possess a highly developed ability to discriminate between the identities of other individuals.

Another cognitive ability that might be central to a cooperative motivational system is the ability to recognize, evaluate, and remember motivational or reputational information about others—known as image scoring. Image scoring involves an evaluation of other organisms and can be seen as fundamental component of reputation systems.⁷⁵ It does not appear that robust cognitive capacities are required to maintain a simple form of an image score. The ability to track behavioral information about others seems to be present in reef fish as they select more helpful cleaner fish to aid in parasite removal.⁷⁶ An avian study of pied flycatchers (*Ficedula hypoleuca*) found that when neighboring birds arrived to help mob an owl model, those neighbors were more likely to receive mobbing assistance when their nests were threatened.⁷⁷ This study also suggests, at the very least, an ability to maintain an image score of other conspecifics; and may indicate an ability to participate in a reciprocity-based defense system. Another study with Eurasian jays (*Cyanistes caeruleus*) suggested that some birds have the capacity to make social decisions based on the perceived hedonic value of a food to their partner versus their own food preferences. In this study, male jays fed the female jays a greater proportion of the type of food that had been withheld from the females' diet. The males only showed this behavior when they were able to witness their mate's food availability.⁷⁸ This study suggests, not only an ability of some avian

⁷⁵ Nowak, Martin A., and Karl Sigmund (1998). Evolution of Indirect Reciprocity by Image Scoring. *Nature*, 393(6685), 573–77. doi:10.1038/31225.

⁷⁶ Bshary, Redouan, and Daniel Schäffer (2002). Choosy Reef Fish Select Cleaner Fish That Provide High-Quality Service. *Animal Behaviour*, 63(3), 557–564.

⁷⁷ Krama, Tatjana, Jolanta Vrublevska, Todd M. Freeberg, Cecilia Kullberg, Markus J. Rantala, and Indrikis Krams. 2012. You Mob My Owl, I'll Mob Yours: Birds Play Tit-for-Tat Game. *Scientific Reports*, 2.

⁷⁸ Ostojić, Ljerka, Rachael C. Shaw, Lucy G. Cheke, and Nicola S. Clayton (2013). Evidence Suggesting That

species to track information related to a conspecific, but also an ability to attach specific motivational information to the image score.

Social Learning

Another cognitive ability we might expect in any species capable of sustainable cooperative behavior is the ability to observe and then to perform the activities of conspecifics – a process generally referred to as social learning. Perhaps the most famous example of social learning was the rapid proliferation of milk bottle opening behavior documented in British tits (*Parus major*).⁷⁹ Sherry and Galef demonstrated a similar adaptation in Black-capped chickadees but they suggested that imitation may not be the primary vehicle for this the proliferation of behavior.^{80 81} They proposed that the exposure of the desirable stimuli was the key factor in the proliferation of this behavior and modeling behavior. Aplin et al, studying wild-caught blue tits (*Cyanistes caeruleus*), came to the opposite conclusion.⁸² They found that not only the result, but the technique the birds used to manipulate objects was proliferated in the population. The disparity between the results found in the Sherry & Galef⁸³ and Aplin et al⁸⁴ studies could be resolved in a number of different ways. But with either of these interpretations, it is clear that the foraging success of one bird can become transferrable to conspecifics in multiple species.

Desire-State Attribution May Govern Food Sharing in Eurasian Jays. *Proceedings of the National Academy of Sciences of the United States of America*, 110(10), 4123–28. doi:10.1073/pnas.1209926110.

⁷⁹ Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds*, 42(11), 347-357.

⁸⁰ Sherry, D. F., & Galef, B. G. (1984). Cultural transmission without imitation: milk bottle opening by birds. *Animal Behaviour*, 32(3), 937-938.

⁸¹ Sherry, D. F., & Galef, B. G. (1990). Social learning without imitation: more about milk bottle opening by birds. *Animal Behaviour*, 40(5), 987-989.

⁸² Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, 85(6), 1225-1232.

⁸³ Sherry, D. F., & Galef, B. G. (1984). Cultural transmission without imitation: milk bottle opening by birds. *Animal Behaviour*, 32(3), 937-938.

⁸⁴ Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, 85(6), 1225-1232.

Social learning is also well documented in avian signaling. Juvenile rehearsal of vocalizations has been demonstrated in multiple species including cowbirds (*Monothrus ater*),⁸⁵ sparrows (*Zonotrichia leucophrys*),⁸⁶ and zebra finches (*Taeniopygia guttata*).⁸⁷ Both black-capped chickadees and Carolina chickadees are exposed to the calls of their parents throughout their incubation, hatchling, fledging, and post-fledging periods. The use of general call appears as early as 10 days after hatching.⁸⁸ Thus, we can say with a high degree of confidence, that during the short infancy and adolescence of chickadees, a rapid period of biological development and social demonstration interact to create the rudiments of the chickadee call system.

Emotional Signaling

Up to this point we have discussed a definition of morality as consisting of two parts – an *ethos*, and set of shared cultural norms. We have also argued that morality can be viewed as existing on a continuum of complexity versus existing as categorical phenomenon only experienced in species with a complex set of cognitions. One of the important features of this two-part morality that has yet to be discussed directly is communication. Communication is an essential element of morality connecting the subjective Morality (*Ethos*) with the shared Morality (*Cultural*) of the group. Within this dual morality model, there is not a categorical difference between moral and non-moral communication. However, some signals and some signalers would be expected to possess a larger impact on the Morality (*Culture*) than others.

⁸⁵ West, M. J., & King, A. P. (1985). Social guidance of vocal learning by female cowbirds: validating its functional significance. *Ethology*, 70(3), 225-235.

⁸⁶ Marler, P., & Peters, S. (1982). Subsong and plastic song: their role in the vocal learning process. *Acoustic communication in birds*, 2, 25-50.

⁸⁷ Johnson, F., Soderstrom, K., & Whitney, O. (2002). Quantifying song bout production during zebra finch sensory-motor learning suggests a sensitive period for vocal practice. *Behavioural brain research*, 131(1), 57-65.

⁸⁸ Brewer, R. (1961). Comparative notes on the life history of the Carolina Chickadee. *The Wilson Bulletin*, 348-373.

Morality (*Culture*) is related to norms and expectations. Signalers higher on a dominance hierarchy would be expected, in many instances, to have greater influence on the Morality (*Culture*), perhaps through the enforcement of norms or even norm creation, than more subordinate members of a group. A signal bearing little relationship to the group's norms and expectations would only be tangentially connected to morality. Thus, communicating environmental information, such as the presence of a food source becomes moral signaling when there is a corresponding expectation to communicate that information. Evidence of these expectations would come in the form of either punishing behavior from the group, such as exclusion or agonism, or rewarding behavior, such as enhanced reputation or increased mating opportunities.⁸⁹

The type of communication being investigated as a part of this dissertation is food-associated calls made by the Carolina chickadee. Chickadees possess a complex and versatile vocal communication system, making them an excellent target species for investigating the motivational aspects of signaling. Chickadees often use a *chick-a-dee* call,^{90 91} hereafter referred to as the “general call,” consisting of multiple note types.^{92 93} A-notes and B-notes are high frequency notes that usually precede the more broadband C-notes and D-notes. The acoustic characteristics of these broadband C-notes and D-notes make their source easier to locate by

⁸⁹ Trivers, R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*. 46:35-57.

⁹⁰ Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. 83:820–833.

⁹¹ Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am*. 113: 2127–2136.

⁹² Soard CM, Ritchison G. (2009). ‘Chick-a-dee’ calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Anim Behav*. 78:1447–1453.

⁹³ Templeton CN, Greene E, Davis K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*. 308:1934–1937.

conspecifics or predators.^{94 95} Thus, the use of C-notes and D-notes in calls may function to recruit individuals to the location of the signaler. C-notes have been associated with flight.^{96 97} The D-notes have been observed in multiple contexts including predator contexts⁹⁸ or food recruitment.⁹⁹ The general call of the Carolina chickadee, especially the D-notes embedded in these calls, are the focal communication investigated in this dissertation.

Animal food signaling: The motivational question

In order to test our hypothesis that some avian species possess both the motivational capacity and the rudimentary cognitive abilities (in the form of image scoring, individual recognition, and social learning) to form a moral *ethos*, we must find an appropriate behavior as a basis for investigation. The target behavior in the study of cooperation should be an instance of helping.¹⁰⁰ If the cooperative behavior involves mobbing or other forms of aggression, it is unlikely that the motivational states preceding the behavior stem from the “parental and filial affections” proposed by Darwin. One type of behavior that potentially meets the requirements of this affiliation-based test is food sharing.

There are many species that communicate the availability of food to conspecifics. Some

⁹⁴ Wiley RH, Richards DG. (1982). Adaptations for acoustic communication in birds: sound transmission and signal design. In: Kroodsma DE, Miller EH, Ouellet H, editors. *Acoustic communication in birds*. New York: Academic Press. p. 131–181.

⁹⁵ Bradbury JW, Vehrencamp SL. (1998). *Principles of animal communication*. Sunderland (MA): Sinauer.

⁹⁶ Mahurin, E. J., Freeberg, T.M. (2009) Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behav Ecol* 20:111–116

⁹⁷ Freeberg TM, Lucas JR. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Anim Behav.* 63:837–845.

⁹⁸ Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool.* 83:820–833.

⁹⁹ Clemmons, J., & Howitz, J. L. (1990). Development of early vocalizations and the chick-a-dee call in the black-capped chickadee, *Parus atricapillus*. *Ethology*, 86(3), 203-223

¹⁰⁰ de Waal, Frans BM. (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy. *Annu. Rev. Psychol.*, 59, 279–300.

primates, which we assume to possess a relatively high degree of cognitive complexity, may be quite sensitive to the presence of conspecifics when signaling about food availability – known as an audience effect. During one field study, researchers played chimpanzee (*P. troglodytes*) “pant hoots” from a member of the same band as they approached a conspecific at a food source.¹⁰¹ The researchers then observed if the food-finding chimpanzee returned the call with a “rough grunt” – a vocalization associated with food discovery. Their subsequent analysis indicated that chimpanzees are more likely to call to more dominant “friends” in this exchange. This same research group was able to build upon these findings when examining alarm calls in response to model snakes. They found evidence in their analysis that these calls were a) socially directed and given to the arrival of friends, b) linked with gaze monitors and alternations, and c) goal directed, since the calls ceased once recipients were safe from the predator.¹⁰² Chimpanzees also are more likely to recruit conspecifics for tasks when they had a history of successfully cooperating with them.¹⁰³ Thus, it appears quite likely that some non-human primates have an incredibly complex and robust (often food-related) reciprocity system.

Food sharing appears to be quite common in non-primates as well. Honeybees (*Apis Linnaeus*) relay food location through their dance patterns,¹⁰⁴ an intriguing discovery that led to a Nobel Prize. Food-related signaling exists in species as diverse as ants (*Leptothorax*),¹⁰⁵ dolphins

¹⁰¹ Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, 86(5), 955-965.

¹⁰² Ibid.

¹⁰³ Melis, A. P. (2006). Chimpanzees Recruit the Best Collaborators. *Science*, 311(5765), 1297–1300. doi:10.1126/science.1123007.

¹⁰⁴ von Frisch, Karl (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA, US: Harvard University Press.

¹⁰⁵ Möglich, M. (1978). Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insectes Sociaux*, 25(3), 205-225.

(*Tursiops truncatus*),¹⁰⁶ and ravens (*Corvus corax*).¹⁰⁷ How these other species communicate the food location may differ in mode—such as odor trails in mole rats (*Heterocephalus glaber*),¹⁰⁸ movement patterns such in bees,¹⁰⁹ or vocalizations in primates¹¹⁰—but it is generally accepted that many animals communicate the location of food to conspecifics. What is not generally agreed upon is the set of motivations that compel this signaling. Functional explanations for behavior are not the same as motivational explanations for behavior.¹¹¹ The motivational reason why any animals (both primates and non-primates) are motivated to reveal food locations to conspecifics, instead of merely consuming the food, remains an important question in animal psychology.

Two Hypotheses

Given the immense complexity inherent in any moral system, and the goal of discovering the fundamental motivational components that compose that system, a comparative approach might prove beneficial. An ideal biological system or species for studying a multi-level morality would, ideally, be as simple as possible while still containing many of the same elements of the human variety of morality. This target species should possess some set of social motivations, such as the Darwin's "filial affections" found in Panksepp's CARE system, and at least in some

¹⁰⁶ Janik, V. M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1446), 923-927.

¹⁰⁷ Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others?. *Behavioral Ecology and Sociobiology*, 28(1), 13-21.

¹⁰⁸ Judd, Timothy M., and Paul W. Sherman (1996). Naked Mole-Rats Recruit Colony Mates to Food Sources. *Animal Behaviour*, 52(5), 957-969.

¹⁰⁹ von Frisch, Karl (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA, US: Harvard University Press.

¹¹⁰ Schino, Gabriele, and Filippo Aureli (2009). Chapter 2 Reciprocal Altruism in Primates: Partner Choice, Cognition, and Emotions. In *Advances in the Study of Behavior*, edited by Timothy J. Roper H. Jane Brockmann Marc Naguib, Katherine E. Wynne-Edwards, John C. Mitani and Leigh W. Simmons, 39, 45-69. Academic Press.

¹¹¹ de Waal, Frans BM. (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy. *Annu. Rev. Psychol.* 59, 279-300.

basic “intellectual powers” that allow for sustained cooperative behavior between conspecifics. One species that might meet this criterion of affection, basic cognitions, and simplicity is the Carolina chickadee, *Poecile carolinensis*.

M.S. Ficken observed that black-capped chickadees, a close relative of the Carolina chickadee, often emit calls upon the discovery of a new food source. She suggested that this type of food-related communication might qualify as altruism.¹¹² That is, the chickadees were believed to incur a fitness cost in the recruiting of flock-mates to, and the sharing of, a food source in order to convey the benefit of the available food to conspecifics. However, this interpretation has not been universally accepted. Several alternative explanations for this calling behavior have been proposed, including various ‘predation-defense’ hypotheses. Since the focus of this dissertation is on the subjective motivations of the *ethos*, we will need to translate these functional or phylogenetic hypotheses into motivational hypotheses. The act of behavior-to-emotion translation, whether across languages or time periods, can hold many perils. We must always be willing to revise our translations as new information arises. Thus, these translations should be viewed as tentative. We begin our translation process with the “predation defense” hypothesis.

The Predator Defense → FEAR Hypothesis

The predator defense theories attempt to explain flock recruitment to a food source by highlighting the advantage of having additional conspecifics in the area. These added conspecifics function to decrease the probability that the calling bird will fall victim to predation.

¹¹² Ficken, M. S. (1981). Food Finding in Black-Capped Chickadees: Altruistic Communication? *The Wilson Bulletin*, 393–394.

The vocalizing birds may be attempting to dilute predator risk by recruiting more potential predator targets to the foraging area. Or, the callers may be attempting to recruit other birds to the food source in order to increase the amount of predator surveillance present. A partial summary of some of these predator-defense hypotheses are included in **Table 2.1**. In light of these predator defense explanations, the claim that this food-related calling was cooperative or altruistic was often met with serious skepticism. Most of these predator defense hypotheses assume a non-altruistic motivation behind the calling behavior. One literature review went so far as to state that there is no evidence of reciprocal altruism among avian species.¹¹³

Translating the predation defense hypothesis to motivational language, the best homeological fit into a Pankseppian formulation is a motivation of FEAR-Avian. Whether or not the food-associated vocalizations become associated with FEAR via genetically-based neurological connectivity, or this connectivity is acquired through experience is not here explored. What we are exploring is that the subjective experience of the bird immediately preceding the food-associated calls is a negatively-valenced emotion; and that this emotion is experienced in response to the perception of increased danger.

One of the most commonly cited studies used to support the predator defense theory is Elgar's house sparrow (*Passer domesticus*) study. In this series of experiments the researcher altered the distance a) between himself and the feeding apparatus and b) between a common perch and the feeding apparatus. Elgar found a decrease in chirrup calls—associated with food resources—when the feeding apparatus was farther away from him, but nearer to the common

¹¹³ Klein, B. C. (1988). Weather-dependent mixed-species flocking during the winter. *J. Theor. Biol.*, 38, 419–422.

Table 2.1: A summary of “Predator Defense” hypotheses adapted from Sridhar et al., 2009.¹¹⁴

Effect	Effect Description	Source
<i>Herd Effect</i>	reduced risk in relation to the position of group members	Hamilton 1971
<i>Dilution Effect</i>	reduced probability of targeting by a predator	Foster & Treherne 1981
<i>Encounter Effect</i>	reduced probability of being encountered by a predator	Inman & Krebs 1987
<i>Confusion Effect</i>	reduced ability of a predator to single out individual prey	Neill & Cullen 1974
<i>Many-eyes Effect</i>	increased probability of a predator being detected	Pulliam 1973
<i>Disturbance</i>	physical disturbance of predators by many birds	Charnov & Krebs 1975

¹¹⁴ Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78(2), 337–347. <http://doi.org/10.1016/j.anbehav.2009.05.008>

perching area. He interpreted this finding to suggest the perceived increase in threat, caused by his own proximity to the feeding station, resulted in more recruitment calling. A FEAR-based interpretation is quite consistent with this finding; as predation-stimulated FEAR increases, so does the amount of sparrow vocalizations.

Comparative analysis between phylogenetically-related mainland and island species has also been used to support a predator defense model for food recruitment. For example, Beauchamp proposed that when predation pressure becomes relaxed on isolated islands, flocking decreases compared to related mainland species.¹¹⁵ Using the adapted Pankseppian model for these findings we again find that FEAR-Avian would be a consistent motivation with the inducement of flocking behavior and conspecific recruitment.

Some of the neurological correlates of a FEAR-Avian system have been documented in a variety of species. Similar to a mammalian fight-or-flight system,¹¹⁶ birds have a stress response system modulated largely by a HPA (Hypothalamus-Pituitary-Adrenal) axis. Endocrine changes, such as elevations in Corticosterone or ACTH can occur in response to stressful stimuli or alter the behavior response to stimuli. Alaskan redpolls (*Acanthis flammea*), for example show elevations in glucocorticoid level after an hour in captivity,¹¹⁷ just as many mammalian species do. And white-crowned sparrows (*Zonotrichia leucophrys oriantha*) treated with corticosterone more readily relocated from high-elevation breeding grounds to the warmth of lower

¹¹⁵ Beauchamp, G. (2004). Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society B: Biological Sciences*, 271(1543), 1039.

¹¹⁶ Cannon, W. B. (1929). Bodily changes in pain, hunger, fear and rage.

¹¹⁷ Wingfield, J. C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G., Freed, L., & Lepson, J. (1997). *Environmental stress, field endocrinology, and conservation biology. Behavioral approaches to conservation in the wild*. Cambridge University Press, Cambridge, 95-131.

elevations.¹¹⁸ However, there are also some differences in how the HPA axis is utilized in avian and mammalian species. Avian species can exhibit stronger seasonal fluctuations in their stress-related endocrine systems that interact with social status and other factors, which also influence mammalian hormones.¹¹⁹ But these differences aside, from a 5th-Aim perspective, it is highly probable that the majority of avian species possess a FEAR homeologue experienced as a negatively-valenced emotion in response to threat.

The Homeostatic → SEEKING Hypothesis

There are some data that suggest that food-associated vocalizations may not be motivated by FEAR-based emotion. In the previously described house sparrow study, the raw data show, counterintuitively, that the second fewest number of calls occurred when the feeder was closer to the observer and farthest away from the perch.¹²⁰ If the motivational cause of the chirrup calls was FEAR—evoked by the perception of an increased predation risk (via the nearby observer)—the far away perch condition might have been expected to generate the most perceived threat and the highest rate of chirrup calling. And one of the least emphasized aspects of the Elgar studies is the effect of temperature on chirrup call rate. Elgar noted this confound and found a significant negative correlation between calling rates and temperature—above and beyond the effects of the experimental manipulations. What is not apparent is if the effects of experimental design would still be significant if the effects of site temperature had been removed from analysis. Thus, it would appear that measurement of the temperature of the feeding sites during foraging

¹¹⁸ Breuner, C. W., & Hahn, T. P. (2003). Integrating stress physiology, environmental change, and behavior in free-living sparrows. *Hormones and Behavior*, 43(1), 115-123.

¹¹⁹ Kotrschal, K., Hirschenhauser, K., & Möstl, E. (1998). The relationship between social stress and dominance is seasonal in greylag geese. *Animal Behaviour*, 55(1), 171-176.

¹²⁰ Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, 19(6), 433-438. <http://doi.org/10.1007/BF00300546>

experiments is crucial for identifying the motivation associated with this calling phenomenon.

In light of these problems connected with a FEAR-based motivational explanation for food-associated calls, another hypothesis is warranted. One possibility that has received much less examination is that the signaler's own homeostatic energy regulation system might play a role in modulating food-associated calls.¹²¹ Homeostatic drives are closely related to the Panksepp's SEEKING-Avian system. The SEEKING system is related to general motivation and associated with approach or appetitive states of an animal. States of food deprivation unconditionally arouse the SEEKING-Avian system.¹²² Just as with Skinner's superstitious pigeons,¹²³ food-associated calls may be related to an appetitive motivation. In humans we call this appetitive motivation hunger. Our hypothesis here is that SEEKING-related motivation maybe a strong proximate emotion influencing the food-associated call.

There are several studies that suggest the possibility of a SEEKING basis for food-associated calling. The first string of evidence comes from the required energetic intake over the winter for non-migratory birds.¹²⁴ The need for constant food intake is significant. At 23°C the night-time weight losses are equivalent to between 2.7 and 3.9 kcal/g in typical birds, depending on activity level. These energetic demands increase sharply in the sub-freezing conditions common for chickadees during the winter. A study that examined energy expenditure in the Carolina chickadee, the focal species of this study, found chickadees used 42% more energy per

¹²¹ Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 357(1427), 1549-1557.

¹²² Panksepp, Jaak, and Lucy Biven (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. WW Norton & Company, p 211.

¹²³ Skinner, B. F. (1992). "Superstition" in the pigeon. *Journal of Experimental Psychology: General*, 121(3), 273.

¹²⁴ Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78(2), 337-347.

day during nonbreeding season than during breeding season.¹²⁵ During winter black-capped chickadees three times their basal rate of expenditure during the winter.¹²⁶ Black-capped chickadees appear to disband their mixed flocks when temperature rises above 25° C.¹²⁷ Similar to Beauchamp's argument that predation pressure is related to flocking behavior, temperature, and the associated energetic demands, are also potential pressure influencing flocking behavior.

Some species display temperature-dependent calling behavior. Cliff swallows (*Petrochelidon pyrrhonota*) often use a squeak call that attracts conspecifics to the foraging site.¹²⁸ After flushing insects from the provisioning site, the researchers observed increases in squeak calls from the swallows. The authors suggested that the added conspecifics may function to help track the insect swarms. But this effect was only observed when temperatures were below 17° C. It is not immediately clear why the advantage of extra insect-tracking help would dissipate under a given temperature. Another study designed specifically to address the predator defense versus a homeostatic-based, foraging efficiency hypothesis, by altering food supplementation, suggested predation defense alone cannot account for the changes in flocking that occur near a food source.¹²⁹ Grubb concluded that a type of foraging efficiency must play a role in this flocking behavior.

Evidence linking food-associated calls and homeostatic motivation has also been

¹²⁵ Doherty Jr, P. F., Williams, J. B., & Grubb Jr, T. C. (2001). Field metabolism and water flux of Carolina Chickadees during breeding and nonbreeding seasons: a test of the "peak-demand" and "reallocation" hypotheses. *The Condor*, 103(2), 370-375.

¹²⁶ Karasov, W. H., Brittingham, M. C., & Temple, S. A. (1992). Daily energy and expenditure by Black-capped Chickadees (*Parus atricapillus*) in winter. *The Auk*, 109(2), 393-395.

¹²⁷ Johnston, V. R. (1942). Factors influencing local movements of woodland birds in winter. *The Wilson Bulletin*, 192-198.

¹²⁸ Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42(4), 551-564.

¹²⁹ Cimprich, D. A., & Grubb, T. C. (1994). Consequences for Carolina chickadees of foraging with tufted titmice in winter. *Ecology*, 75(6), 1615-1625.

documented in Carolina chickadees. A captive study using Carolina chickadees revealed an association between an increase in non-song vocalizations to less food availability and lower body density.¹³⁰ The chickadee general call, especially the number of D-notes used in the call, has been associated with food discovery.¹³¹ These experiments suggest that embedded within these calls is information used by the receivers to locate potential food sources. They also found that signalers produced more D-notes in their calls when they were the first bird to arrive and before the second chickadee arrived, compared to calls produced after the second chickadee arrived. This pattern suggests a recruiting function. There was also a shorter latency for receivers to approach a novel food source when recorded calls with 7-11 “D” notes were played than recordings with 2-5 “D” notes.¹³² The calls may or may not be functionally referential (specific) to food stimuli. The calls may be general calls to approach the signaler or they may be mere indications of positive affective state. The important aspect of these D-note laden calls is that they function as a recruitment call for flock-mates. A follow-up study replicated these findings and suggested that it was not the total number of notes, but the relative frequency of these calls, or duty cycle, that is the primary structural component that attracts conspecifics to a feeding site.¹³³

¹³⁰ Lucas, J. R., Schraeder, A., & Jackson, C. (1999). Carolina chickadee (Aves, Paridae, *Poecile carolinensis*) vocalization rates: effects of body mass and food availability under aviary conditions. *Ethology*, *105*(6), 503-520.

¹³¹ Clemmons, J., & Howitz, J. L. (1990). Development of early vocalizations and the chick-a-dee call in the black-capped chickadee, *Parus atricapillus*. *Ethology*, *86*(3), 203-223.

¹³² Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, *20*(1), 111-116.

¹³³ Wilson, D. R., & Mennill, D. J. (2010). Black-capped chickadees, *Poecile atricapillus*, can use individually distinctive songs to discriminate among conspecifics. *Animal Behaviour*, *79*(6), 1267-1275.

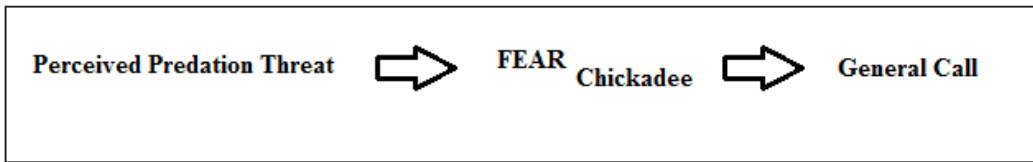
Hypotheses Summarized

We can now summarize the motivational hypotheses that will be tested in the experiments described in chapters three and four. The first set of hypothesis is the FEAR-based hypothesis for the general call of the chickadee. This hypothesis proposes that a negatively-valenced, FEAR homeologue is the proximate emotion promoting the food-associated calls in the Carolina chickadee. The second hypothesis is that a positively-valenced SEEKING homeologue is the proximate emotion promoting the food-associated call in the Carolina chickadee.

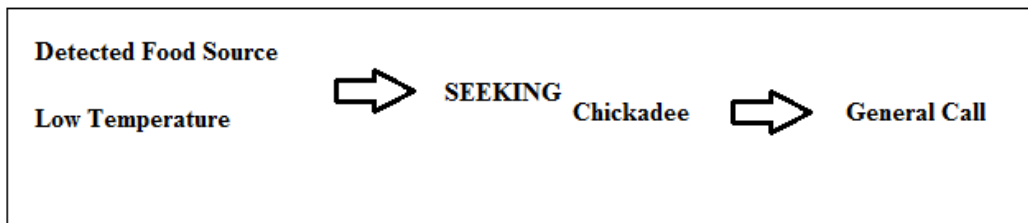
A third hypothesis, which will only be tested if the SEEKING hypothesis is supported, is the SEEKING + CARE hypothesis. This hypothesis suggests a connection between the general call of the chickadee and in interaction between the homeostatic-related, SEEKING system and the social attachment-related CARE system in producing the general call. Social network analysis has demonstrated that the order of arrival at new food patches was non-random and predicted by the strength of social affiliations in multiple species of Parids.¹³⁴ This finding suggests a connection between food recruitment and the social relationships formed with the CARE system. If a SEEKING hypothesis is supported with the empirical work of chapters three and four, the next step will to tests the influence of the CARE system on this system. All three of these hypotheses are summarized in **Figure 2.2**.

¹³⁴ Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1745), 4199-4205.

FEAR Hypothesis



SEEKING Hypothesis



SEEKING + CARE Hypothesis

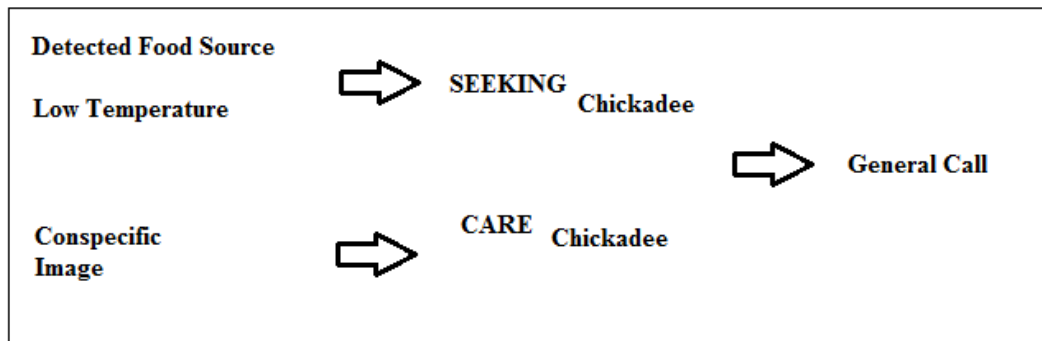


Figure 2.2: A summary of the FEAR and SEEKING hypotheses tested in chapters 3 and 4, and a proposed hypothesis linking the CARE and SEEKING systems.

CHAPTER 3: CHICKADEE FOOD DISCOVERY AND CALLING

Motivational Hypothesis Testing

“Without emotion you have a dead study. How can you possibly sit for months and look at something you don’t particularly like, that you simply see as an object?”¹³⁵

The primary purpose of the following experiments is to examine the possible motivational forces which influence food-related calling in the Carolina chickadee. In order to test whether food-related calling is best explained by a FEAR-related emotion connected to a perceived predation risk or a SEEKING-based affect connected to the perceived hedonic value of a discovered food source, we developed two separate experiments involving: 1) variations in the quantity and quality of the food type and 2) cues of predator presence. In the first study, the type and quantity of food was manipulated and the vocalizations of chickadees were recorded upon the discovery of the food source. If food-related calling is motivated by the salience of the food in the SEEKING system, we would anticipate an increase in calling rate when a large supply of food, or a more desirable type of food, is available. However, if the calling is more motivated by a FEAR system homeologue, we would anticipate an increase in calling when a cue of predator presence is presented at the feeding site compared to a non-threatening species.

Focal Species

The primary species studied in this experimental series was the Carolina chickadee, (*Poecile carolinensis*). Multiple studies conducted with this species confirm that it does not

¹³⁵ Schaller, George “Feral and Free—An Interview with George Schaller,” *New Scientist*, April 5, 2007, 46-47.

migrate over the winter months and individuals are often observed as members of small semi-stable flocks.¹³⁶ These flocks typically maintain a consistent foraging area they will defend from other such flocks. Carolina chickadees can often be found within the same areas as tufted titmice, (*Baeolophus bicolor*) and white-breasted nuthatches, (*Sitta carolinensis*); and this grouping is often referred to as a mixed-species flock.¹³⁷ However it is uncertain if this arrangement is more symbiotic or parasitic for any of these species.¹³⁸ Carolina chickadees are, on average, the smallest species in the mixed flock and are subordinate to both titmice and nuthatches. However, on rare occasion chickadees have been observed supplanting members of the other species.¹³⁹

Call Characteristics

Chickadees possess a complex and versatile vocal communication system, making them an excellent target species for investigating the motivational aspects of signaling. Chickadees often use a *chick-a-dee* call,^{140 141} hereafter referred to as the “general call,” consisting of multiple note types.^{142 143} A-notes and B-notes are high frequency notes that usually precede the more broadband C-notes and D-notes (See **Figure 3.1**). The acoustic characteristics of these broadband C-notes and D-notes make their source easier to locate by conspecifics or

¹³⁶ Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology*, *64*(7), 1187–1198.

¹³⁷ Morse, D. H. (1970). Ecological Aspects of Some Mixed-Species Foraging Flocks of Birds. *Ecological monographs*, *40*(1), 119-168.

¹³⁸ Ibid.

¹³⁹ Ibid.

¹⁴⁰ Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. *83*:820–833;

¹⁴¹ Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am*. *113*: 2127–2136.

¹⁴² Soard CM, Ritchison G. (2009). ‘Chick-a-dee’ calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Anim Behav*. *78*:1447–1453.

¹⁴³ Templeton CN, Greene E, Davis K. (2005). Allometry of alarm calls:black-capped chickadees encode information about predator size. *Science*. *308*:1934–1937.

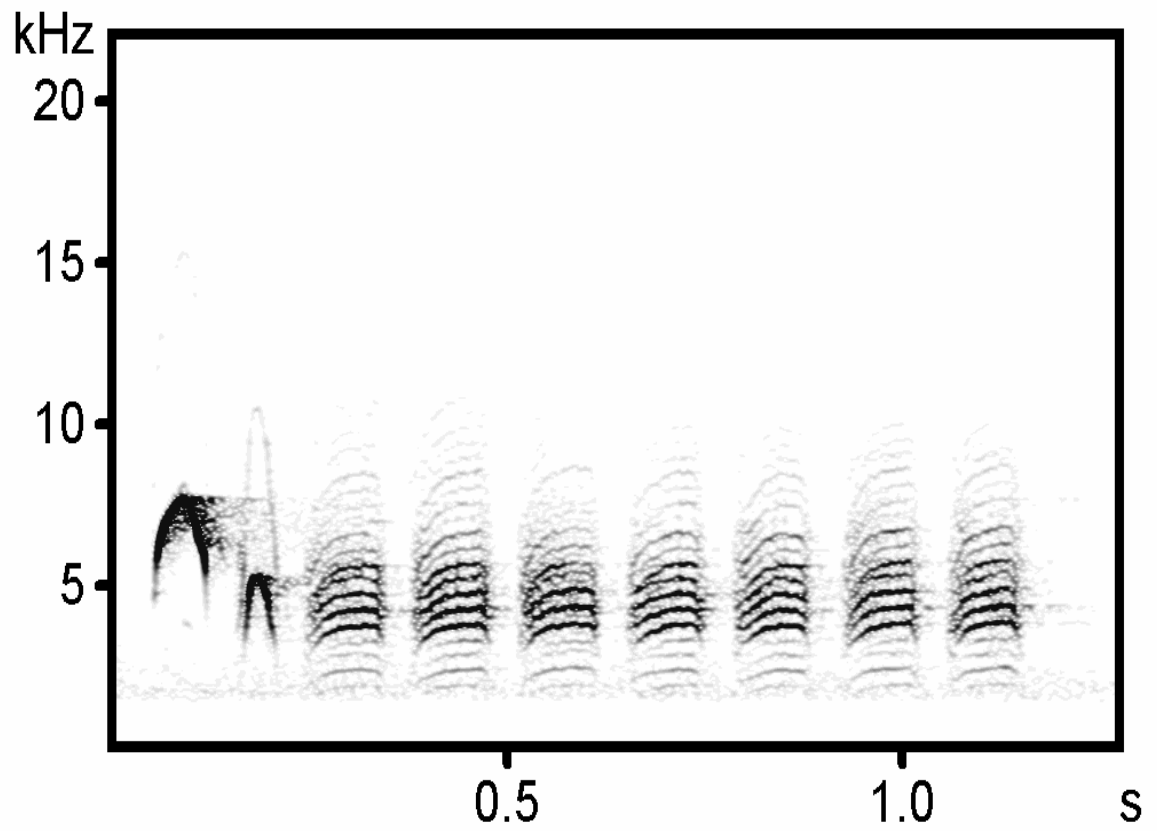


Figure 3.1: A Spectrogram depicting introductory (A and B) and D-notes found in the general call of the chickadee.

predators.¹⁴⁴ ¹⁴⁵Thus, the use of C-notes and D-notes in calls may function to recruit individuals to the location of the signaler. C-notes have been associated with flight and food discovery.¹⁴⁶ ¹⁴⁷The D-notes have been observed in multiple contexts including predator contexts¹⁴⁸ or food recruitment.¹⁴⁹

Since these experiments are attempting to discover the proximate emotion for food-associated calling, we have avoided using stimuli that may be immediately threatening, such as predator models. Predator models or novel stimuli are likely to produce mobbing behavior.¹⁵⁰ The mobbing of a predator may be considered altruistic,¹⁵¹ but the underlying motivation factors generating the aggressive mobbing behavior may be quite distinct from the motivation elements provoking food-related calls,¹⁵² which are presumably directed at flock mates.

¹⁴⁴ Wiley RH, Richards DG. (1982). Adaptations for acoustic communication in birds: sound transmission and signal design. In: Kroodsma DE, Miller EH, Ouellet H, editors. *Acoustic communication in birds*. New York: Academic Press. p. 131–181.

¹⁴⁵ Bradbury JW, Vehrencamp SL. (1998). *Principles of animal communication*. Sunderland (MA): Sinauer.

¹⁴⁶ Mahurin, E. J., Freeberg, T.M. (2009) Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behav Ecol*, 20:111–116.

¹⁴⁷ Freeberg TM, Lucas JR. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Anim Behav*. 63:837–845.

¹⁴⁸ Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. 83:820–833.

¹⁴⁹ Ficken MS. (1981). Food finding in black-capped chickadees: altruistic communication? *Wilson Bull*. 93:393–394.

¹⁵⁰ Templeton CN, Greene E, Davis K. (2005). Allometry of alarm calls:black-capped chickadees encode information about predator size. *Science*. 308:1934–1937.

¹⁵¹ Krama, T., Vrublevska, J., Freeberg, T. M., Kullberg, C., Rantala, M. J., & Krams, I. (2012). You mob my owl, I'll mob yours: birds play tit-for-tat game. *Scientific Reports*, 2. Retrieved from <http://www.nature.com/srep/2012/121112/srep00800/full/srep00800.html>

¹⁵² de Waal, F. B. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.*, 59, 279–300.

Site Locations

There were 20 observation sites used in this study. These sites were located in Eastern Tennessee and North/Central Kentucky at multiple nature reserves, state parks, and private residences (see **Table 3.1**).

Table 3.1: The location of the feeding sites for both food variation and predator cues studies.

<i>Fort Boonesborough State Park, KY</i>	<i>3 Sites, 6 observations</i>
<i>Blue Licks Battlefield State Resort Park, KY</i>	<i>3 Sites, 4 observations</i>
<i>Norris Dam State Park, TN</i>	<i>7 Sites, 20 observations</i>
<i>Ijams Nature Center, TN</i>	<i>4 Sites, 11 observations</i>
<i>Private Residences, KY</i>	<i>3 Sites, 4 observations</i>

Equipment

Two previous pilot studies investigating food-related calling were terminated early due to a) significant calling prior to the chickadees arriving at the site – possibly due to expectations associated with the presence of the recording apparatus and b) calling seemingly provoked by novel apparatus on or near the feeding platform. Vocalizations were observed when the approaching birds were a significant distance from the feeding station, leaving open the multiple possibilities that they could see the food on an open platform at large distances, were calling for unrelated reasons, or that they were vocalizing expectations of food availability. Due to our inability to distinguish between these possibilities, both present studies incorporated a “seed

house” that obscured the amount of food available, if any, until the birds reached the opening of the house. We have observed in previous studies that some members of the flocks frequently check the location for food. Since most of these foraging attempts will result in an empty seed house, we hoped to diminish possible anticipatory calling by offering no clues as to the contents of the seed house until the target bird landed on the seed house.

Each research site consisted of a feeding platform modified with one of the seed houses. The feeding platform was a wooden board approximately 60 cm X 30 cm, secured to the top of a pole rising approximately 1.5 m from the ground. On top of the platform the seed house was mounted with wood screws. The type and volume of food could not be observed by the birds until the chickadees landed on the opening of the seed house. The seed house was an approximately 26 cm X 26 cm X 31 cm wooden box with a triangular roof. The seed house contained a large, approximately 22 cm X 24 cm, opening on the front to allow birds to enter and take seed. A small, cylindrical, metal (tuna) can with an attached black button was attached to the opposite side of the feeding platform. The black button served as a mock camera lens. During experimental observation, the metal can with the mock lens was replaced by a metal can containing a sports camera with a protruding black lens. The vocalizations, arrival at the site, and foraging behavior of the birds were captured by the attached sports camera (**Figure 3.2**).

Subsequent sound analysis was conducted using Raven 1.5.

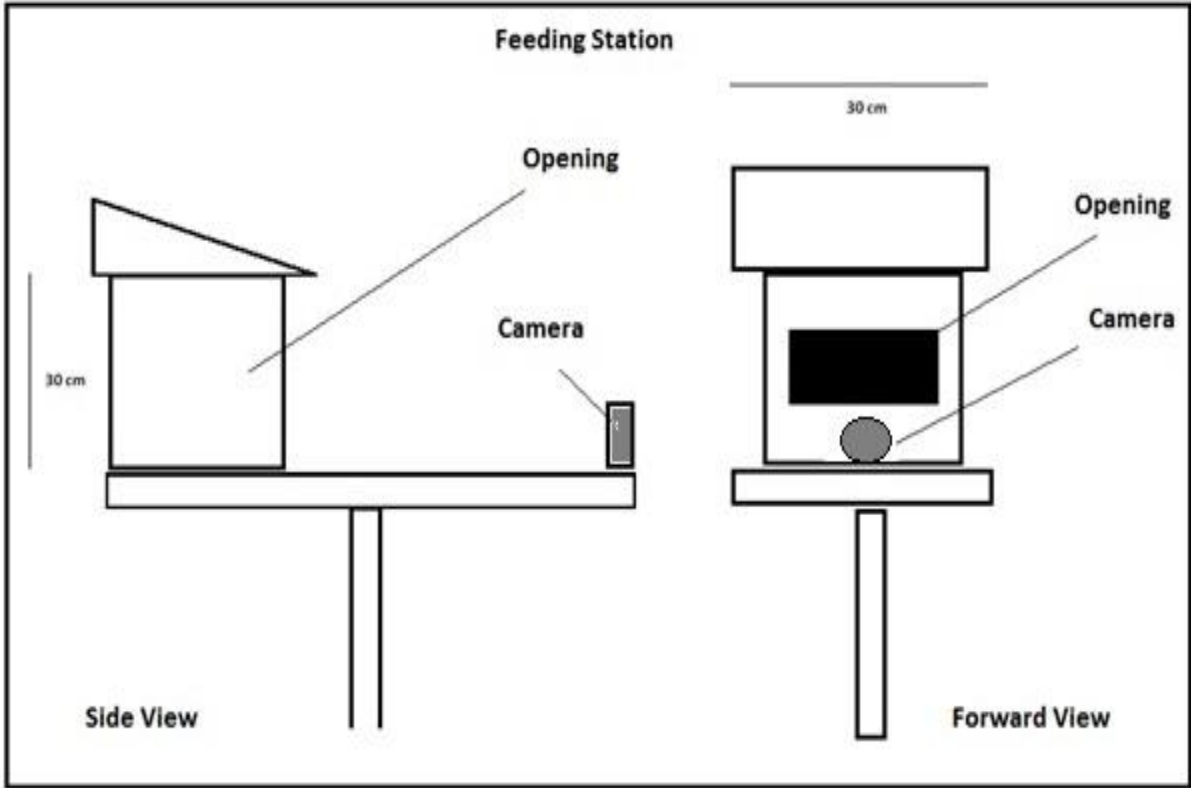


Figure 3.2: Experimental Apparatus used in Experiments 1 and 2.

Habituation Period

At least ten days of habituation to the seed house took place before any observations were recorded. During the habituation period the seed houses were stocked with ¼ cup of sunflower seed with 5 dried meal worms on at least three days. Additionally, once the camera and audio recording devices were activated, the researcher left the area to avoid any confounds related to human presence. We anticipated that these changes would greatly reduce, if not eliminate, the apparent expectancy calling and apparatus-related neophobia observed in the pilot studies.

Preferred Food Type Test

In order to document the difference in hedonic value of the food types used in this experiment we first observed the food preferences of chickadees at five research sites. Several different food types were placed on a seed stand at Ijams Nature Center in Eastern TN: black oil sunflower seed, safflower seed, two varieties of suet, live mealworms, and dried mealworms. Although chickadees have been observed eating all of these items on previous occasions, they did not take suet or live mealworms during any of these presentations. On a separate day, 20 sunflower seeds, 20 safflower seeds, and 20 dried mealworms were presented on a platform and recorded with a video camera. This process was repeated at two other sites for a total of three sessions. At all of these sites the chickadees showed a clear preference for black oil sunflower seed over safflower seed and a clear preference for safflower seeds over dried mealworms. The results of this food preference test are shown in **Appendix 1**.

Conditions for Experiment 1 (Food Variation)

Following the ten day habituation period, we started audio and video recording of food discovery reactions in foraging birds. The independent variable for this study was the amount

and type of discoverable food available in the seed house. Our first session captured the feeding behavior and vocalizations of the **BASELINE** condition. During the baseline condition the seed house was stocked with ¼ cup sunflower seed used during habituation. During habituation, a few mealworms were added to ensure that dried mealworms were not a novel food item for the foraging chickadee. After at least one day following this baseline recording, the seed house was stocked with one of the three experimental conditions: five sunflower seeds (**SCARCE** condition), two cups of sunflower seed (**ABUNDANCE** condition), or ¼ cup of dried mealworms (**MEALWORM** condition). The selection of these experimental conditions was determined by a die roll between the closest research sites and counter-balanced to minimize the influence of seasonal conditions. Following the recording session of the first experimental condition, the site was restocked with **BASELINE** mix and left idle for at least one day. This process of recording an experimental condition followed by a one day rest period was repeated until all experimental conditions had been recorded.

Conditions for Experiment 2 (Predator Cue)

Following the study involving food variation at 20 sites, we conducted Experiment 2 using the same research sites from Experiment 1. Both conditions for Experiment 2 were similar to the **BASELINE** condition in Study 1 in many respects. The same experimental apparatus was used, including the seed house and sports camera, and ¼ cup of sunflower seed was placed in the seed house. However, in Experiment 2 each condition was also accompanied by one of two audio playbacks. One condition (**OWL**) consisted of 10 seconds of an Eastern screech owl (*Megascops asio*) whinny call followed by 65 seconds of silence played on a loop. The other condition (**GOOSE**) consisted of 10 seconds of a Canada goose (*Branta Canadensis*) calling followed by

65 seconds of silence played on a loop. Both recordings were acquired from the Xeno-canto database and edited to make the 75 second recordings.¹⁵³ Playback audio was broadcast from a speaker and iPod hidden in a camouflaged bag approximately 5 m from the seed house. A summary of the conditions for both studies is included in **Table 3.2**.

Recording Durations

The time between recording onset and bird arrival varied in each session. However, each session lasted at least five minutes after a bird arrived on the feeding station. Due to concerns surrounding observer interference we established a few a priori observation exclusion rules. *Exclusion Rule 1:* If during any recording session a bird was observed before the researcher could activate the recording device and retreat to the 50 m safe distance, that recording session was terminated, the seed house was restocked with **BASELINE** mix, and attempts to observe the site were abandoned for an addition 20 hour period. *Exclusion Rule 2:* If a chickadee was not the first bird to discover the food source, another attempt was made to capture chickadee food discovery following another BASELINE restocking.

Experimental Measures

The primary dependent variable in all conditions of both studies was the number of general calls in the 30 second target window of food discovery. The target window of 30 seconds was chosen because it was judged to be long enough to record the initial reaction to the available food source, and a longer observation period might have captured general calls that were unrelated to food source in the seed house. This 30 window began once a chickadee landed on the seed house

¹⁵³ Xeno Canto audio files: XC153434-eastern_screech_owl_whinny_Todd Wilson // Canadian Goose1_XC289219-CANG Garrett MacDonald

Table 3.2: A summary of experimental conditions for studies 1 and 2.

Study 1 Conditions	Food Type/Volume in Seed House	Playback Stimuli
BASELINE	1/4 cup of Sunflower Seed	None
SCARCE	5 Sunflower Seeds	None
ABUNDANCE	2 cups of Sunflower Seed	None
MEALMORM	1/4 cup of Dried Mealworms	None
Study 2 Conditions	Food Type/Volume in Seed House	Playback Stimuli
OWL	1/4 cup of Sunflower Seed	10 seconds of Owl per 75 seconds
GOOSE	1/4 cup of Sunflower Seed	10 seconds of Goose per 75 seconds

opening. If the hedonic value of the discovered food is an important stimulus in motivating food-related calls, we would expect an increase in this calling when large amounts of food are discovered (**ABUNDANCE**) versus small amounts of food (**SCARCE**) or less desired food (**MEALWORM**). If the motivation for calling is more closely linked to mitigating predation threat, we would anticipate more calling when predator cues are present (**OWL**) than non-predatory bird (**GOOSE**). We used a mixed-model ANOVA to compare the general calls of chickadees across food conditions in Study 1. A paired t-test was used to compare calls between the **GOOSE** and **OWL** conditions in Study 2.

Results

Out of the total number of 80 data collection attempts in the food variation study (4 conditions at 20 sites) we were able to obtain 45 usable observations. Observations were excluded from analysis for several reasons: chickadees did not appear at the site during video recording (28 instances), other species arrived at the site before the target species and interrupted their foraging (6 instances), the researcher presence during camera maintenance interfered with naturalistic observation and violated our a priori exclusion rule (1 instance) Out of the total number of 40 data collection attempts in the predator cue study, (2 conditions at 20 sites) we were only able to collect 24 paired, usable observations. Chickadees did not appear at the site during video recording in 14 instances. Two other observations were excluded because only one of two conditions was captured for that site.

The results from the food variation study did not align with our *a priori* predictions. In the first study, where we manipulated the amount and type of food available at the seed station, we detected no difference in calling between any of the conditions $F(3,41) = 1.427, p = .25$.

There was no statistical difference between large and small amounts of food and no difference between preferred food types over non-preferred types (**Figure 3.3**). A similar, non-significant result was also obtained with D-notes $F(3,41) = 1.15$, $p = .34$, and C-notes $F(3,41) = 0.44$, $p = .72$. Not only were there no significant differences between conditions, only the minority (18 out of 45, or 40%) of these observations, across all conditions, had detectable calling in the 30 seconds after landing on the seed house. In most of the recordings no calling was observed. Additional data are located in **Appendices 2, 3, and 4**.

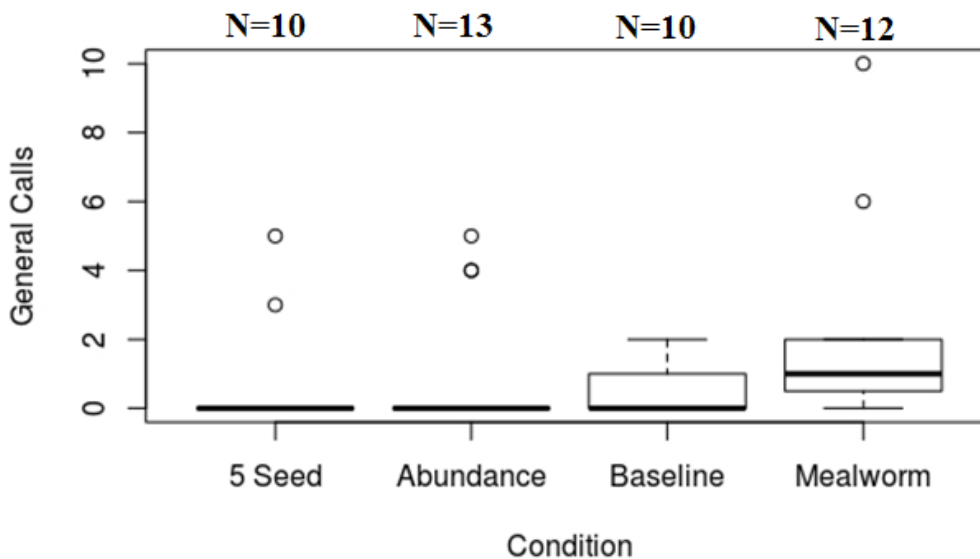


Figure 3.3: Number of chickadee general calls under various conditions.

The results of Study 2, our predator cue study, were also unanticipated. When calling patterns were compared during an Eastern Owl or Canadian Goose playback, there was again no detectable difference between these conditions $t(11) = -0.41$, $p = .69$. Just as in the food variation study, we detected chickadee calling only in a minority (7 of 26, or 27 %) of the total

analyzed recordings. See **Figure 3.4**.

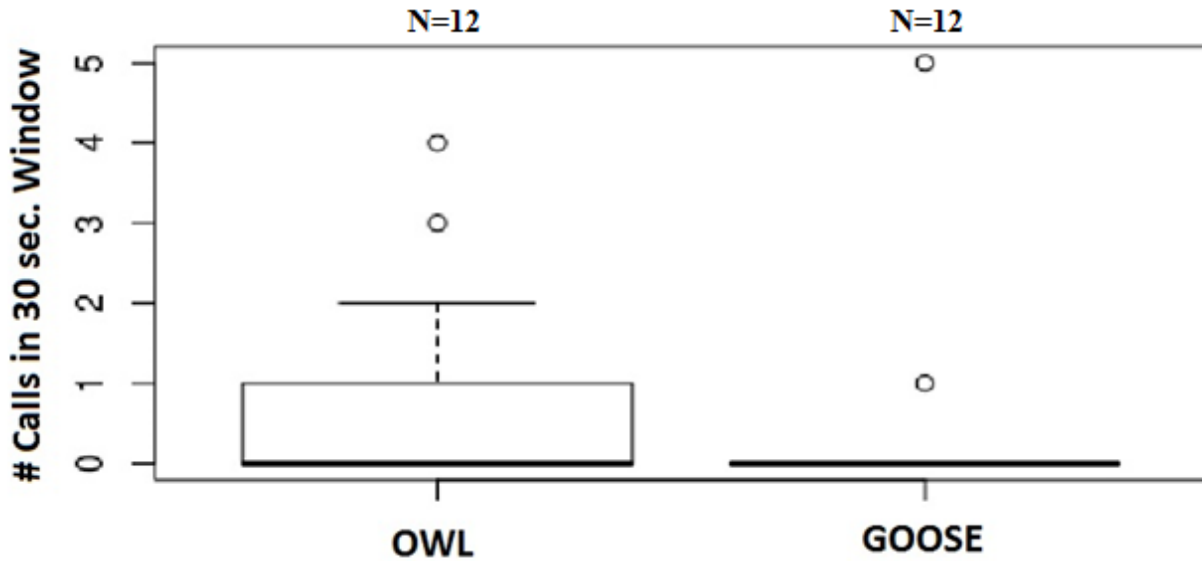


Figure 3.4: General calls while foraging when owl or goose calls played.

Analysis and Interpretation

As discussed in Mahurin & Freeberg, the lack of consistent calling by Carolina Chickadees when arriving at a food source suggests that what has been described as “food-related calling” is unlikely to be referential to food.¹⁵⁴ The birds may be responding to the presence or absence of specific conspecifics, subtle changes in the experimental apparatus, nearby semi-hostile avian species, or other motivational or environmental factors. It is also possible that the chickadees are conditionally responding to the presence of food, albeit under a yet undetermined set of conditions.

Neither primary hypothesis, that avian calling near a food sources has a FEAR-based motivation, as might be predicted by predator defense hypothesis, or a SEEKING-based

¹⁵⁴ Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, 20(1), 111–116.

motivation, which might be expected in cooperative foraging, were directly supported in this study. If the avian homeologue of fear of predation had been the primary motivation, we would have expected to see an increase in calling when owl vocalizations were played versus goose vocalizations. No such calling increase was observed. If the avian homeologue of hedonic arousal had been the primary motivational factor, we should have observed an increase in calling when large amounts of highly preferred food were available compared to small amounts of food or less-preferred food types. However, calling differential by food characteristics was not observed.

In order to interpret our unanticipated results, we must first address some of the limitations of our study. One such limitation concerns the continued effects of novelty. While we observed much less novelty-related calling prior to the chickadees arriving at the feeding platform, there was some evidence that at least some chickadees noticed a difference between the apparatus present during experimental sessions and the apparatus present during habituation or between experimental observations. A few of the birds appeared to inspect the camera lens during their foraging. Thus, we cannot rule out the experimental apparatus introduced a potential confound into our data by disproportionately affecting one condition more than another. However, we have no reason to suspect that this observational noise, however robust, would operate differentially across the conditions, and the counter-balancing of the food/sound presentations should have mitigated the risk of this confound.

There is also the possibility that the owl and goose playback stimuli we used in our second study were perceived by the chickadees as either neutral stimuli or more as an auditory novelty than as a cue of predator presence. The primary reason why we entertain this possibility is that there was no increased latency to approach and subsequently forage from the seed house

when the owl stimulus was playing than when the goose stimulus was playing. There are several possible explanations for the lack of approach latency. The chickadees may not perceive Eastern screech owls, or at least their whinny, to be a significant indication of a predatory threat, at least during daylight hours – and all of our data were captured after sunrise. However, this possibility is contradicted by previous research showing increases in chickadee calling in response to owl vocalizations.¹⁵⁵ We also have heard both goose calls and owl calls at most of the research sites in previous seasons. It is possible that chickadees, at these specific locations, have ceased perceiving these calls as any indication of threat. It may be the silent owls that are the primary source of threat. Another possibility is that the repetitive aspect of the looped calls may have allowed for rapid habituation to the calls, or lead to the determination that they were from an inauthentic source of predation threat. Whatever may be the reason for the lack of calling in response to our playback stimuli, as a pseudoreplicated design, we are hesitant to interpret our results as representative of a typical chickadee response to predation threat.¹⁵⁶

Despite these caveats, there is still reason for us to believe that the general *chick-a-dee* call is not closely linked to imminent predation threat. When we had the chance to observe a predator, such as a hawk, entering the research area the typical reaction consisted of either ceasing vocalizations completely, or emitting only soft, high-frequency vocalizations. Instead of perching conspicuously on or near the feeder, when a significant danger was detected, the chickadees would retreat to nearby foliage and scan their surroundings.¹⁵⁷ These observations

¹⁵⁵ Nolen, M. T., & Lucas, J. R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour*, 77(5), 1137-1146.

¹⁵⁶ Johnson, W. T., & Freeberg, T. M. (2016). Pseudoreplication in use of predator stimuli in experiments on antipredator responses. *Animal Behaviour*, 119, 161-164.

¹⁵⁷ Zachau, C. E., & Freeberg, T. M. (2012). Chick-a-dee call variation in the context of “flying” avian predator stimuli: a field study of Carolina chickadees (*Poecile carolinensis*). *Behavioral Ecology and Sociobiology*, 66(5), 683-690.

also suggest that our playback stimuli used in this study did not provoke significant predation defense behavior. No hiding or conspicuous scanning was noticed. These chance observations with live predators in the field suggest that the general call is not utilized when predation threat is high and the predator is not actively targeting a flock-member. These observations raise significant question about how Carolina chickadees evaluate predation threat in response to the presentation playback stimuli.

The pilot studies preceding Experiments 1 & 2 suggested that the first bird to arrive at the site would most often be a Carolina chickadee. During these pilot studies, Carolina chickadees were disproportionately the most frequent first visitor, followed by the tufted titmouse, and on rare occasions, the white-breasted nuthatch. This, however, was not the pattern that we observed during Experiments 1 & 2. For unknown reasons, possibly related to the differences in chickadee and titmouse memory, neophobia directed at the added seed houses, or an undetermined set of ecological influences, tufted titmice were more likely to be the first visitor to check the seed houses for food. The call data from the titmice have not been analyzed, but the initial indications suggest that titmice also do not call in response to food discovery.

This set of experiments was initially devised to test whether the general call was more likely to be motivated by the perceived hedonic value of a discovered food source or more likely motivated by the FEAR of a predation threat. Our results suggest that there is no significant link between the general calls and food discovery – at least during the late winter conditions of Eastern Tennessee and Kentucky. There are certainly many other means by which the chickadees could communicate the presence of a food source, but the general *chick-a-dee* call does not appear to be primary mechanism for this information.

As for the hypothesis that the general call is motivated by a predation-induced FEAR, we

are much more tentative in our interpretation. Our observations during these studies and prior lab experiments suggest to us that imminent threats suppress calling and moderate threat cues increase calling. At this point we cannot determine if the owl vocalizations failed to promote calling because they did not generate enough perceived threat, they reached a threshold of threat that suppresses calling, or the general call is not closely linked predation threat. Only future studies can address these and other explanations for the sparse calling observed in Study 2. We then arrive at a tentative conclusion based on study 1 and 2 that the perceived hedonic values of food are unlikely to be an adequate motivational explanation of what has been called “food-related calling” in the Carolina chickadee. Our results also did not support the hypothesis of a FEAR-related motivation for the general call, but due to the limitations of our stimuli, this hypothesis remains a plausible explanation. Only further experimentation will be able to determine the likely motivation factors that precede the general call of the Carolina chickadee.

CHAPTER 4: REPLICATIONS AND REVISIONS

A Hypothesis Rejected, A Hypothesis Proposed

“Perhaps the most basic emotion that motivates cooperative behavior is affiliation—a sense of liking and a feeling of closeness.”¹⁵⁸

In the previous chapter, we attempted to determine if the apparent food-related calls of the Carolina chickadee are more likely to be motivated by the negative affect of predation threat, or motivated by a positive affect related to hedonic value of food. We tested this assertion in two ways. In the first experiment, we varied the type and amount of food available within a seed house that obscured the type of food available. Once a chickadee landed upon the seed house the type and amount of food available would be visible to the chickadee. If the general call of the chickadee was indeed motivated by SEEKING-related affect, we should see variations in the amount of these calls upon the differences in hedonic value of the discovered food. But this “hedonic hypothesis” was not supported by our observations. We found no evidence that the chickadees used their general call any differently according to variations in food type or volume of food available.

In our second experiment we examined the effect of predator cues on the chickadee’s general call. We placed a moderate amount of food in the seed house while either a goose or owl recording played on a loop. If the general call was motivated by a FEAR related to predation, we should see an increase in these calls when subtle cues of a predator, like an owl recording, were

¹⁵⁸ Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press.

present. This hypothesis was also not supported by our observations. There was no apparent difference in the use of the general call when an owl or goose call was played at the site. The findings from both of these experiments raise many important questions concerning the general call of the Carolina chickadee in both of the hypothesized affective explanations. Our experiments reveal an inconsistent connection, a weak association, or no association at all between available food and the general call. These experiments also suggest that certain auditory cues are insufficient for producing FEAR-motivated calls, if indeed the general call is motivated by a FEAR homeologue.

In order to better interpret these findings, it was important to verify that there is little association between the general call and food discovery. In order to test this connection we conducted a simple experiment where the call patterns of chickadees were compared when they discovered food in a seed house versus when they arrived at an empty seed house. If there is no difference in the patterns of general calls used when food is available or not available in the seed house, this is strong evidence against a SEEKING-based motivation for the general call.

Methods

Focal Species and Vocalizations

As in the previous experiments, the focal species in this study was the Carolina chickadee, (*Poecile carolinensis*). Also, as in the previous studies, the chickadee general call was the target vocalizations for observations. The D-notes used in these calls are broadband signals that possess the greatest acoustic capacity for being detected, and for their location to be

triangulated by the signal receiver.¹⁵⁹ The D-notes in the general call were also the focus of the 2009 Mahurin and Freeberg playback study using calls with a various number of D-notes per call.¹⁶⁰ In that study they found that the latency to arrive to a feeding stand was shorter for chickadees when the playback vocalizations contained more D-notes. In the present study we are attempting to focus on the role of the signaler food availability. We are attempting to test whether chickadees emit more general calls (with embedded D-notes) when they discover food in the seed houses versus an empty seed house.

Site Locations

There were 22 observation sites used in this study. These sites were located in Eastern Tennessee and North/Central Kentucky at multiple nature reserves, state parks, and private residences (see **Table 4.1**).

Table 4.1: Locations of the research sites used in Study 3.

<i>Fort Boonesborough State Park, KY</i>	<i>2 Sites, 4 Observations</i>
<i>Blue Licks Battlefield State Resort Park, KY</i>	<i>3 Sites, 6 Observations</i>
<i>Norris Dam State Park, TN</i>	<i>4 Sites, 6 Observations</i>
<i>UTK Forestry Station, TN</i>	<i>10 Sites, 14 Observations</i>
<i>Private Residences, KY</i>	<i>3 Sites, 2 Observations</i>

¹⁵⁹ Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, 111(981), 855-869.

¹⁶⁰ Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, 20(1), 111–116.

Equipment

The equipment used in this experiment was similar to studies described in Chapter 3 with a few alterations. Just as in the previous study we used a 26 cm X 26 cm X 31 cm seed house mounted on a feeding stand approximately 1.5 m from the ground. However, in this experiment the seed house was altered to change the position of the camera. On the altered seed house for experiment 3, the camera was mounted the back of the seed house (see **Figure 4.1**). This location of the camera was changed for two reasons. First, a camera mounted on the back of the seed house contained within a plastic container would be less conspicuous for birds entering from the front of the seed house. There was what appeared to be neophobia by some birds directed toward the camera mount in experiments 1 and 2 after the habituation period had ended. There was also one instance where a tufted titmouse pecked at the camera lens. Whatever the motivation for this pecking, we believed it would be best to move the camera assembly to a less conspicuous area.

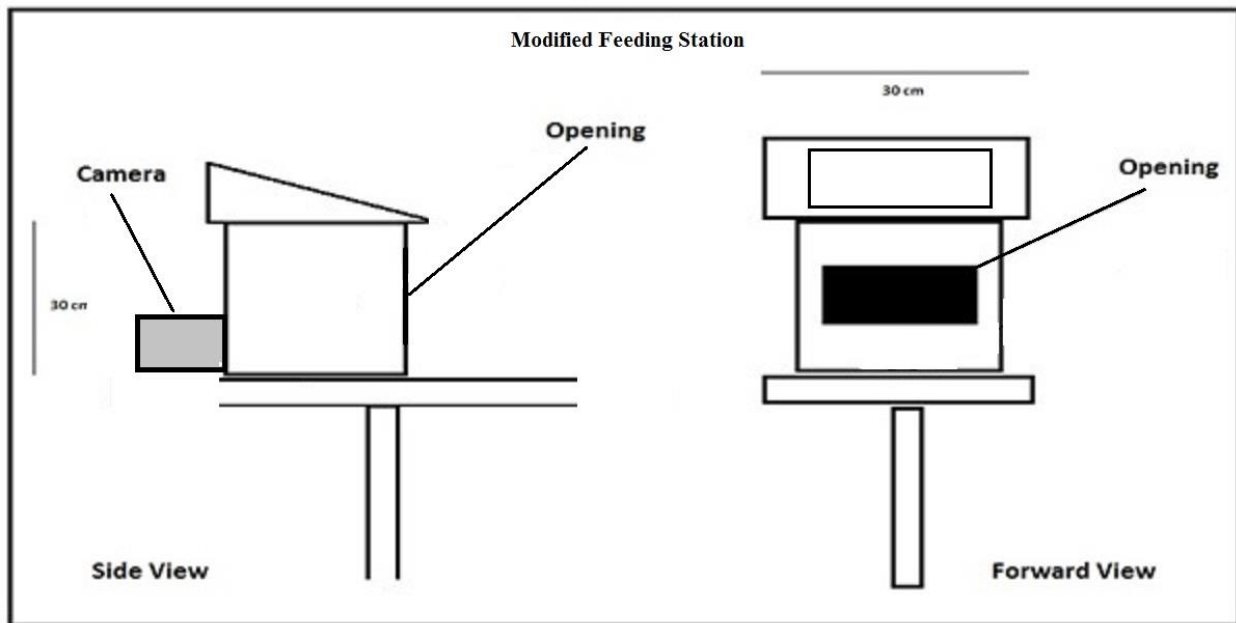


Figure 4.1: Experimental apparatus, with rear-mounted camera used in Experiments 1 and 2.

The second reason why the camera assembly was relocated to the back of the seed house was to increase the recording capacity of the sports camera. The original experimental setup allowed for approximately two hours of recording with that standard battery capacity of the sports camera. By relocating the camera to the rear of the seed house we were able to add a USB power source that increased the recording capacity of the sports camera to approximately nine hours of 1080p @ 30fps footage. The camera and power source were located in a removable plastic container painted black to obscure its contents. In order to ensure that there was sufficient light for recording, we also replaced a circular section of wood on top of the seed house with a translucent white plastic. The plastic allowed enough light to enter the seed house to allow the camera to capture video without revealing the contents of the seed house. In addition to the adapted seed houses, we also used three seed houses with a new design. These seed houses were similar to the original seed houses except that the sides of the new seed houses were also translucent white plastic and they contained a perch on the front of the seed house that provided landing position for the chickadees that was within the field of view of the camera (see **Figure 4.2**).

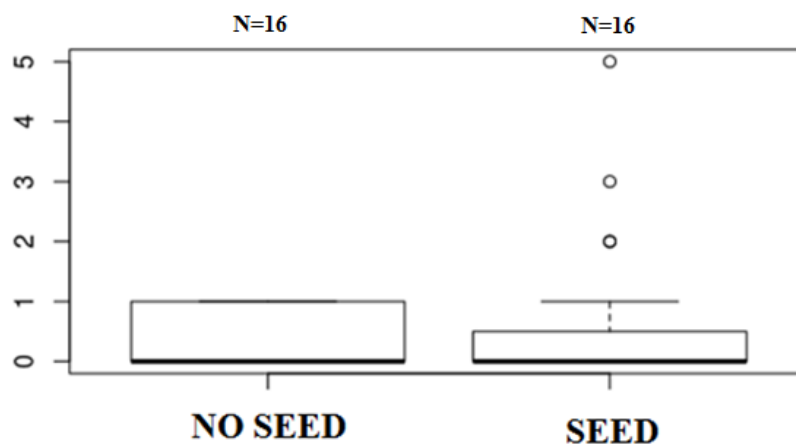


Figure 4.2: The Number of General Calls between the NO SEED and SEED conditions.

Habituation

At least ten days of habituation for the seed house took place before any observations were recorded. During the habituation period, seed houses were stocked with approximately $\frac{1}{4}$ cup of sunflower seed on at least three separate occasions.

Conditions and Recording Procedure

Following the habituation period, recording for the experimental and control conditions began. The researchers set up the camera and began recording around sunrise each morning. The cameras were left recording for at least five hours, but usually until the battery was depleted approximately nine hours later. After the camera setup, the seed house was immediately prepared for the experimental conditions. There were only two conditions in this study. Either the seed house contained approximately $\frac{1}{4}$ cup of sunflower seed (SEED condition) or it was left empty (NO SEED condition). The time between recording onset and bird arrival varied for each session. However, each session lasted at least five minutes after a bird arrived on the feeding station. Due to concerns surrounding observer interference we maintained the primary data exclusion rule used in experiments 1 and 2. If during any recording session a bird was observed before the researcher could activate the recording device and retreat to the 50 m safe distance, that recording session was terminated.

Experimental Measures

The primary dependent variable in this experiment, as in the prior experiments, was the number of general chickadee calls and the D-notes contained in these calls during the target temporal window of food discovery. From the moment when a chickadee landed on the seed house we compared the general call 15 seconds after landing, and 15 seconds prior to landing

between the SEED and NO SEED conditions (see **Table 4.2**). This time window was reduced from 30 seconds used in Study 1 & 2 in order avoid including calls unrelated to food-discovery that may have been captured in the prior studies and to allow for a comparison for calls made before and after landing on the seed house.

Table 4.2: Experimental Conditions for Experiment 3.

Condition	Target Measure
Seed	# General Calls 15 seconds before landing
	# General Calls 15 seconds after landing
No Seed	# General Calls 15 seconds before landing
	# General Calls 15 seconds after landing

Replication Results

Of the total 20 research sites, we were able to obtain data for both **NO SEED** and **SEED** conditions from 16 sites. Four of the sites were missing one of the conditions because either birds did not arrive at the site during a recording period (3), or a corrupted audio file (1). Using a standard paired t-test, we found no significant difference between the number of calls emitted by chickadees after arriving at the seed house when there was seed present in the seed house versus when the seed house was empty $t(15) = -0.84$, $p = .42$ (see **Figure 4.2**). Similar results were obtained with the analysis of D-notes $t(15) = 1.23$, $p = .24$, and C-notes $t(15) = -1.26$, $p = .23$ (see **Appendices 7 and 8**). In 67 % of all of our observations of the general call, covering both conditions (24 of 36 obs.), they maintained the same pattern of vocalizations before and after landing on the seed house. If they emitted no vocalizations before landing on the seed house,

they emitted no detectable vocalizations after landing. If they were calling prior to landing, they continued to call afterward. During the **NO SEED** condition there were six instances (16.7%) and during the **SEED** condition there were three instances (8.3%) where detectable calling was observable after landing on the seed house, but no calling was observed prior to landing. Conversely, during the **NO SEED** condition there were two instances (5.5%) where calling was detected prior to landing, but not after. There was once instance (2.8%) in the **SEED** condition where calling was detected prior to landing, but not after. These findings are not consistent with a strong link between food availability and the general call of the Carolina chickadee.

There were numerous supplants and other agonistic behavior during these observations. Most of these instances of aggression were interspecific. Tufted titmice supplanted chickadees and white-breasted nuthatches supplanted titmice and chickadees. We mention these occurrences because there seemed to be greater reluctance on the part of the chickadees to enter the seed house than in previous studies. Although we believe the seed houses were effective in obscuring the seed from view, using them may have also created a more dangerous foraging environment for the chickadees. The avenues for escape within the seed house were much more limited than when seed is placed on an open seed stand, the most common stimulus display method used in previous studies. This change in apparatus may or may not have affected the calling behavior of the chickadees in this experiment.

We also analyzed regional differences in calling behavior. When we combined all of our observations from Study 1, 2, and 3 into one data pool, we found no differences between sites located in Kentucky and Tennessee $t(106) = -0.35, p = .72$. Thus, whatever the explanation for the lack calling between conditions, they do not appear to be influenced by differences in regional ecology (see **Appendix 9**).

Discussion

The results of this study and the studies conducted in the previous chapter combine to indicate that the general call of the Carolina chickadee is not, in any significant way, referential to food. This possible dissociation between food availability, certain owl vocalizations, and the general call of the Carolina chickadee have important implications for the motivational question of the general call. In light of these findings, it is useful to review the documented use of the general call in Carolina chickadees, and closely-related black-capped chickadees, in multiple contexts. That is, we start at the beginning:

(1) The general call is ubiquitous. It can be heard any time of year and there is often no obvious stimulus which provokes the call. This suggests that the motivation for using the call must be commonly experienced.^{161 162 163}

(2) Novelty increases the use of the general call. When novel stimuli are present on feeding apparatus chickadees emit robust calling behavior.¹⁶⁴ In our own pilot studies, we noticed that any alternation to the feeding platform greatly increased the call. Since the presence of this novelty delayed their foraging, this might suggest that the motivation leading to the call possesses a negative valence.

(3) During Experiments 1-3, and the preceding pilot studies, the general call was often heard prior to, and at significant distances from, the chickadees arriving at the research site. This

¹⁶¹ Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

¹⁶² Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am*. 113: 2127–2136.

¹⁶³ Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. 83:820–833.

¹⁶⁴ Browning, S. A. (2015). Mixed-species Flock Members' Reactions to Novel and Predator Stimuli. Retrieved from http://trace.tennessee.edu/utk_graddiss/3327/

suggests that the motivation was influenced by either the anticipation of foraging at the seed house or related to the movement of the flock.¹⁶⁵

(4) Exposure to, and orientation of, predator models increases the use of the general call.¹⁶⁶ There are multiple other examples where predator models elicit general calls.¹⁶⁷ Again, the subjective experience of the chickadee calling under these conditions would more likely be negative than positive.

(5) The general call is also emitted by the male after returning with food to a nest with hatchlings.¹⁶⁸ The motivational experience of the male in this context is difficult to interpret. The male may be experiencing the excitement of a return to the nest, or signaling a longing for their mate, or some other motivation.

(6) The earliest use of the general call in hatchlings occurs between nine to twelve days.¹⁶⁹ The use of the call on a least one of these occasions corresponded with fellow hatchlings being removed from the nest.¹⁷⁰ There is a strong probability here that the motivation valence was negative.

(7) The general call is also linked to territorial disputes and disturbances at the nest.¹⁷¹ In both of these instances we would anticipate a high degree of motivation and a negative emotional

¹⁶⁵ Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, 20(1), 111–116.

¹⁶⁶ Book, D. L., & Freeberg, T. M. (2015). Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. *Animal cognition*, 18(5), 1155.

¹⁶⁷ Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

¹⁶⁸ Brewer, E.P. (1961). Comparative notes on the life history of the Carolina chickadee. *The Wilson Bulletin*, 73(4), 349-373.

¹⁶⁹ Clemmons, J., Howitz, J.L., (1990). Development of early vocalizations and the chicka-a-dee call in the black-capped chick-a-dee, *parus atricapillus*. *Ethology*, 86, 203-223.

¹⁷⁰ Brewer, E.P. (1961). Comparative notes on the life history of the Carolina chickadee. *The Wilson Bulletin*, 73(4), 349-373.

¹⁷¹ Clemmons, J., Howitz, J.L., (1990). Development of early vocalizations and the chicka-a-dee call in the black-capped chick-a-dee, *parus atricapillus*. *Ethology*, 86, 203-223.

valence.

(8) Although not well-documented in the empirical studies included in this dissertation, there was more than one instance in these experiments and in previous pilot studies when a chickadee arrived at the site, took a few seeds, and then left the area using the general call. Several minutes later, a flock of chickadees arrived at the site. The motivation behind the general call here was originally assumed to be positive – a response to a highly-desired reinforcer. However, the calling bird in this instance could have been also motivated by their isolation from their flock mates, such as in the FEAR-based hypothesis summarized in chapter 3.¹⁷²

(9) The general call from the chickadee also can be elicited, not from direct contact with a threatening stimulus, but from the response of tufted titmice exposure to a predator.¹⁷³ This eavesdropping can be difficult to interpret from a motivational standpoint. We must assume that chickadees have some sense of how titmice respond to various stimuli, including predator presence. However, given the nature of the original stimulus, it is more likely that the general call, used here, reflects a negative emotion.

(10) Nesting mate pairs will also use the general call during the search for a nest location. A portion of one of these occurrences was captured on video. During this exchange a pair of chickadees approximately 2 m away and oriented toward a nest box reciprocated general calls for approximately 70 seconds. The apparent object of interest was the nest box. Similar nesting exchanges have been documented by other researchers as well.¹⁷⁴

¹⁷² Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, 20(1), 111–116.

¹⁷³ Hetrick, S.A. Sieveing, K.E. (2012) Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behav Ecol*, 23:83–92.

¹⁷⁴ Brewer, E.P. (1961). Comparative notes on the life history of the Carolina chickadee. *The Wilson Bulletin*, 73(4), 349-373.

Revised Motivational Models for General Call

A simultaneous examination of all of these contexts where the general call has been observed reveals at least two possible motivational explanations for this behavior. The first explanation centers on an observer effect. In all of these contexts there was, we assume, a human researcher present to observe and/or record the calling. It is a possible and parsimonious hypothesis that the presence of a human observer is an unintentional motivational source for this calling. Similar to a FEAR-based motivational hypothesis related to predation, the presence of a human observer may also have a FEAR-related emotional root as one of the chief motivational elements producing the general call. The much-cited Elgar study discussed in chapter 2 used the researcher as the threat source in evaluating house sparrow calls.¹⁷⁵ Our own evidence for this hypothesis can be summarized by the common element of a human observer across all of the conditions in our pilot study and the unanticipated finding in our experiments that as the “observational footprint” in our methodology decreases, so does the amount of observed general calls. This is not to say that humans are the primary stimulus responsible for the general call of the chickadee, but one or more of the above contexts may have been misinterpreted due to observer effects. We must face the possibility that our presence with the chickadees is creating, at least in some contexts, the phenomena we observe.

A second possibility that has been suggested is that simple arousal, and not one of Panksepp’s primary emotions, may be the motivational factor provoking the chickadee general call across these various contexts. At present we are unconvinced that arousal is a likely motivational candidate for at least two reasons. The first reason is that simple arousal is too

¹⁷⁵ Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, 19(6), 433–438. <http://doi.org/10.1007/BF00300546>

vague of a concept to fit into a 5th Aim ethology. All of Panksepp's primary emotions could be described as types, or subtypes, of arousal. LUST is the emotional root of sexual arousal.

SEEKING is the raw desire promoting appetitive behavior. All out these primary emotions would have, to some degree, an influence on a general arousal. Panksepp has added specificity to the types of arousal experienced by the organism making the classical conceptualization of arousal somewhat obsolete. The second reason why we do not pursue simple arousal as an explanation is that it is not consistent with our empirical evidence. We discovered no significant difference in the amount general calls produced when large amounts of food were available, small amounts, or no food at all was present. There was also no detectable difference in calling when owl or goose vocalizations were played at the sites. We would anticipate some difference in one of these conditions if general arousal was the motivational driver. We thus do not pursue arousal as likely motivational force preceding the general due to its conceptual incompatibility with our emotional model and its inability to explain our experimental results.

A third explanation, and with the current evidence we believe is the most probable, is that the general call is motivated by a pervasive "desire to affiliate" in chickadees. This hypothesized motivation is similar to Panksepp's GRIEF/PANIC system¹⁷⁶ in that it would be experienced as a negative emotion prompted by environmental stressors, such as novelty or predators cues, or by isolation, such as when conspecifics are conspicuously absent. This general desire to affiliate could be communicated by chickadees, most often, via the general call under a number of diverse circumstances. This proposed desire to affiliate, and the accompanying general call,

¹⁷⁶ Panksepp, Jaak, and Lucy Biven (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. WW Norton & Company.

together would form the basis of a “social cohesion”¹⁷⁷ effect of the call, or what was once referred to as “the herd instinct”— although “flocking instinct” may be a better descriptor for an avian species. **Figure 4.3** illustrates these two motivational models within the context of the observable call patterns of the chickadees.

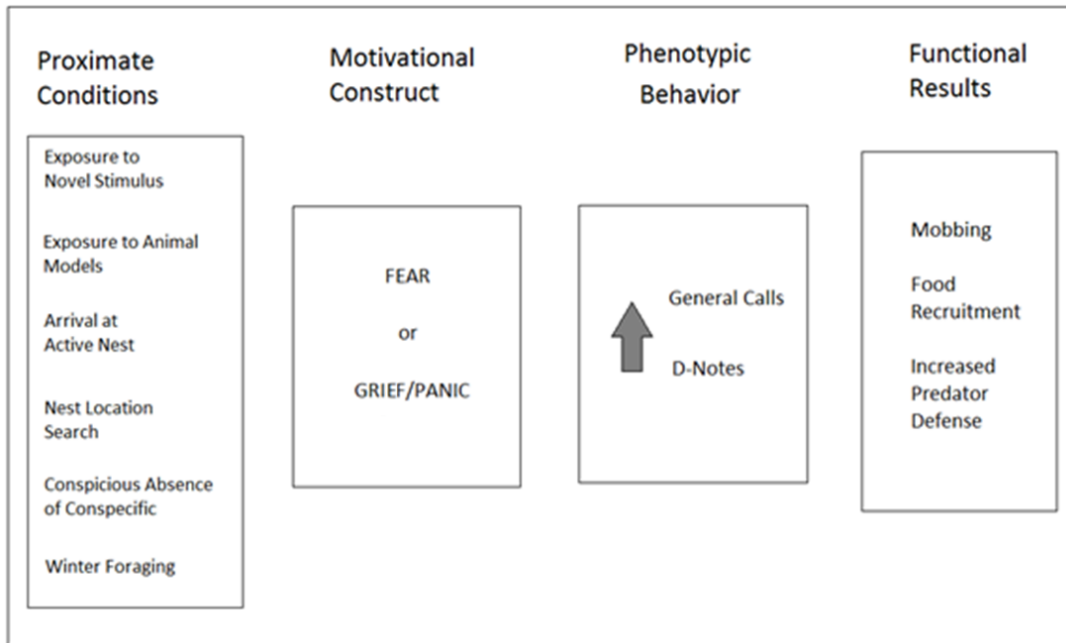


Figure 4.3: A revision of the hypothesized motivations for the chickadee general call.

Although speculative, there is some evidence to suggest that the motivational role of this general call, within the “desire to affiliate” motivational hypothesis, might not merely relate information about the motivational state of one bird to other conspecifics. The general call (or at least some components of the call such as D-notes) may also have a role in emotional contagion. Upon hearing the general call, a signal receiver might experience an increase in the desire to

¹⁷⁷ Brown, E. D., & Farabaugh, S. M. (1997). What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. *Social influences on vocal development*, 98-127.

affiliate, and an increased probability of generating the call themselves. If the general call of the chickadee does play a role in emotional contagion, this might explain many instances of the general call, such as mobbing behavior, or a response to stimulus that is hidden to conspecifics, such as in the Hetrick and Sieving study. In this experiment the researchers played recordings of tufted titmouse vocalizations as they responded to different predator types. They found that chickadee vocalizations reflected aspects of the titmouse call patterns adding the additional prospect that intraspecific emotional contagion can occur via homologous motivational signals.

A general “desire to affiliate” motivational hypothesis could explain many of the functional effects of the general call. A general call motivated by a conspicuous absence from a mate could readily function as a food recruitment mechanism. One of the reasons chickadees might have failed to use a general call in our experiments is that in most instances they arrive at the site with their mate, or perhaps other flock members, already in close proximity. The hypothesized desire to affiliate would already have been satisfied. Mobbing could be explained as: 1) a novel or threatening stimulus activates a desire to affiliate, 2) a call is generated, 3) this call attracts other chickadees, and 4) the call increases the likelihood of other calls being emitted via emotional contagion or exposure to the original stimulus. A general desire to affiliate could also help explain how a call used during mobbing, could be the same as the call used during the care of offspring. In summary, a core motivational system based on a fundamental desire to affiliate, with an accompanying signal that communicates and proliferates this motivation, could function to “close formation” in multiple contexts where an increase in proximity would be adaptive.

The “desire to affiliate” motivational hypothesis also aligns with Darwin’s emphasis on

“filial affections,”¹⁷⁸ Preston’s evolutionary model of cooperation based upon offspring care,¹⁷⁹ any many other proposals and findings described in the previous chapters. This motivational hypothesis is also parsimonious in that it does not rely on higher-order cognitive capacities. The chickadee need only be able to recognize the presence of, and form bonds with, select conspecifics, and possess the ability to associate certain stimuli, such as threatening objects, with that motivational system.

Despite the failure of our three experiments to determine the motivational basis of the chickadee general call, we still possess some clues about the chickadee *ethos* based upon the work of other researchers and our significant field experience. If we are to informally describe the *ethos* of the chickadee, with our own observations and other available evidence, we might conclude that they are a “family-centered” species. Adult chickadees invest heavily into the well-being of their mates and hatchlings. From courtship and mating to when fledglings are escorted into their new environments, parenting plays a very large role in the life cycle of the Carolina chickadee. Chickadees also seem to be a wary bird. They display very acute sensitivity to changes in their environment. The smallest change in our stimulus can create a significant apprehension to approach a pile of sunflower seed. Chickadees also appear much less aggressive than other species with which they congregate. Chickadees do display intraspecific aggression in the form of supplants and other harassing behavior. However, we have not yet witnessed the degree of belligerence a nuthatch might direct at titmice and chickadee. Some of these agonistic encounters could only be described as brutal – an aggression used with a goal to harm the other bird instead of using force with a goal of getting a seed. If chickadees use these intense forms of

¹⁷⁸ Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London.

¹⁷⁹ Preston, Stephanie D (2013). The origins of altruism in offspring care. *Psychological bulletin* 139(6), 1305.

aggression, from what we can determine, it is only on rare occasions.

Given this short ethological narrative of the chickadee, they still appear to possess a set of qualities that make them an excellent candidate for investigations into the fundamentals of character morality. Their substantial parental investment is congruent with a Darwinian proposal that moral behavior emerges from offspring care. Their subdued aggression suggests that outright physical dominance is not the primary tool in their evolutionary kit of adaptations. However, their wariness of novelty and change makes them difficult to study. We hope in future research to be able to better assess the motivational character of the chickadee. Their sensitivity to both equipment and human presence carries with it a constant threat of confounds. If we study the subtleties of chickadee motivation, we must ourselves be subtle.

In light of our findings we can now return to a question raised in a previous chapter. Is the use of the general call elicited in proximity to food, as proposed by Ficken,¹⁸⁰ an example of altruism? We believe the answer to this question depends more upon the perspective of the scientist than the data itself. Using a 5th-Aim ethology approach, we believe that the best current motivational explanation for the chickadee general call is some sense of social deprivation – the call represents a felt desire to affiliate. One researcher may frame this motivation as “selfish”—the bird calls in order to satisfy their own desire for affiliation. Another researcher might consider a desire to share experiences, both positive and negative, with conspecifics as the opposite, or nearing the opposite, of selfishness. One researcher may focus on the shared advantages of this motivation in mobbing contexts, recruitment, early warnings, etc., and find many examples of cooperation, or in some instances, altruism. Another researcher may focus on

¹⁸⁰ Ficken, M. S. (1981). Food Finding in Black-Capped Chickadees: Altruistic Communication? *The Wilson Bulletin*, 393–394.

the advantages to the individuals using the general call and classify the behavior as an example of mutualism. We leave these interpretive decisions to the reader and their chosen philosophy.

CHAPTER 5: IMPLICATIONS AND DIRECTIONS

Narratives, Parallels, Dangers

“If it were not so frightening it would be amusing to observe the pride and complacency with which we, like children, take apart the watch, pull out the spring and make a toy of it, and are then surprised when the watch stops working.”¹⁸¹

Character, or *ethos*, has been the consistent theme of this entire dissertation. Throughout these chapters we have been looking for the emotional roots that compose the *ethos* of the Carolina chickadee. We have made progress on this front, but are still at a mere beginning in our understanding of the chickadee *ethos*. We thus arrive at one obvious criticism that could be directed at this dissertation: it presents a significantly ambitious theoretical framework for morality and adds little empirical evidence in support of this framework. This is a certainly a just criticism. Our framework describes morality as either, 1) a matrix of an individual’s emotions associated with various objects or concepts (*Ethos*), or 2), a shared set of behavioral rules, norms, or expectations of a group (*Culture*). Our empirical work altogether ignores, for now, the cultural aspects of morality in chickadees. Our work with chickadees leads us to suspect that some social norms or expectations may exist in this species, but we have added no evidence to support or refute this claim. The empirical work is also quite narrow in its capacity to reveal the chickadee *ethos*. The experiments described in chapters three and four are designed to examine the link between a specific emotion and one behavior – the general call of the chickadee.

We started by examining how chickadees use their general call when they discover food.

¹⁸¹ Tolstoy, L. (1987). *A confession and other religious writings*. Penguin UK.

We have concluded, at least during the late winter months in Eastern Kentucky and Tennessee, that they do not use their call consistently when they do discover a food source. Chickadees may behave differently at other times of year. They may use their call before arriving at our seed houses. There are many possible explanations for our findings. But at present, it appears unlikely that a Pankseppian SEEKING system plays a significant motivational role in the general call of the chickadee.

We also examined the role of predation FEAR as a motivational factor behind the chickadee call. Again, the results of the study do not support this interpretation. The particular study performed here was quite limited. We compared the vocal reactions of the chickadees to the calls of two other avian species, an owl and a goose. We may have obtained substantially different results had we used different stimuli – hawk instead of a goose, or a different type of owl vocalization. But even with these limitations, there is other research suggesting that FEAR is also an unlikely motivation source of the general call. FEAR does not explain the frequent use of the general call near the nest or in seemingly innocuous foraging conditions. Failing to support either hypothesis we are left to speculation. A new hypothesis is warranted.

Evaluating these finding in light of our larger framework, we must admit that our model has developed very little as a result of these experiments. We are much more confident in our falsification of SEEKING as a probable proximate emotion for the general call than our hypotheses of FEAR or GREIF/PANIC being the primary emotional explanation. We find ourselves in a position much like an architect with a grand set of blueprints and vacant parcel of land. In our experiments we hoped to discover our first usable emotional “brick” in the construction of a chickadee *ethos*. However, we have found this particular “brick” to be incompatible with our empirical evidence. Our only progress on this framework is falsifying one

proposed proximate emotion for one type of vocal behavior. Yet, we still believe our approach is defensible for two important reasons.

The first reason comes from the history of the sciences. Important advances in the sciences often come from a major reconceptualization of an important phenomenon. Both natural selection and quantum mechanics did not emerge quickly and seamlessly from a belief in a static ecology or Newtonian physics. The advance in the sciences only came through a steady presentation of (for many, disquieting) evidence. We cannot compare our moral framework to natural selection or quantum mechanics in its importance or genius. The gulf between our contribution to science and those of Darwin or Bohr is comically vast. We do, however, argue that same principle of assumption re-evaluation applies to morality as it does to the nature of heredity or the mysteries of the atom. The very concept of morality, with all of its entanglements with the ever-changing spirit of the age, various religious traditions, post-modern philosophy, and a ‘red in tooth-and-claw’ evolutionary perspective is ripe for a fresh reconceptualization. A new wineskin for the new wine of an objective moral science.

The second reason that may help to justify our ambitious framework is that it helps expand upon other important scientific models. One of these models, and the one we are best qualified to speak about, is the Social Complexity Hypothesis for Communication (SCHC). The SCHC argues that increased social complexity of a species predicts an increased complexity in that species’ vocalizations.¹⁸² This complexity has been measured in numerous ways including group size, group density, diversity of roles, the status of group members, or the

¹⁸² Freeberg, T.M., (2005). Social complexity can drive vocal complexity: Group size influences vocal information in Carolina chickadees. *Psychological Science*, 17(7), 557-560.

number of relationships with group members.¹⁸³ Many of these conceptualized measures can be visualized using various statistical or visual modeling techniques. We propose here that emotional complexity, though much harder to quantify, may prove to be an important component linking communication with social complexity. The general call is believed to play a significant functional role in the social cohesion of chickadee or mixed species flocks.^{184 185 186} Variation in the acoustic structure and note composition of the general call has been associated with phenotypic variations in individuals, flocks, or environmental cues.^{187 188} One of the chief goals within our studies is to discover the emotion underpinning this social cohesion and to understand an additional level of phenotypic variation that likely exists in the chickadee. Social complexity, we assume, begins with individual complexity. Hence, to study emotion is to study the fundamentals of sociality. And the very concept of complexity is exceedingly abstract until we are able to describe it in ways identifiable to an observer. Emotion, even in its most primal form as described in a Pankseppian system, provides a small bridge to understanding the concept of social complexity beyond the calculus of population metrics.

In order to illustrate the potential connection of emotion to social complexity we begin with a description of a simple organism capable of experiencing only one emotion in a

¹⁸³Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

¹⁸⁴Freeberg, T.M., & Lucas, J.R. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour*, 63, 837–845. 560.

¹⁸⁵Hailman, J.P., Ficken, M.S., & Ficken, R.W. (1985). The ‘chick-a-dee’ calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English. *Semiotica*, 56, 191–224.

¹⁸⁶Templeton, C.N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, 308, 1934–1937.

¹⁸⁷Hailman, J.P., & Ficken, M.S. (1996). Comparative analysis of vocal repertoires, with reference to chickadees. In D.E. Kroodsma & E.H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 136–159). Ithaca, NY: Comstock Publishing Associates of Cornell University Press.

¹⁸⁸Lucas, J.R., & Freeberg, T.M. (2007). “Information” and the chickadee call: Communicating with a complex vocal system. In K.A. Otter (Ed.), *Ecology and behaviour of chickadees and titmice: An integrated approach*. Oxford, England: Oxford University Press.

dichotomous on/off state – though we are uncertain whether such an organism could exist in nature. Perhaps an insect that was capable of only experiencing pain or to remain in a state of no experience. This dichotomous emotional capacity would be the simplest imaginable form of motivational complexity. Other organisms, which are able to experience multiple emotions that range on a continuum of affect, would possess much greater motivational complexity. As these various emotions become associated with various stimuli, an increasing complex moral character, or *ethos*, emerges. The complexity of the *ethos*, and the *ethos* of other group members, influences the complexity of the culture *via* vocal communication. Emotional complexity, as viewed through the lens of the SCHC, becomes an individual-level predictor of communication and social complexity, and vice versa. The more complex the emotional range of the individual, we would predict the more complexity found within social organization and communication.¹⁸⁹ A simplified depiction of this connection is depicted in **Figure 5.1**.

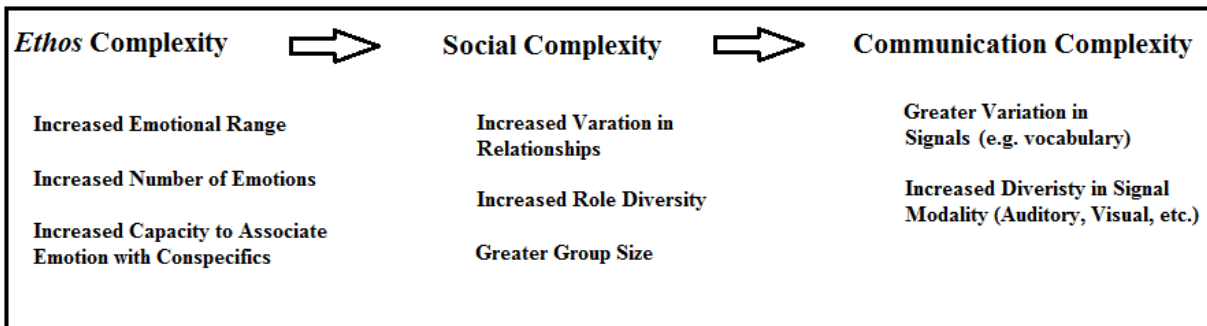


Figure 5.1: The hypothetical connection between an *ethos*, social complexity and communicative complexity.

According to our moral framework and the SCHC we should not be surprised when individuals of an emotionally complex species (as estimated with Burghardt’s critical

¹⁸⁹ Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, 111(981), 855-869.

anthropomorphism or Panksepp's triangulation method) are able to express high levels of socially complex behavior. Chimpanzees appear to target their food-related calls at specific conspecifics,¹⁹⁰ while ants utilize a less complex and more colony-targeted chemical signaling system.¹⁹¹ These are just two examples of the comparative of correlational evidence supporting the SCHC.¹⁹² ¹⁹³ ¹⁹⁴ But there is a need to experimentally test the SCHC by examining the relationship between social dynamics and communication at the individual, population, and species levels to determine if longer-term changes in social structure might serve as a selection pressure for vocal system complexity.¹⁹⁵ We believe the experiments included in the previous chapters provide a modest start in pursuing the empirical evidence required to support or falsify the SCHC.

Philosophical and Scientific Parallels

As we have investigated morality from an evolutionary perspective, certain parallels begin to emerge between evolutionary models and classical philosophy. These parallels are too numerous to relate here, but a couple of them deserve brief mention. Aristotle proposed a set of human virtues and argued that an excess or deficiency in these virtues created a vice.¹⁹⁶ Courage,

¹⁹⁰ Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955-965.

¹⁹¹ Möglich, M. (1978). Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insectes Sociaux*, *25*(3), 205-225.

¹⁹² Wilkinson, G.S. (2003). Social and vocal complexity in bats. In F.B.M. de Waal & P.L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 322–341). Cambridge, MA: Harvard University Press.

¹⁹³ Blumstein, D.T., & Armitage, K.B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, *150*, 179–200.

¹⁹⁴ McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*, 381–385.

¹⁹⁵ Freeberg, T.M., (2005). Social complexity can drive vocal complexity: Group size influences vocal information in Carolina chickadees. *Psychological Science*, *17*(7), 557-560.

¹⁹⁶ Aristotle (1976). *The ethics of Aristotle: The Nicomachean ethics*. Penguin Books.

for example, could be deficient in the form of cowardice or seen in the excess of rashness.

Augustine conceptualized virtue as the ordinate state of emotions.¹⁹⁷ To translate this concept into psychological terms, the Augustinian view proposed that with a given set of stimuli, such as death of a loved one, there were some valid or invalid emotional responses for the individual, such as grief or joy. Moral behavior, for Augustine, arose from the proper alignment of our affections with nature. For both Aristotle and Augustine, nature, at least in part, was a judge of morality. It was not a mere social innovation.

These two conceptualizations of morality can be translated into two hypotheses of a scientific model. The hypothesis we would derive from Aristotle is that moral emotions are adaptive in moderation. Any moral emotion, such as Panksepp's FEAR system would only be adaptive when in an intermediate zone. A complete lack of FEAR disables an individual from perceiving and reacting against threat. An over-abundance of FEAR will interfere with other motivations, such as those involved in resource seeking. This principle of the optimal intermediate value is widely accepted in psychology under the Yerkes-Dodson Law.¹⁹⁸

The Augustinian view that morality is attached to objects requires a little more explanation. We can start this process by envisioning a certain stimulus. This stimulus may be rewarding or threatening to the individual. From an Augustinian view, morality arises by the proper calibration of the individual's emotions to the stimulus. Threats should evoke FEAR in a person or animal. Close relationships should evoke CARE. These simple examples can be expanded to include all emotions and potential stimuli. The result of such an expansion would be a type of emotional matrix for each of the stimuli to which the individual might be exposed.

¹⁹⁷ Gregory, E. (2008). *Augustine and politics as longing in the world*. University of Missouri Press.

¹⁹⁸ Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of comparative neurology*, 18(5), 459-482.

Given the lifespan of an individual, this matrix would be extremely large: each potential stimulus would have a corresponding weight from each emotion. Fortunately, the human brain seems well-adept at such massive calculations. Just as DNA plays an incomprehensibly large role in the formation of a person's or animal's physical structure, these massive matrices together would form the *ethos* of that individual. But the Augustinian model becomes even more complex as we envision these sets of matrices, or moral characters, interacting with each other. The forces of psychology and sociology come to act at this level of operation. It is here that we should add to the Augustine model the reminder that the forces of evolution are also functioning during these interactions. There are objective fitness consequences for these exchanges. Changes in shared cultural morality could lead to a type of egalitarianism, where every individual benefits from the membership of the collective, to a repressive tyranny where a select few benefit at the expense of many, or the extinction of humanity. The evolutionary map of humanity is open and uncertain.

Some Dangers of Manipulating Morality

As our understanding of morality increases, a serious problem is almost certain to emerge. This problem is highlighted in multitudes of dystopian novels and films and lucidly described to certain educated audiences during the last World War.¹⁹⁹ Scientific discoveries that unlock the power to manipulate our world are often a double-edged sword. We see this in physics, where unlocking the secrets of the atom produce both quantum computing and nuclear bombs. We see this in microbiology, where unlocking the secrets of DNA produce the ability to cure ancient diseases or to end civilization with a pandemic. The accumulation of knowledge,

¹⁹⁹ Lewis, C. S. (2001). *The abolition of man, or, reflections on education with special reference to the teaching of English in the upper forms of schools*. San Francisco, HarperSanFrancisco.

especially scientific knowledge, can hold dangers. The fruits of science can be used by humanity to cure disease and fight oppression, or can be used to create disease or forge the tools of oppression. The difference in how these tools are used is a moral question. But the subject of these investigations is morality. This raises a paradox for scientists. How can a scientist objectively study morality without sacrificing their own moral character, which might prevent these discoveries from being converted into tools of oppression and destruction? Complete objectivity, in the field of morality, is both impossible and undesirable. It would be like taking out our own eyes to examine them more closely. A dangerous moral blindness to one's own motivations can only result.

To many, the answers to moral problems reside in technology and education. It may be very tempting to try to improve human moral nature as soon as tools for doing so become available. Gene therapy, in utero hormone treatment, and moral conditioning in infancy/early childhood could be employed in an attempt to improve human moral nature. But until a comprehensive model of morality is fully formulated we are mostly working in the dark. J.B.S. Haldane reminded us long ago that the rule in evolution was not change for the better, but degeneration. Most genetic lines end in extinction. Most mutations are malevolent.²⁰⁰ The popular notion that evolution will inevitably lead to human progress is completely unsupported in the sciences of physics or biology. The evolutionary odds, and the arrow of entropy, point in the other direction.

It is hoped that Haldane's reminder might give us pause if we ever consider using the scientifically-derived powers of manipulation to drastically alter human moral sentiments.

²⁰⁰ Haldane JBS (1933) The part played by recurrent mutation in evolution. *American Naturalist* 67: 5–19.

Knowing so little of the relationship between the *ethos*, the group's Morality (*Culture*), and the prospects for long-term adaptiveness, what assurance do we have that we can beat Haldane's odds of degeneration? And who can be trusted with this great power to alter human nature? Can we safely assume that architects of such a moral improvement initiative will be the most compassionate and fair-minded among us? And how would these moral innovators maintain their own sense of compassion and fairness once they learn the biological "ingredients" and the conditioning procedure which create compassion and fairness in their subjects? Since I do not know the answers to these questions, it seems imperative to seriously question what is meant by those who use words such as moral or social "progress" or "improvement." With the science of morality in its infancy, it is quite sensible to want a clear and specific definition of what constitutes moral progress before enacting irrevocable changes toward such a vaguely defined goal. Change only becomes progress if it succeeds in overcoming "Haldane's odds."

Proponents of moral improvement may object to this reticence by claiming that humans have always attempted to improve morality either directly through education and or indirectly by mate selection. The claim could be made that moral innovators are merely attempting to use better tools to accomplish this ancient goal. There is, at the very least, a veneer of validity to this criticism. It is certainly true that humans have always attempted to create certain moral phenotypes through education and parenting. And we can safely assume that an individual's moral reputation played some role in the sexual selection in human history. But the difference moving forward will be dramatic. Gene therapy, almost by definition, replaces the process of natural selection with the process of artificial selection. Modern education is replacing social modeling, conducted in all the diversity of a working society, with abstract instruction, conducted in the artificial homogeneity of the classroom. The powers to alter human morality

will be orders of magnitude greater with emerging scientific tools. We may be looking toward a future where the power to generate our moral phenotypes will be greatly magnified and under the control of a small cohort of technical specialists. The central question remains concerning the morality of these technical specialists. Will the science of morality be mastered by those who truly know how morality operates and seek the betterment of all, malevolent manipulators who view morality as a tool to their own ends, or meddling novices who are quite willing to chart a new course for humanity based upon scanty and insufficient evidence? We know not.

The opinion offered here is here is that science should move very cautiously in the field of morality. We also propose that scientists studying morality have a duty to strengthen their own moral characters with the study of history, philosophy, religion, and daily practice. I would not trust, as one small example, someone who delighted in being cruel to their own dog to chart the future of human morality. That is, the scientists of morality should be moral themselves, and we need vast amounts of time to know what being moral means.

We have chosen to contribute to the field of moral research a study examining the *ethos* of the Carolina chickadee. Investigating the cooperative system of chickadees provides several advantages. The relative simplicity of both the social system and neuroanatomy of the chickadee provides an opportunity to examine the rudiments of cooperation in a less perplexing context. Chickadees, being an avian species, allow an additional opportunity to examine some convergent aspects of moral development. Perhaps the most important advantage to using a comparative approach for studying moral systems is that the negative consequences for manipulating these systems would be less catastrophic for humanity. Tolstoy long ago observed humanity's tendency to dismantle our objects of study, like a watch, to understand their internal mechanisms. If we are to attempt this procedure with morality, might it not be prudent to begin with a different species?

A simple watch is easier to study than a more complex one; and to lose “the spring” in human morality is to jeopardize all.

LIST OF REFERENCES

Chapter 1 References

- Bacon, Francis (2016). *Novum organum*. Jazzybee Verlag.
- Badyaev, A. V. (2009). Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364(1520), 1125-1141.
- Baldwin, J. Mark (1896). A new factor in evolution. *The American Naturalist*, 30(354), 441-451.
- Bartal, I. B. A., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, 334(6061), 1427-1430.
- Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press.
- Brosnan, Sarah F., and Frans BM De Waal (2003). Monkeys reject unequal pay. *Nature*, 425(6955), 297-299.
- Burghardt GM. (1977) The ontogeny of communication. In: Sebeok TA, editor. *How Animals Communicate*. Bloomington, Ind, USA: Indiana University Press; pp. 67–93
- Burghardt, Gordon M (1985). Animal awareness: Current perceptions and historical perspective. *American Psychologist*, 40(8), 905.
- Burghardt, G.M. (1997). "Amending Tinbergen: A fifth aim for ethology". In R.W. Mitchell; N. S. Thompson; H. L. Miles. *Anthropomorphism, anecdotes and animals*. Albany: State University of New York Press.
- Damasio, A. (1994). *Descartes' error: Emotion, reason, and the human brain*. Avon Books.
- Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London.
- Darwin, Charles (2003). *On the Origin of Species by Means of Natural Selection*. Ed. Joseph Carroll. Peterborough, Ont.: Broadview.
- Dawkins, Richard (1989). *The selfish gene*. Oxford: Oxford University Press.
- de Waal, Frans (2016). *Are we smart enough to know how smart animals are?* WW Norton &

Company.

Descartes, René (1968). *Discourse on Method and the Meditations*. Penguin UK.

Dunbar, Robin IM (1992). Neocortex size as a constraint on group size in primates. *Journal of human evolution*, 22(6), 469-493.

Freud, Sigmund (1961). *Civilization and its Discontents*. W.W. Norton & Company.

Gert, Bernard and Gert, Joshua, "The Definition of Morality", *The Stanford Encyclopedia of Philosophy* (Spring 2016 Edition), Edward N. Zalta (ed.), URL = [<https://plato.stanford.edu/archives/spr2016/entries/morality-definition/>](https://plato.stanford.edu/archives/spr2016/entries/morality-definition/).

Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York: Pantheon Books.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of theoretical biology*, 7(1), 17-52.

Jensen, Keith (2010). Punishment and spite, the dark side of cooperation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1553), 2635-2650.

Kahneman, D. (2011). *Thinking, fast and slow*. New York: Farrar, Straus and Giroux

Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

Lewis, C. S. (1964). *The discarded image: An introduction to medieval and renaissance literature*. Cambridge University Press.

Masserman, J. H., Wechkin, S. & Terris, W. (1964) "Altruistic" behavior in rhesus monkeys. *American Journal of Psychiatry*, 121:584-585.

Mercier, H., & Sperber, D. (2011). Why do humans reason? Arguments for an argumentative theory. *Behavioral and brain sciences*, 34(2), 57-74.

Morris, Simon Conway (2003). *Life's solution: inevitable humans in a lonely universe*.

Cambridge University Press.

Panksepp, Jaak (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and cognition*, 14(1), 30-80.

Panksepp, Jaak, and Lucy Biven (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. WW Norton & Company.

Preston, Stephanie D (2013). The origins of altruism in offspring care. *Psychological bulletin* 139(6), 1305.

Rice, George E., and Priscilla Gainer (1962). 'Altruism' in the albino rat. *Journal of comparative and physiological psychology*, 55(1), 123.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

Rilling, James K., and Larry J. Young (2014). The biology of mammalian parenting and its effect on offspring social development. *Science*, 345(6198), 771-776.

Ruse, M. (2003) Is evolution a secular religion? *Science* 299.5612 p. 1523-1524.

Singer, P. (2011). *The expanding circle: Ethics, evolution, and moral progress*. Princeton

University Press. Sober, E., & Wilson, D. S. (1999). *Unto others: The evolution and psychology of unselfish behavior* (No. 218). Harvard University Press.

Sober, E., & Wilson, D. S. (1999). *Unto others: The evolution and psychology of unselfish behavior* (No. 218). Harvard University Press

Spencer, Herbert (1876). *First principles of a new system of philosophy*. D. Appleton.

Tinbergen, Niko (1963). On aims and methods of ethology. *Ethology*, 20(4), 410-433.

Van der Braak, H. (2013). *Evolutionary Psychology*. Pearson Education Limited.

Van Oudenhove, L., & Cuypers, S. E. (2010). The philosophical "mind-body problem" and its relevance for the relationship between psychiatry and the neurosciences. *Perspectives in biology and medicine*, 53(4), 545-557.

Von Uexküll, Jakob (1992). A stroll through the worlds of animals and men: A picture book of invisible worlds. *Semiotica*, 89(4), 319-391.

Tinbergen, Niko (1963). On aims and methods of ethology. *Ethology*, 20(4), 410-433.

Webster, Noah (1966). *Webster's dictionary of the English language, unabridged*. Publishers International Press.

Wilson, David Sloan, and Edward O. Wilson (2007). Rethinking the theoretical foundation of sociobiology. *The Quarterly review of biology*, 82(4), 327-348.

Wilson, E. O. (1999). *Consilience: The unity of knowledge*. Vintage.

Chapter 2 References

- Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, 85(6), 1225-1232.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1745), 4199-4205.
- Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press
- Beauchamp, G. (2004). Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society B: Biological Sciences*, 271(1543), 1039.
- Bradbury JW, Vehrencamp SL. 1998. *Principles of animal communication*. Sunderland (MA): Sinauer.
- Breuner, C. W., & Hahn, T. P. (2003). Integrating stress physiology, environmental change, and behavior in free-living sparrows. *Hormones and Behavior*, 43(1), 115-123.
- Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. 83:820–833.
- Brewer, R. (1961). Comparative notes on the life history of the Carolina Chickadee. *The Wilson Bulletin*, 348-373.
- Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42(4), 551-564.
- Bshary, Redouan, and Daniel Schaffer (2002). Choosy Reef Fish Select Cleaner Fish That Provide High-Quality Service. *Animal Behaviour*, 63(3), 557–564.
- Byrne, R., & Whiten, A. (1989). *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford Science Publications.

- Cannon, W. B. (1929). *Bodily changes in pain, hunger, fear and rage*.
- Cimprich, D. A., & Grubb, T. C. (1994). Consequences for Carolina chickadees of foraging with tufted titmice in winter. *Ecology*, 75(6), 1615-1625.
- Clemmons, J., & Howitz, J. L. (1990). Development of early vocalizations and the chick-a-dee call in the black-capped chickadee, *Parus atricapillus*. *Ethology*, 86(3), 203-223.
- Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London.
- de Waal, Frans BM (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy. *Annu. Rev. Psychol.*, 59, 279–300.
- de Waal, F. (2009). *The age of empathy*. New York: Harmony.
- de Waal, F. B. (2013). *The bonobo and the atheist: In search of humanism among the primates*. WW Norton & Company.
- Doherty Jr, P. F., Williams, J. B., & Grubb Jr, T. C. (2001). Field metabolism and water flux of Carolina Chickadees during breeding and nonbreeding seasons: a test of the “peak-demand” and “reallocation” hypotheses. *The Condor*, 103(2), 370-375.
- Donaldson, Z. R., and L. J. Young (2008). Oxytocin, Vasopressin, and the Neurogenetics of Sociality. *Science*, 322(5903), 900–904. doi:10.1126/science.1158668.
- Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, 19(6), 433–438.
<http://doi.org/10.1007/BF00300546>
- Edgar, J. L., J. C. Lowe, E. S. Paul, and C. J. Nicol (2011). Avian Maternal Response to Chick Distress. *Proceedings of the Royal Society of London B: Biological Sciences*, 22;278 (1721):3129-34.
- Ficken, M. S. (1981). Food Finding in Black-Capped Chickadees: Altruistic Communication? *The Wilson Bulletin*, 393–394.
- Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds*, 42(11), 347-357.

Freeberg TM, Lucas JR. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Anim Behav.*, 63:837–845.

Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am.* 113: 2127–2136.

Goodson, J. L., Schrock, S. E., Klatt, J. D., Kabelik, D., & Kingsbury, M. A. (2009). Mesotocin and nonapeptide receptors promote estrildid flocking behavior. *Science*, 325(5942), 862-866.

Hamilton, W. D. (1964). *The Genetical Evolution of Social Behaviour*. I.

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others?. *Behavioral Ecology and Sociobiology*, 28(1), 13-21.

Johnson, F., Soderstrom, K., & Whitney, O. (2002). Quantifying song bout production during zebra finch sensory-motor learning suggests a sensitive period for vocal practice. *Behavioural brain research*, 131(1), 57-65.

Johnston, V. R. (1942). Factors influencing local movements of woodland birds in winter. *The Wilson Bulletin*, 192-198.

Judd, Timothy M., and Paul W. Sherman (1996). Naked Mole-Rats Recruit Colony Mates to Food Sources. *Animal Behaviour*, 52(5), 957–969.

Karasov, W. H., Brittingham, M. C., & Temple, S. A. (1992). Daily energy and expenditure by Black-capped Chickadees (*Parus atricapillus*) in winter. *The Auk*, 109(2), 393-395.

Klein, B. C. (1988). Weather-dependent mixed-species flocking during the winter. *J. Theor. Biol.*, 38, 419–422.

Kotrschal, K., Hirschenhauser, K., & Möstl, E. (1998). The relationship between social stress and dominance is seasonal in greylag geese. *Animal Behaviour*, 55(1), 171-176.

Krama, Tatjana, Jolanta Vrublevska, Todd M. Freeberg, Cecilia Kullberg, Markus J. Rantala, and Indrikis Krams (2012). You Mob My Owl, I'll Mob Yours: Birds Play Tit-for-Tat Game. *Scientific Reports*, 2. <http://www.nature.com/srep/2012/121112/srep00800/full/srep00800.html>.

- Lucas, J. R., Schraeder, A., & Jackson, C. (1999). Carolina chickadee (Aves, Paridae, *Poecile carolinensis*) vocalization rates: effects of body mass and food availability under aviary conditions. *Ethology*, *105*(6), 503-520.
- Janik, V. M. (2000). Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London B: Biological Sciences*, *267*(1446), 923-927.
- Johnston, V. R. (1942). Factors influencing local movements of woodland birds in winter. *The Wilson Bulletin*, 192-198.
- Judd, Timothy M., and Paul W. Sherman (1996). Naked Mole-Rats Recruit Colony Mates to Food Sources. *Animal Behaviour*, *52*(5), 957-969.
- Mahurin, E. J., Freeberg, T.M. (2009) Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behav Ecol* *20*:111-116
- Marler, P., & Peters, S. (1982). Subsong and plastic song: their role in the vocal learning process. *Acoustic communication in birds*, *2*, 25-50.
- Melis, A. P. (2006). Chimpanzees Recruit the Best Collaborators. *Science*, *311*(5765), 1297-1300. doi:10.1126/science.1123007.
- Mock, Douglas W., and Masahiro Fujioka (1990). Monogamy and Long-Term Pair Bonding in Vertebrates. *Trends in Ecology & Evolution*, *5*(2), 39-43.
- Möglich, M. (1978). Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insectes Sociaux*, *25*(3), 205-225.
- Nowak, Martin A., and Karl Sigmund (1998). Evolution of Indirect Reciprocity by Image Scoring. *Nature*, *393*(6685), 573-77. doi:10.1038/31225.
- Odum, E. P. (1942). Annual cycle of the black-capped chickadee: 3. *The Auk*, *59*(4), 499-531.
- Ostojić, Ljerka, Rachael C. Shaw, Lucy G. Cheke, and Nicola S. Clayton (2013). Evidence Suggesting That Desire-State Attribution May Govern Food Sharing in Eurasian Jays. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(10), 4123-28. doi:10.1073/pnas.1209926110.

Panksepp, Jaak, and Lucy Biven (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. WW Norton & Company, p 211.

Preston, Stephanie D (2013). The origins of altruism in offspring care. *Psychological bulletin*, 139(6), 1305.

Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., & Wild, M. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology*, 473(3), 377-414.

Royle, N. J., A. F. Russell, and A. J. Wilson (2014). The Evolution of Flexible Parenting. *Science*, 345(6198), 776–81. doi:10.1126/science.1253294.

Schino, Gabriele, and Filippo Aureli (2009). Chapter 2 Reciprocal Altruism in Primates: Partner Choice, Cognition, and Emotions. In *Advances in the Study of Behavior*, edited by Timothy J. Roper H. Jane Brockmann Marc Naguib, Katherine E. Wynne-Edwards, John C. Mitani and Leigh W. Simmons, 39, 45–69. Academic Press.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, 86(5), 955-965.

Sherry, D. F., & Galef, B. G. (1990). Social learning without imitation: more about milk bottle opening by birds. *Animal Behaviour*, 40(5), 987-989.

Sherry, D. F., & Galef, B. G. (1984). Cultural transmission without imitation: milk bottle opening by birds. *Animal Behaviour*, 32(3), 937-938.

Skinner, B. F. (1992). "Superstition" in the pigeon. *Journal of Experimental Psychology: General*, 121(3), 273.

Soard CM, Ritchison G. (2009). ‘Chick-a-dee’ calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Anim Behav*. 78:1447–1453.

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78(2), 337–347.

<http://doi.org/10.1016/j.anbehav.2009.05.008>

Templeton CN, Greene E, Davis K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*. 308:1934–1937.

Trivers, R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*. 46:35-57.

Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 357(1427), 1549-1557.

von Frisch, Karl (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA, US: Harvard University Press.

West, M. J., & King, A. P. (1985). Social guidance of vocal learning by female cowbirds: validating its functional significance. *Ethology*, 70(3), 225-235.

Wiley RH, Richards DG. (1982). Adaptations for acoustic communication in birds: sound transmission and signal design. In: Kroodsma DE, Miller EH, Ouellet H, editors. *Acoustic communication in birds*. New York: Academic Press. p. 131–181.

Wilson, D. R., & Mennill, D. J. (2010). Black-capped chickadees, *Poecile atricapillus*, can use individually distinctive songs to discriminate among conspecifics. *Animal Behaviour*, 79(6), 1267–1275.

Wingfield, J. C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G., Freed, L., & Lepson, J. (1997). *Environmental stress, field endocrinology, and conservation biology. Behavioral approaches to conservation in the wild*. Cambridge University Press, Cambridge, 95-131.

Chapter 3 References

Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology*, *64*(7), 1187–1198.

Bradbury JW, Vehrencamp SL. (1998). *Principles of animal communication*. Sunderland (MA): Sinauer.

Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. *83*:820–833.

de Waal, F. B. (2008). *Putting the altruism back into altruism: the evolution of empathy*. *Annu. Rev. Psychol.*, *59*, 279–300.

Freeberg TM, Lucas JR. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Anim Behav*, *63*:837–845.

Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am.*, *113*: 2127–2136.

Ficken MS. 1981. Food finding in black-capped chickadees: altruistic communication? *Wilson Bull*, *93*:393–394.

Krama, T., Vrublevska, J., Freeberg, T. M., Kullberg, C., Rantala, M. J., & Krams, I. (2012). You mob my owl, I'll mob yours: birds play tit-for-tat game. *Scientific Reports*, *2*. Retrieved from <http://www.nature.com/srep/2012/121112/srep00800/full/srep00800.html>

- Johnson, W. T., & Freeberg, T. M. (2016). Pseudoreplication in use of predator stimuli in experiments on antipredator responses. *Animal Behaviour*, *119*, 161-164.
- Mahurin, E. J., Freeberg, T.M. (2009) Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behav Ecol*, *20*:111–116.
- Morse, D. H. (1970). Ecological Aspects of Some Mixed-Species Foraging Flocks of Birds. *Ecological monographs*, *40*(1), 119-168.
- Nolen, M. T., & Lucas, J. R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour*, *77*(5), 1137-1146.
- Schaller, George. (2007) Feral and Free—An Interview with George Schaller. *New Scientist*, 46-47.
- Soard CM, Ritchison G. (2009). ‘Chick-a-dee’ calls of Carolina chickadees convey information about degree of threat posed by avianpredators. *Anim Behav.*, *78*:1447–1453.
- Templeton CN, Greene E, Davis K. (2005). Allometry of alarm calls:black-capped chickadees encode information about predator size. *Science*, *308*:1934–1937.
- Wiley RH, Richards DG. (1982). Adaptations for acoustic communication in birds: sound transmission and signal design. In: Kroodsma DE, Miller EH, Ouellet H, editors. *Acoustic communication in birds*. New York: Academic Press. p. 131–181.
- Zachau, C. E., & Freeberg, T. M. (2012). Chick-a-dee call variation in the context of “flying” avian predator stimuli: a field study of Carolina chickadees (*Poecile carolinensis*). *Behavioral Ecology and Sociobiology*, *66*(5), 683-690.

Chapter 4 References

- Bekoff, Marc, and Jessica Pierce (2009). *Wild justice: The moral lives of animals*. University of Chicago Press.
- Book, D. L., & Freeberg, T. M. (2015). Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. *Animal cognition*, 18(5), 1155.
- Bloomfield LL, Phillmore LS, Weisman RG, Sturdy CB. (2005). Note types and coding in parid vocalizations III: The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Can J Zool*. 83:820–833.
- Brewer, E.P. (1961). Comparative notes on the life history of the Carolina chickadee. *The Wilson Bulletin*, 73(4), 349-373.
- Brown, E. D., & Farabaugh, S. M. (1997). What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. *Social influences on vocal development*, 98-127.
- Browning, S. A. (2015). *Mixed-species Flock Members' Reactions to Novel and Predator Stimuli*. Retrieved from http://trace.tennessee.edu/utk_graddiss/3327
- Clemmons, J., Howitz, J.L., (1990). Development of early vocalizations and the chick-a-dee call in the black-capped chick-a-dee, *parus atricapillus*. *Ethology*, 86, 203-223.
- Darwin, Charles (1871). *Sexual Selection and the Descent of Man*. Murray, London.
- Preston, Stephanie D (2013). The origins of altruism in offspring care. *Psychological bulletin*, 139(6), 1305.

Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*, 19(6), 433–438.

Freeberg TM, Lucas JR, Clucas B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: identity and redundancy within note types. *J Acoust Soc Am*, 113: 2127–2136.

Ficken, M. S. (1981). Food Finding in Black-Capped Chickadees: Altruistic Communication? *The Wilson Bulletin*, 393–394.

Hetrick, S.A. Sieveing, K.E. (2012) Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behav Ecol*, 23:83–92.

Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, 367(1597), 1879-1891.

Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, 20(1), 111–116.

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, 111(981), 855-869.

Panksepp, Jaak, and Lucy Biven (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions*. WW Norton & Company.

Preston, Stephanie D (2013). The origins of altruism in offspring care. *Psychological bulletin* 139(6), 1305.

Chapter 5 References

- Aristotle (1976). *The ethics of Aristotle: The Nicomachean ethics*. Penguin Books.
- Blumstein, D.T., & Armitage, K.B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, *150*, 179–200.
- Freeberg, T.M., & Lucas, J.R. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour*, *63*, 837–845.
- Freeberg, T.M., (2005). Social complexity can drive vocal complexity: Group size influences vocal information in Carolina chickadees. *Psychological Science*, *17*(7), 557-560.
- Gregory, E. (2008). *Augustine and politics as longing in the world*. University of Missouri Press.
- Hailman, J.P., & Ficken, M.S. (1996). Comparative analysis of vocal repertoires, with reference to chickadees. In D.E. Kroodsma & E.H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 136–159). Ithaca, NY: Comstock Publishing Associates of Cornell University Press.
- Hailman, J.P., Ficken, M.S., & Ficken, R.W. (1985). The ‘chick-a-dee’ calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English. *Semiotica*, *56*, 191– 224.
- Haldane JBS (1933) The part played by recurrent mutation in evolution. *American Naturalist* *67*: 5–19.
- Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Phil. Trans. R. Soc. B*, *367*(1597), 1879-1891.

Lewis, C. S. (2001). *The abolition of man, or, reflections on education with special reference to the teaching of English in the upper forms of schools*. San Francisco, HarperSanFrancisco.

Lucas, J.R., & Freeberg, T.M. (2007). “Information” and the chick-adee call: Communicating with a complex vocal system. In K.A. Otter (Ed.), *Ecology and behaviour of chickadees and titmice: An integrated approach*. Oxford, England: Oxford University Press.

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*, 381–385.

Möglich, M. (1978). Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insectes Sociaux*, *25*(3), 205-225.

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955-965.

Sieving, K. E., Hetrick, S. A., & Avery, M. L. (2010). The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. *Oikos*, *119*(2), 264-276.

Templeton, C.N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, *308*, 1934–1937.

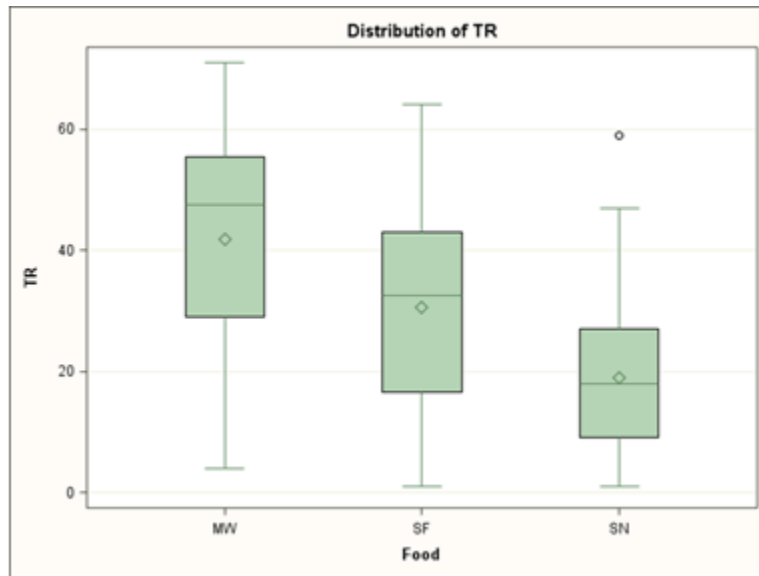
Tolstoy, L. (1987). *A confession and other religious writings*. Penguin UK.

Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of comparative neurology*, *18*(5), 459-482.

Wilkinson, G.S. (2003). Social and vocal complexity in bats. In F.B.M. de Waal & P.L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 322–341). Cambridge, MA: Harvard University Press.

APPENDICES

Appendix 1: Carolina Chickadee Food Preferences



MW = Mealworms, SF= Safflower, SN = Sunflower

TR = Preference, low number indicate high preference.

Tukey's Studentized Range (HSD) Test for TR

Note: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	310
Error Mean Square	220.0144
Critical Value of Studentized Range	3.33051

Comparisons significant at the 0.05 level are indicated by ***.

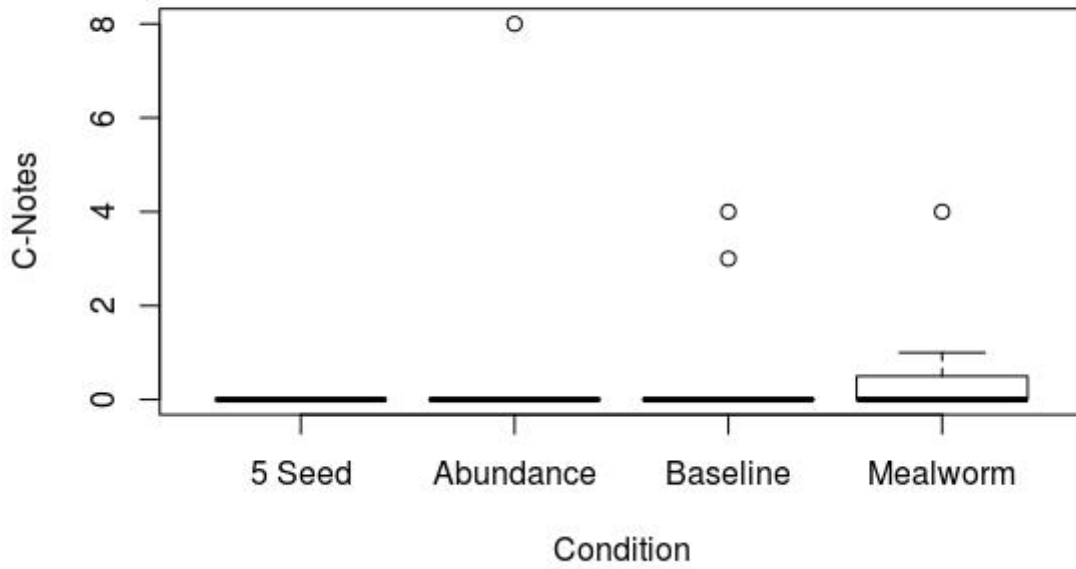
Food Comparison	Difference Between Means	Simultaneous 95% Confidence Limits		
MW - SF	11.388	5.450	17.326	***
MW - SN	22.903	17.065	28.740	***
SF - MW	-11.388	-17.326	-5.450	***
SF - SN	11.515	7.215	15.816	***
SN - MW	-22.903	-28.740	-17.065	***
SN - SF	-11.515	-15.816	-7.215	***

Appendix 2: Food Type Raw Data

Site	Cond	Calls	Intro	C	Dh	D
Boone Camp	Abundance	0	0	0	0	0
Boone Camp	Baseline	0	0	0	0	0
Boone Camp	Mealworm	2	2	4	0	9
Boone Farm	5 Seed	0	0	0	0	0
Boone Farm	Abundance	0	0	0	0	0
Boone Farm	Mealworm	1	0	0	1	1
Boyscout	5 Seed	0	0	0	0	0
Boyscout	Abundance	5	5	0	0	40
Boyscout	Baseline	2	2	4	0	9
Boyscout	Mealworm	6	7	0	0	45
Circle	5 Seed	0	0	0	0	0
Circle	Abundance	0	0	0	0	0
Circle	Baseline	0	0	0	0	0
Circle	Mealworm	1	0	0	0	0
Dads	5 Seed	5	16	0	0	4
Dads	Abundance	0	0	0	0	0
Dads	Baseline	2	7	3	0	9
Dads	Mealworm	0	0	0	0	0
Dam	Abundance	0	0	0	0	0
Dam	Mealworm	2	2	1	0	13
Dump	Mealworm	0	0	0	0	0
E Cabin	5 Seed	0	0	0	0	0
E Cabin	Abundance	0	0	0	0	0
E Cabin	Mealworm	2	2	0	0	6
E Camp	Abundance	0	0	0	0	0
E Camp	Baseline	0	0	0	0	0
Fitness	5 Seed	0	0	0	0	0
Fitness	Abundance	4	4	8	0	7
Fitness	Baseline	0	0	0	0	0
Fitness	Mealworm	1	2	1	5	0
Homestead	5 Seed	0	0	0	0	0
Homestead	Abundance	0	0	0	0	0
Homestead	Baseline	0	0	0	0	0
Marine	5 Seed	0	0	0	0	0
Marine	Abundance	0	0	0	0	0
Marine	Baseline	0	0	0	0	0

Marine	Mealworm	10	9	0	6	28
Quarry	5 Seed	3	6	0	0	5
Quarry	Abundance	0	0	0	0	0
Quarry	Baseline	1	1	0	0	3
Quarry	Mealworm	0	0	0	0	0
Riverbend	5 Seed	0	0	0	0	0
Riverbend	Abundance	4	12	0	1	49
Riverbend	Baseline	0	0	0	0	0
Riverbend	Mealworm	1	1	0	0	1

Appendix 3: Study 1, C-Notes by Condition



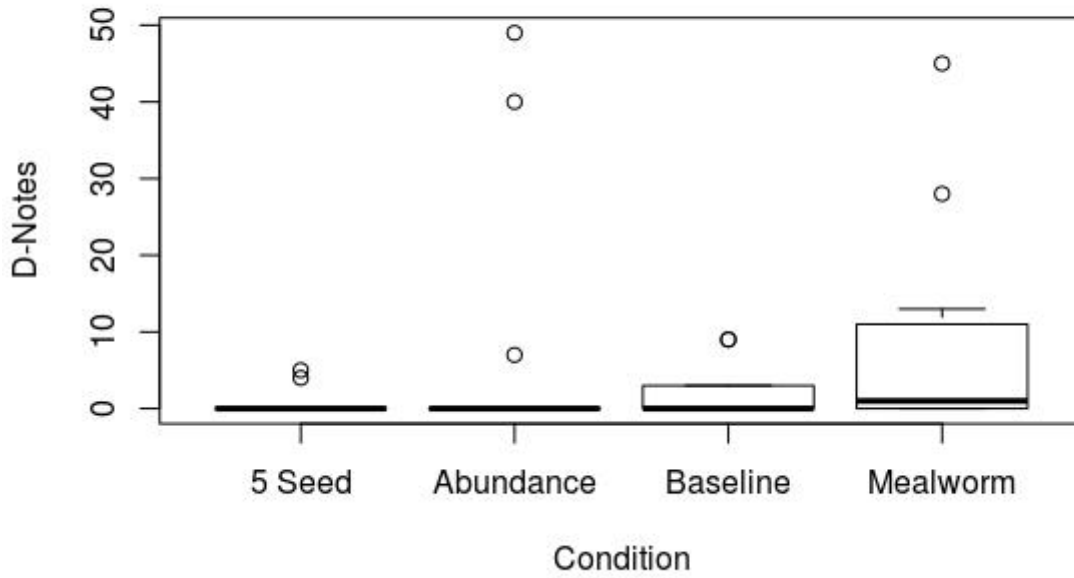
N=10 (5 Seed)

N=13 (Abundance)

N=10 (Baseline)

N=12 (Mealworm)

Appendix 4: Study 1, D-notes by Condition



N=10 (5 Seed)

N=13 (Abundance)

N=10 (Baseline)

N=12 (Mealworm)

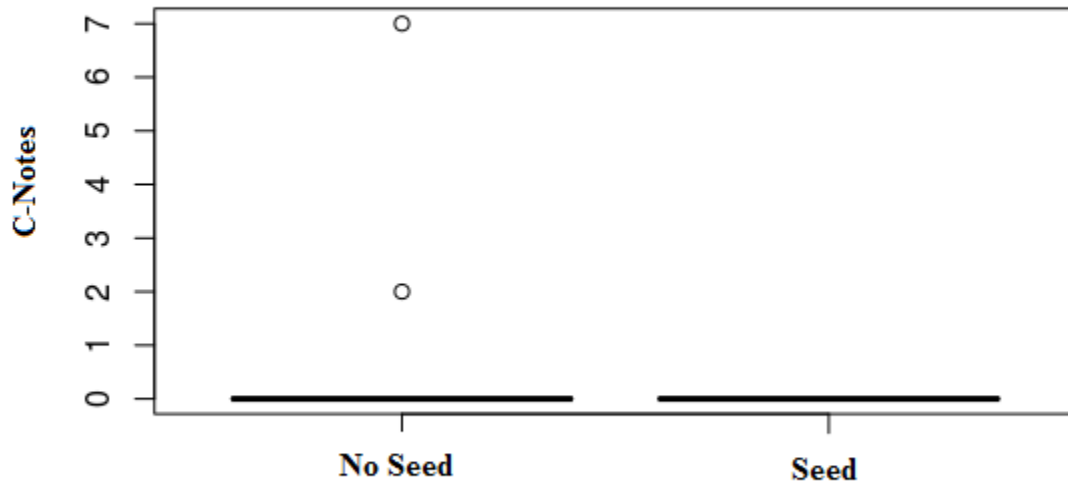
Appendix 5: Study 2, Owl vs. Goose Call Raw Data

Site	Cond	Bird T#	Calls	intro	C	Dh	D
Boone Camp	Goose	1	0	0	0	0	0
Boone Camp	Owl	2	0	0	0	0	0
Boone Farm	Goose	2	0	0	0	0	0
Boone Farm	Owl	2	2	4	0	0	0
Boyscout	Goose	3	1	2	0	0	0
Boyscout	Owl	2	3	0	9	1	13
Dads	Goose	1	0	0	0	0	0
Dads	Owl	2	4	9	0	0	0
Dam	Goose	3	5	2	0	1	39
Dam	Owl	2	0	0	0	0	0
E Cabin	Goose	2	0	0	0	0	0
E Cabin	Owl	1	0	0	0	0	0
E Camp	Goose	3	0	0	0	0	0
E Camp	Owl	4	0	0	0	0	0
X_Fitness	Owl	2	1	5	0	0	0
X_Heritage	Goose	2	2	4	8	0	0
Homestead	Goose	1	0	0	0	0	0
Homestead	Owl	3	0	0	0	0	0
Marine	Goose	3	0	0	0	0	0
Marine	Owl	2	0	0	0	0	0
Ramp	Goose	1	0	0	0	0	0
Ramp	Owl	2	0	0	0	0	0
Quarry	Goose	2	0	0	0	0	0
Quarry	Owl	1	0	0	0	0	0
Riverbend	Goose	2	0	0	0	0	0
Riverbend	Owl	2	0	0	0	0	0

Appendix 6: Seed vs. No Seed Call Raw Data

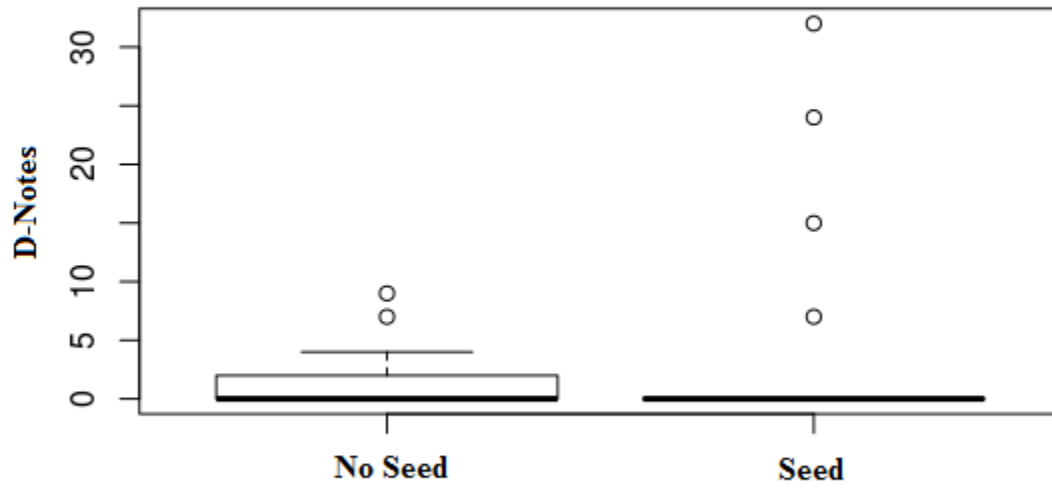
Site	Condition	Calls	Intro	C	D	Condition	Calls	Intro	C	D
10M	NS	0	0	0	0	S	0	0	0	0
15I	NS	1	1	7	2	S	3	8	0	24
17A	NS	1	1	0	2	S	0	0	0	0
1K	NS	0	0	0	0	S	0	0	0	0
4A+	NS	1	5	0	0	S	0	0	0	0
B1B	NS	0	0	0	0	S	0	0	0	0
B3F	NS	0	0	0	0	S	0	0	0	0
BooneCamp	NS	0	0	0	0	S	0	0	0	0
BooneFarm	NS	0	0	0	0	S	0	0	0	0
Boyscout	NS	1	0	0	7	S	1	4	0	7
Circle	NS	1	0	0	4	S	0	0	0	0
Dads	NS	0	0	0	0	S	0	0	0	0
Ecabin	NS	1	2	0	0	S	2	3	0	15
Fitness	NS	1	2	2	2	S	0	0	0	0
Heritage	NS	1	1	0	9	S	2	21	0	0
Ramp	NS	0	0	0	0	S	5	4	0	32
17L						S	0	0	0	0
B2AR7	NS	0	0	0	0					
Yard						S	0	0	0	0
Ecamp						S	0	0	0	0

Appendix 7: Study 3, C-Notes by Condition



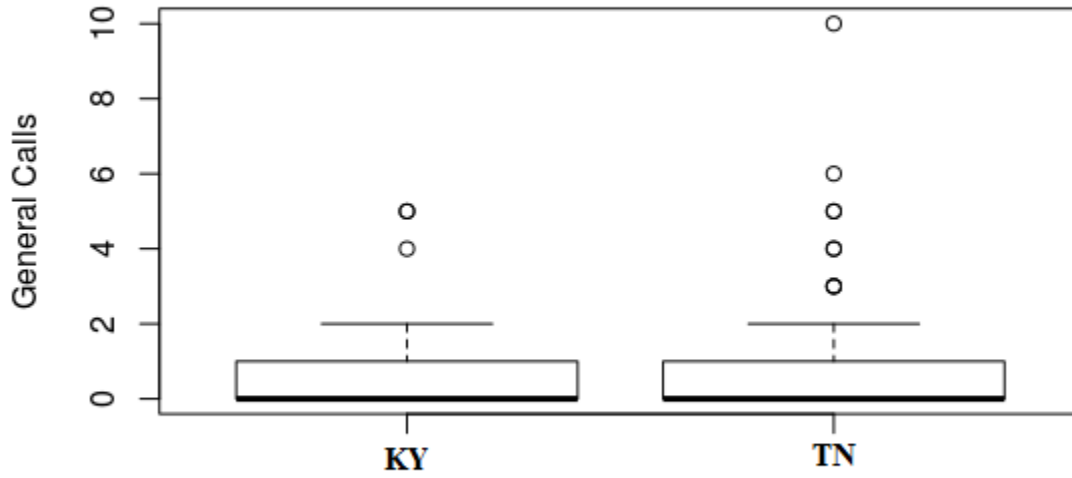
N=16 (Seed and No Seed)

Appendix 8: Study 3, D-Notes by Condition



N=16 (Seed and No Seed)

Appendix 9: Regional Analysis



N=36 (KY)

N=71 (TN)

VITA

D.L. Book was born in Ann Arbor, Michigan. He received an M.A. in Pastoral Counseling in 2009 from Cincinnati Christian University, a M.S. in Experimental Psychology in 2011 from Morehead State University, and is submitting this dissertation to fulfil the requirements of a Ph.D. in Experimental Psychology at the University of Tennessee. David's research interests include moral motivation and relationship between matter and sentience. He resides in Winchester, Kentucky with his wonderful family and precocious cat.