

Acoustic communication in colonial seabirds: individual, sexual, and species-specific variation in acoustic signals of *Pterodroma* petrels

Matthew W. McKown

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Approved by:
R. Haven Wiley (Advisor)
Sabrina S. Burmeister
Karin S. Pfennig
Theodore R. Simons
Peter S. White

ABSTRACT

Matthew W. McKown

Acoustic communication in colonial seabirds: individual, sexual, and species-specific variation in acoustic signals of *Pterodroma* petrels
(Under the direction of R. Haven Wiley)

Acoustic communication is an integral component of social interactions in procellariid seabirds (petrels), and a substantial amount of research has been devoted to the vocalizations and vocal behavior in this family. This work has shown that petrels' calls contain information about the species, sex, and identity of the caller. Experiments have confirmed that these features are used to recognize conspecifics, mates, and other individuals in many species. Relatively little is known, however, about vocalizations in the genus *Pterodroma*, which contains 40% of the species in the family. My research on *Pterodroma externa* in the Islas Juan Fernández confirmed sexual dimorphism in the calls of this species and showed that their burrow calls differ among individuals. Both Linear Discriminant Functions and Probabilistic Neural Nets classified individuals by their calls with high accuracy. Acoustic censuses in a mixed colony of *Pterodroma externa* and *P. longirostris* showed that both of these nocturnal species increased vocal activity on nights with moonlight. Different tradeoffs between the risk of predation and the risk of collision in the dark might explain differences in the timing of their nocturnal activity. In addition, I compared aerial vocalizations in a closely related group of *Pterodroma* species in the subgenus *Cookilaria*. The similarities in the calls produced by these species suggest that vocalizations can provide useful information for understanding the phylogenetic relationships

of species in this genus. Differences among the calls and activity patterns of these species, on the other hand, suggest a range of adaptations to the different environments they inhabit. One implication of these findings is that each colony of seabirds on remote islands might have an optimal pattern of activity that differs from those of colonies elsewhere. If immigrant individuals cannot adjust, these colony-specific patterns of activity could contribute to reproductive isolation between populations and thus to speciation in these birds.

DEDICATION

To my grandmother, Helen McKown, for introducing me to birds, and to my father and mother, for encouraging my interest in the natural world.

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INTRODUCTION

Seabirds are top level marine predators that consume 7% of marine primary productivity (Brooke, 2004b). They are the most threatened marine group, representing 25% of all marine extinctions (Dulvy et al., 2003) and 30% are at risk of extinction (IUCN, 2007). The order includes 125 recognized species in 4 families – the Diomedidae (Albatrosses), Hydrobatidae (Storm Petrels), Procellariidae (the petrels, shearwaters, prions, fulmars, and similar), and the Pelicanoididae (the diving petrels). Thorough reviews of the biology and ecology of these birds have been presented by Warham (1990; 1996) and Brooke (1990; 2004a), and the general material I present in this brief introduction, and many of the details I present throughout this dissertation are gleaned from these references.

Largely unseen by human eyes, these species gather in staggering aggregations at their oceanic foraging grounds and island breeding sites. Though much of their lives are spent at sea, the Procellariiformes, like some other marine predators (the pinnipeds, sea turtles, and even the anadromous salmonids), are tied to terrestrial sites for reproduction. Reproduction is energetically costly (with eggs for some small species weighing up to 29% of female body mass), and breeding periods can last from 4 to 13 months for the smallest and largest species (Brooke 2004, Warham 1990). All species in the order lay only one egg, and both sexes share the responsibilities of incubation and chick rearing. The high degree of

cooperation required to successfully rear a chick is thought to explain the complex social behavior between mates, and the long-term pair bonds found in many species.

Adults, their egg, and chicks are extremely vulnerable to predators during the breeding period. For this reason, most Procellariiformes breed on islands devoid of mammalian predators (with some notable exceptions such as Hornby's Storm Petrel *Oceanodroma hornbyi* and Markham's Storm Petrel *O. markhami* which breed in some mainland sites in the deserts of Southern Peru and Northern Chile). Many species dig underground nesting chambers (burrows), probably to avoid avian predation and possibly to help insulate the egg and chick from drastic changes in temperature and humidity.

Because individuals of these species forage over large areas of the ocean, behavior that precedes mating is concentrated at these colonies, where individuals gather in large vocal aggregations to court and establish nest sites. Colony attendance is highly synchronized for breeding pairs and for un-paired individuals displaying at colony sites during each breeding season. Most Procellariiformes do not breed in the first years of their lives, but young unpaired individuals visit colonies for a number of years before attempting to breed for the first time. Thus non-breeders make up a large portion of the total population of many species and often outnumber breeding birds at colony sites during some stages of the breeding season. As a result, breeding colonies are busy, chaotic, and spectacular sites during the breeding season, with breeders and non-breeders gathering offshore, and interacting in the air, on the ground, and at nesting sites in a synchronized mass.

Within the family Procellariidae, colony attendance for roughly 61 of the 79 species occurs strictly after sunset (Brooke, 2004a). Individuals interacting at the colony therefore face the challenge of communicating in the dark. So, instead of the complex visual displays seen in the diurnal Diomedidae, the procellariids (petrels) rely predominantly on acoustic and olfactory signals to interact with mates, potential mates, and/or rivals in the darkness. Variation in the properties of these signals (amplitude, timing, and frequency) have been shown to convey information about the species, sex, and individual identity of the caller in many petrel species (Warham, 1996; Bretagnolle, 1996). Patterns of communication at colonies also vary within nights, among nights in a season, among species at a colony, and among colony sites.

This is especially true of the petrels in the genus *Pterodroma*. Containing 40% of the species in the Family Procellariidae, and 25% of all of the species in the Order, the *Pterodroma* breed on islands throughout the mid and low latitudes of the Pacific, Atlantic, and Indian Oceans. Nearly a third of the recognized *Pterodroma* breed on only one island or island group, higher than the number of found in any of the other species in the order. Similarities in plumage patterns within the group may mask other cryptic island endemics within the group. Because of the important role of acoustic signals in the reproductive behavior of these species, it is likely that similarities in the vocalizations and vocal behavior of populations of *Pterodroma* petrels may provide information of the taxonomy of this group. Likewise, differences in the communication behavior of species breeding in different locations may help to improve our understanding of the phylogeny of this group as well as some clues about potential mechanisms of diversification in the genus. The current

phylogeny of the species in the genus *Pterodroma* was developed by Imber in the 1980's and needs to be revised and updated with additional molecular and behavioral data.

My research investigates three aspects of vocal communication in *Pterodroma* petrels. In *Chapter 2*, I provide the first detailed investigation of sexual dimorphism and individual variation in the vocalization of a *Pterodroma* species – the Juan Fernandez Petrel *P. externa*. Though sexually monomorphic in plumage, sexually dimorphic vocalizations, have been found in most procellariid species studied to date (Brooke, 2004a; Bretagnolle, 1996; Warham, 1996). Individual variation, and individual recognition by voice have also been found in species throughout the family (Brooke, 1978b; Warham, 1990; Bretagnolle, 1996; Brooke, 2004a; Mackin, 2005; James, 1985b; James & Robertson, 1985b; James & Robertson, 1985a). That the acoustic signals of these petrels contains information about sex and individual identity is perhaps not surprising, given the nocturnal nature of many of these species, the number of different types of social interactions that occur at colony sites, and the high degree of cooperation that must be achieved between breeding pairs in order to successfully raise a chick each season. To date there has been no study of individual or sexual variation in the calls of any of the 32 or so petrel species in the genus *Pterodroma*, though evidence for sexual variation has been suggested in at least two *Pterodroma* species (Grant et al., 1983a; Tomkins & Milne, 1991). Here I provide the first detailed study of sexual dimorphism and individual variation in the vocalizations of a *Pterodroma* species – the Juan Fernandez Petrel *P. externa*, and present a measure of the amount of individual information in vocalizations produced at the nesting burrow. I also use the set of carefully measured calls from individual petrel and two multivariate analysis techniques (linear

discriminant function analysis, and probabilistic neural networks) to explore the challenges presented by any classification problem, including how classification rates are affected by the number of discriminatory variables available for classification, the number of exemplars used to define each category, the number of categories to be classified, and the variability of the signals within and among categories.

In *Chapter 3*, I describe the patterns of vocal behavior of two seabirds, the Juan Fernandez Petrel *Pterodroma externa* and Stejneger's Petrel *P. longirostris*, at a large colony on Isla Alejandro Selkirk, in the Juan Fernandez archipelago of Chile. I compare the timing of aerial activity for these two species in order to learn more about the factors that might influence activity patterns in seabirds. I evaluate whether variation in activity is correlated with moonlight, meteorological conditions, and the progression of the breeding season, and the presence of a diurnal avian predator. The nocturnal behavior of many seabird species is thought to have evolved in response to the presence of diurnal avian predators, and many species avoid breeding colonies in moonlight where these predators can hunt by moonlight (Watanuki, 1986b; Bretagnolle, 1990; Mousseot & Bretagnolle, 2000a; Mousseot & Bretagnolle, 2000b). In the absence of nocturnal predation pressure I predicted that there would be no relationship between vocal activity of the species breeding on Isla Alejandro Selkirk and the lunar cycle. Instead I present the unexpected results that both petrel species increase their activity in moonlight, and that both species have largely exclusive activity periods during the night, and then review possible explanations for these patterns.

Finally, in *Chapter 4* I compare the vocalizations of the *Cookilaria* petrels, 6 closely related species (and 1 sub-species) currently described as a subgenus within the *Pterodroma*. I present the first published descriptions of the vocalizations of two species in the group (Stejneger's Petrel *Pterodroma longirostris* and DeFilippi's Petrel *P. defilippiana*). I also measure and compare the features of the aerial calls from all taxa in the *Cookilaria* group in order to compare these homologous characters within the entire group.

Despite the similarity in the vocalizations in the *Cookilaria*, my observations show intriguing differences in the call features and vocal behavior at different breeding sites. Other studies of the vocalizations within procellariid species and between closely related species have found geographic variation. Given the important role that acoustic signals play in mediating reproductive behavior in the petrels, the emergence of variation in these signals could have important implications on the ability of individuals to disperse between colonies. Several factors may influence the development of geographic variation in these reproductive signals, including a environmental variables that can influence the potential costs and benefits of signals, signal preferences, and signaling strategies (*Reviewed in Chapter 1*). The islands on which the *Cookilaria* species breed differ in a number of environmental factors and in this final chapter I test whether there is evidence that 3 of these factors – predators, co-occurring species, and habitat, have influenced the evolution of communication behavior in these seabirds. The *Cookilaria* species provide a series of useful contrasts to compare the characteristics of calls of closely related species communicating in differing environments.

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CHAPTER 1

Biotic and abiotic constraints on acoustic communication – a review of behavioral adaptations to the signaling environment

ABSTRACT

Communication is an integral part of reproduction. Divergence in reproductive signals, signal preferences, and/or patterns of communication activity between populations could reduce the reproductive success of immigrants in novel environments. Behavioral changes may arise through the actions of mutation, genetic drift, natural selection and sexual selection. Historically, changes in breeding signals leading to reproductive isolation were thought to arise either as a byproduct of local adaptations related to resource acquisition, or as a result of natural selection against sterile or otherwise handicapped hybrid offspring. I review another potential avenue to the development of reproductive isolation: behavioral adaptations to the local signaling environment. In this scenario, reproductive signals and signaling behavior that increase detection and/or reduce the potential costs (in terms of reproductive success or survival) of communicating in a given environment would be favored by receivers. The natural world differs in physical (abiotic) and biological (biotic) characteristics that can constrain communication. Populations breeding in different areas may thus evolve reproductive signals, signal preferences, and activity patterns that are favored in that environment. Here I review research on the types of abiotic and biotic constraints to communication, discuss examples where animals signals seem to have adapted to local signaling constraints, and point to some limited evidence that such changes can lead to reproductive isolation. I conclude with suggestions for further research and present examples using several procellariiform species as a system in which these questions may be addressed.

INTRODUCTION

The mechanisms behind the formation of new species are still debated (Turelli et al., 2001; Coyne & Orr, 2004; Sawamura & Tomaru, 2002; Servedio & Noor, 2003; Doebeli et al., 2005; Losos & Glor, 2003; Rundle & Nosil, 2005; Orr & Smith, 1998; Price, 1998; McKinnon et al., 2004). Given the complexity of natural systems it not surprising that scientists still find it difficult to define what a species is (Boughman, 2001; Boughman et al., 2005; Nosil et al., 2002; Nosil, 2004; Christianson et al., 2005; Helbig et al., 2002; Biermann et al., 2004; Smith et al., 1997; Coyne & Orr, 1997; Gavrillets & Boake, 1998; Irwin & Price, 1999; Higashi et al., 1999; Irwin et al., 2001; Hochberg et al., 2003). It is generally agreed that a critical step towards speciation is the development of reproductive barriers that prevent (or limit) genetic exchange between different populations (Dobzhansky, 1937; Mayr, 1942; Mayr, 1963). There are likely many factors contributing to the development of reproductive barriers either before or after mating. Here I explore changes in reproductive communication that may arise as a result of environmental signaling constraints and whether or not these alone might lead to reproductive isolation.

In this paper, I review evidence that 1) local signaling constraints can lead to the divergence of signals and signal preferences, and 2) that locally adapted signals can lead to reproductive isolation among populations. I begin by summarizing the literature on the physical and biological characteristics of natural environments that can inhibit communication, or change the potential costs of communication. The effectiveness of a signal in eliciting an appropriate response from a receiver may be impaired by physical interactions in the environment (abiotic constraints) as well as a myriad of potential

interactions (such as predation or competition) with other organisms in the biological community (biotic constraints) (Wiley & Richards, 1982b). Changes (either plastic responses or genetic changes) that lead to improved, transmission, efficiency, and reliability under local conditions should be favored over less robust signals (Endler, 2000; Endler, 1992b; Endler & Basolo, 1998). Given the central role of communication in regulating reproductive interactions, such local adaptations may have obvious evolutionary implications (Boughman, 2002). Individuals using reproductive signals adapted to different environments may encounter problems recognizing suitable mates or interpreting important information about available mates. Individuals that have evolved to signal/monitor at specific times in one location may not find mates if local factors favor different signaling strategies in another location. Communication errors such as these might contribute to a reduction in genetic exchange between populations.

In this review, I focus primarily on acoustic signals, though the underlying principles are transferable to signals in any sensory modality (e.g. electrical, chemical, and visual signals). I review the research on abiotic communication constraints on acoustic communication in natural environments, as well as the smaller number of studies addressing biotic constraints to communication. I then summarize evidence that animal signals have adapted to mitigate the effects of local signaling constraints and experimental evidence that locally adapted signals can lead to reproductive isolation between populations adapted to differing signaling environments. Finally, I suggest that several seabird species offer opportunities to study the ways that communication behavior and reproductive signals might change in the face of novel signaling constraints and signaling costs.

A REVIEW OF ANIMAL COMMUNICATION

To better understand the challenges faced by organisms signaling in the natural world I will quickly review some of the basic principles of animal communication. Wiley (1994) defined communication as:

“Any alteration in a receiver produced by a signaler by means of a signal. A signal is defined as any pattern of energy or matter produced by an individual (signaler) and altering some property of another (the receiver) without providing the power to produce the entire response.”

Communication therefore involves the transfer of information between individuals through some medium (air, water, substrate) by means of a signal. Receivers may use this information to make decisions about their actions in a variety of contexts, including agonistic interactions (conflicts), cooperative interactions, and reproductive interactions (Endler, 1993b; Wiley, 1994). In many cases, signals reach multiple receivers, and communication occurs within a network of participants (McGregor & Dabelsteen, 1996). These networks can include conspecific individuals that eavesdrop on communication between other individuals (Peake et al., 2001), conspecific individuals interacting in complex social groups (Naguib, 2005), and predators or parasites that intercept signals from their prey or host (Mougeot & Bretagnolle, 2000a; Zuk & Kolluru, 1998; Endler, 1988; Arak, 1988; Donelson & van Staaden, 2005).

To accomplish the task of transmitting information between individuals, animals produce signals in a variety of sensory modalities including chemical, visual, acoustic,

electrical, and tactile signals. Consistent patterns of variation in the parameters that define these signals can encode a great deal of information about the signaler. In acoustic signals, for example, information may be encoded through consistent variations in the timing, frequency (pitch) and amplitude (intensity) of a sound. Variations in the parameters that define animal signals have been shown to encode *individual identity* (Hutchison et al., 1968; Moseley, 1979; Beecher, 1989; Bee & Gerhardt, 2002; Godard & Wiley, 1995; Bretagnolle, 1989; Mackin, 2005; Blumstein & Munos, 2005; Wiley, 2005; Falls, 1982), *sex* (Gerhardt & Huber, 2002; James, 1985b; Gerhardt, 1994), some aspects of *physical condition* (Genevois & Bretagnolle, 1994; Brandt & Greenfield, 2004) as well as numerous other biologically relevant types of information. At some point the variation in signal structure encoding one type of information may begin to interact with and mask the structural variation encoding other types of information. These limitations define the total variation of signal parameters within which the signaling system of any species may operate in *signal space* (Nelson & Marler, 1990).

An idealized depiction of how variation may be partitioned in the signals of a given species is depicted in *Figure 1.1a*. Though a receiver's sensory system is likely tuned to detect and process multiple signal parameters at the same time, I depict variation in only two hypothetical parameters (say frequency and timing) in the following examples for ease of explanation. The principles are similar for information encoded in multiple parameters.

Figure 1.1a, portrays the range of acoustic signal types (call types) produced by a hypothetical seabird species (A, B, C, & D). These calls might represent a warning call (A), a call used for mate recognition at the nest site (B), a call used in agonistic interactions (C),

and advertisement calls used in flight (D). The calls of ten hypothetical females (gray ovals) and ten hypothetical males (white ovals) are shown for each call type, highlighting typical variation within and among individuals. In some call types (B), individuals' calls do not overlap, and the sexes cluster into distinct groups based on the value of one parameter. Other call types may not have evolved to vary between individuals or sexes (A). Related species may produce signals that differ in these same parameters (*Figure 1.1b*) or that overlap considerably (*Figure 1.1c*).

The amount of information that can be encoded in a signal is only limited by the number of parameters that can be varied simultaneously without interfering with one another. In practice, signal production and reception are also constrained by anatomical and neurological limitations (Gerhardt & Huber, 2002; Podos et al., 2004a; Ryan & Brenowitz, 1985). In acoustic communication, body mass and the size of the sound producing organs have an effect on the frequencies that an organism can produce, namely small organisms (or individuals) cannot produce low frequency sounds (Bradbury & Vehrencamp, 1998; Ryan & Brenowitz, 1985). Neuro-muscular control may introduce limits on signal production (Podos, 1996). Morphological adaptations for one purpose, such as changes in beak size related to feeding ecology, may have repercussions on signal design when these structures are also used in signal production (Podos et al., 2004b). Signal reception is likewise limited by the design of signal reception organs and the neurological architecture of an organism. Receivers are usually highly sensitive to, though not always limited to, the properties used in intraspecific communication (Slabbekoorn & Ten Cate, 1998; Wilczynski et al., 1992; Wilczynski et al., 2001; Gerhardt & Huber, 2002). Thus, taxonomically related organisms

are more likely to produce signals in the same sensory modalities and with generally similar features because they employ homologous structures for signal production, reception and processing (Ryan et al., 2001). This does not however, preclude innovations nor does it imply that distantly related taxa will not employ similar signals.

One area of signal reception that has received a great deal of attention involves situations where the sensory systems used for resource acquisition and predator avoidance may become involved in intraspecific sexual communication, a process sometimes described as *sensory exploitation* (Proctor, 1991; Fleishman, 1992; Rodd et al., 2002; Basolo & Endler, 1995; Madden & Tanner, 2003; Basolo, 1990; Ryan et al., 1990). Similarly, species may retain sensitivity to features once present in ancestral signals but subsequently lost in the signals of derived taxa (*pre-existing biases* or *hidden preferences*), essentially taxonomic baggage (Basolo & Endler, 1995; Ryan, 1990; Arak & Enquist, 1993; Ryan & Rand, 1993). In both cases, though, novel reproductive signals that exploit these sensitivities should not be evolutionarily stable unless they are beneficial to the receiver (Bradbury & Vehrencamp, 2000). In the next section I will review how receivers might evolve criteria for responding or not responding to a perceived signal based on the costs and benefits of these actions.

Signal detection and classification

In order to be effective, a signal must elicit a response from a receiver. A receiver's sensory system must be able to first detect the presence of such a signal and then classify the signal based on the patterns of variation encoded in its structure. In the natural world, receivers may encounter a range of conspecific, heterospecific and environmental stimuli

with features that overlap with those used in their signaling system. How then do receivers evolve criteria for responding appropriately to different stimuli? One approach to studying this question is through signal detection theory (Green & Swets, 1966; Macmillan, 2005). Wiley and Richards (1982b) and Wiley (1994) pointed out the applicability of signal detection theory (SDT) to questions about animal communication. When a receiver is trying to detect a signal in the presence of background noise that overlaps with that signal, the receiver inevitably faces the possibility of committing an error. Faced with such a task, a receiver may react in four possible ways. It can either react appropriately when a signal is present (*correct detection*), overlook a signal and not react (*missed detection*), react when there is no signal present (*false alarm*), or not react when there is no signal present (*correct rejection*). Each of these different outcomes could have repercussions in terms of reproductive success, survival or some other similar measure (Wiley, 1994). Two of these outcomes may have potentially positive results (*correct detection and correct rejection*), and two may have potentially deleterious costs for the receiver (*missed detection and false alarm*). When a receiver is faced with detecting, and then discriminating between two kinds of signals (male/female, mate/stranger, etc.), there are nine possible outcomes, of which, only *correct detection* and *correct rejection* are positive outcomes (Wollerman & Wiley, 2002a; Wiley, 1994). This makes it unlikely that receivers can completely avoid the possibility of mistakes. Instead, receivers must employ criteria for responding to stimuli that optimize their decisions based on the costs or benefits associated with each possible outcome. This points out an interesting component of the evolutionary relationship between signalers and receivers. A positive outcome for a signaler depends in large part on whether a receiver reacts in the desired manner or not, as the receiver must provide all of the energy for such

responses (Wiley 1994). If the parameters of a signal fall outside those perceived by a receiver, or do not reach its criteria for response, it will be unlikely to elicit a successful outcome. Through these response criteria, then, receivers may cause directional or disruptive selection for signals whose features facilitate detection and discrimination and increase the probability of positive outcomes to costly errors (Bradbury & Vehrencamp, 2000; Wiley, 1994; West -Eberhard, 1983).

BIOTIC AND ABIOTIC CONSTRAINTS AND ANIMAL COMMUNICATION

Variation in signal parameters can have opposing roles in communication. Without variation in the parameters that define signal structure animals could not encode and transmit any information. Too much variation, and receivers may make costly errors. It is therefore of fundamental interest that interactions with the environment may introduce variation to a signal as it propagates from a signaler to a receiver. The energy in acoustic signals may be reflected, absorbed, masked, or otherwise degraded by physical and biological interactions. Habitats and biological communities differ in the qualities that constrain signal transmission. Given these challenges, do animal signals show evidence that they have adapted to mitigate the effects of these? Research has shown that that many signals have features that meet predictions based on local signaling constraints in multiple sensory modalities including electrical (Stoddard, 2002), visual (Endler, 1993a; Endler et al., 2005; Endler & Thery, 1996; McNaught & Owens, 2002), and chemical (Greenfield, 2002) signals. Though I concentrate on acoustic signals in this review, the principles are similar for other channels as well (Endler, 2000; Bradbury & Vehrencamp, 1998).

Abiotic Constraints

Wiley and Richards (1982b) give a detailed review of the physical factors influencing sound transmission in the natural world. They describe a number of abiotic processes by which the energy in an acoustic signal may be dissipated, or its structure altered as it spreads through the environment.

The intensity (amplitude) of a signal may be lessened (attenuated) through two processes known as spherical spreading and atmospheric absorption. Spherical spreading is related to the way that acoustic signals propagate through a medium (air or water). A sound is transmitted through air as pressure waves that propagate from a source as a sphere. As the area of this sphere grows, the initial energy of signal is distributed across its rapidly expanding surface area. At some distance, a signal's intensity will diminish to such an extent that it will equal that of ambient background noise (Brenowitz, 1982). Habitats differ in natural levels of background noise generated by wind, running water, precipitation or other properties (such as other animal signals) (Slabbekoorn, 2004; Morton, 1975; Wiley & Richards, 1982b; Marten & Marler, 1977). The energy in acoustic signals may also be absorbed by interactions with molecules in the atmosphere. This absorption is dependent on air temperature and relative humidity, but higher frequencies are attenuated by absorption under all atmospheric conditions.

A signal's structure may also be degraded by energy that is scattered by objects in its path (reverberations), or by the introduction of unpredictable amplitude fluctuations due to wind turbulence or reflections off of moving objects. The higher the frequency, the smaller

the wavelength, and the greater the chance it will encounter an obstruction. Energy deflected from an object travels a longer path to the receiver, and thus reverberations act to alter the timing pattern of a sound. In environments that contain many reflective surfaces, such as forests, the spaces between notes can be filled by reflected energy (echoes). Receivers would likely perceive signals with rapidly repeated elements of the same frequency as a continuous sound, and not receive any information encoded in the timing between notes. Low frequencies will encounter less reverberation. Neither reverberations nor amplitude fluctuations alter the frequency parameters of a signal in biologically meaningful ways. This implies that encoding information through frequency modulations and using low frequencies is the most reliable method for communicating over long distances.

Morton (1975) was one of the first to compare animal signals to the acoustic properties of the different habitats they inhabited. He played signals of varying frequencies through different habitat types (forest, grassland, and edge) and measured frequency attenuation at different distances. He observed what he described as a “sound window” in neotropical forests, where signals with frequencies between 1.5 and 2.5 kHz had lower attenuation rates than signals below or above this range. Grassland did not exhibit this same property. Based on this finding, he predicted that the songs of birds from neotropical forests would fall within this frequency range. In fact, the mean frequency (2.2 ± 1.0 kHz) of the species he measured fell in the middle of the range of the hypothetical sound window. In contrast, local grassland species, on average, used higher frequency signals than forest birds.

On the face of it, this result seems puzzling. Based on abiotic signaling constraints one would predict that low frequency signals should propagate better than in both habitats. One possibility could be that forest birds are larger, and could thus produce lower frequency sounds. Ryan and Brenowitz (1985) tested whether differences body size and taxonomic relationship might account for the observed differences in song frequency between the species in Morton's study. They found that the forest birds tended to be larger than the grassland birds, but when they controlled for body size and phylogeny, they still found a statistically significant trend for lower frequencies in the songs of forest birds. The important signaling constraint, it seems, was not related to habitat structure, body size or phylogeny, but rather to the signaling behavior of the species being studied. Many of the neotropical species measured for the original study were species that called on or near the ground. Boundary interference can influence signals within 1-2 m of the ground and would likely render any signals above 2 kHz useless for long-range communication (Wiley & Richards, 1982b). Thus, it is likely that neotropical forest birds use low frequency signals because they call near the ground, not because they are avoiding increased scattering in forests.

Are there predictable differences in animal signals related to these habitats? One consistent difference between the structure of acoustic signals of birds in open habitat compared to those in closed habitat is the spacing of elements in these signals (Wiley, 1991; Morton, 1975; Brown & Handford, 2000). In habitat with many reflective surfaces, reverberations obscure information encoded in the time domain through echoes. To avoid this, many forest species increase the time delay between song elements of equal frequency, or encode information in the frequency domain.

In open habitat, air turbulence and sound shadows are the primary constraint rather than reverberation. Air turbulence can result in intermittent and unpredictable signal loss during transmission due to amplitude fluctuations. Sound shadows affect communication near the ground at times when air temperatures differ above the ground. Many birds in open habitat use songs with rapidly repeated short elements, sung from a high perch. These changes may increase detection by receivers. The redundancy of the repeated short signal elements ensure information transfer despite the loss or degradation of portions of the song, and perch height decreases the effects of sound shadows. These differences have been confirmed using experimental signals (Brown & Handford, 2000; Brown & Handford, 1996), and are supported by correlative evidence from broad scale surveys of avifauna (Sorjonen, 1986; Wiley, 1991; Morton, 1975; Blumenstein & Turner, 2005; Saunders & Slotow, 2004) as well as within a species or species complexes (Shy & Morton, 1986; Handford & Loughheed, 1991; Tubaro & Segura, 1995).

Perch height can be an important component of animal signaling for both signalers and receivers in many habitats (Marten & Marler, 1977; Arak & Eiriksson, 1992; Mathevon et al., 2005; Dabelsteen et al., 1993; Parris, 2002). One study found that the songs of several neotropical antbird species were adapted to the acoustic characteristics in forests at specific perch heights (Nemeth et al., 2001). The time when one calls can also affect signal transmission. Some animals may signal at times when they can avoid the effects of air turbulence and sound shadows. Dawn choruses in birds may be an adaptation to the

relatively calm atmospheric conditions in the morning as well as beneficial changes in sound shadows due to morning temperatures (Brown & Handford, 2003; Wiley & Richards, 1982b)

In some interesting cases, organisms may actually use these physical constraints to their advantage. For example, several species may be able to assess the distance to a signaler (known as ranging) based on the reverberation in specific song features (Holland et al., 1998; Naguib & Wiley, 2001; Morton et al., 1986; Slabbekoorn et al., 2002; Richards, 1981; McGregor & Krebs, 1984). Carolina Wrens (*Thryothorus ludovicianus*) can even change their distance estimates based on seasonal changes in acoustic constraints, the presence and absence of leaves on the trees in their territory (Naguib, 1996).

Finally, any noise source may mask a signal or change its detectability (Wiley, 1991; Ryan & Brenowitz, 1985). Klump (1996) lists a number of signaling adaptations that might be predicted to arise in species communicating in areas with high levels of background noise. First, signals that include energy distributed through multiple frequencies may ensure that some part of the signal is outside the range masked by background noise. Organisms may also exploit temporal patterns in background noise, and signal at times when masking noise levels are at a minimum. Finally, signals and signal detection systems that facilitate localization of a sound source may help receivers differentiate signals from background noise. Repeated elements may aid receivers to localize signals, and abrupt changes in amplitude may help to increase detection (Wiley 1982).

Background noise is most challenging when its spectro-temporal properties match those of the signals used for communication (Lohr et al., 2003; Klump, 1996). Many bird

species can adjust their song amplitude to match increases in the amplitude of background noise and maintain a consistent active space for their signal, known as the Lombard effect (Brumm, 2004; Pytte et al., 2003). Slabbekoorn and Peet (2003) found that Great Tits (*Parus major*) in the Dutch city of Leiden compensate for differing background levels of urban noise. Birds with territories that had consistently loud, low-frequency urban noise used songs with higher minimum frequencies than those breeding in more quiet sections of the city. The authors hypothesized that these birds learned to sing songs that would be effective under local noise conditions. In Africa, the songs used by Little Greenbulbs (*Andropadus virens*) differ by habitat. In the forest populations, individuals use low frequencies that are not used by individuals breeding in the savannah/forest ecotone (Slabbekoorn & Smith, 2002; Slabbekoorn, 2004). Background levels of low-frequency noise are more prevalent in the savannah/forest ecotone and may mask the low frequency calls used by forest birds. Finally, similar frequency changes seem to have occurred in the signals used in a group of related warblers found in Asia. Two closely related species that breeding in different habitat types, *Phylloscopus borealoides* and *P. tenellipes*, have songs that differ considerably in their spectral qualities despite general morphological similarities between the species. The spectral qualities of the song of *P. borealoides*, in turn, are more similar to those of a distantly related species, *P. magnirostris*. As it happens, the later two species are found near fast running streams and use high frequency tonal songs that may improve transmission by reducing masking interference from the low frequency noise generated by the rushing water (Martens, 1996).

Biotic constraints

Less work has been carried out on the diverse ways in which biological interactions may constrain communication. Obviously, many of the abiotic factors described above (such as scattering) involve physical interactions of signals with living organisms, namely the plant community. Less well studied, though, are the interactions between the network of individuals in a given biological community. A prime example of a biotic constraint to communication is increased background noise due to multiple signalers. In some tropical forests, insects, frogs, mammals and birds may all be communicating with acoustic signals at the same time.

One way that individuals or species may avoid masking by background noise is to signal when masking noise is at a minimum. Species might call at different times of the day, or individuals of a given species might alternate signaling in order to avoid interference (Ficken et al., 1974; Luther, 2008). Similarly, species can use signals and signaling behavior (such as signaling location) that reduce masking (Sueur, 2002). Or, one can cease signaling all together. In frogs and crickets, for example, satellite males may approach signaling males in an attempt to mate with any females attracted by the signaling male (Arak, 1988; Donelson & van Staaden, 2005).

Background noise is especially acute where many individuals gather to call, such as in leks, choruses, or breeding colonies (Wollerman & Wiley, 2002a; Cooley & Marshall, 2004; Aubin & Jouventin, 2002b). These gatherings can include staggering numbers of individuals. For examples, in some seabird colonies tens of thousands of individuals of the

same species are calling in the same area at the same time (Robisson et al., 1993). In these situations, background noise coupled with similar conspecific or heterospecific signals may lead to increased errors by receivers. The noise in these areas will have similar amplitude, timing and frequency values to the those of an individual's own signals, a phenomenon known as the "cocktail-party effect" (Cherry, 1966). Penguins, for example, may congregate in colonies of several hundred thousand individuals during the breeding season. Individuals recognize their mate and offspring based on nest site location and voice or, in some species, by voice and general location. These calls of these species contain a wide range of frequencies (generated as harmonic overtones) and have abrupt changes in amplitude, features that are predicted to increase detection in noisy environments. Individual information is encoded in the frequency values and relative intensities of the harmonic bands each call (Aubin & Jouventin, 2002a; Jouventin & Aubin, 2002). The calls of non-nesting species, such as the Emperor Penguin (*Aptenodytes forsteri*), are more complex than those of nesting species, reflecting the increased complexity of recognizing kin without the aid of additional cues (Searby et al., 2004).

Background noise at frog choruses in Central America hint that not all species can rely on complex coding schemes for discrimination between individuals. Laboratory studies have shown that female frogs often have preferences for conspecific signals based on its frequency and timing parameters (Gerhardt, 1994). In the natural world, though, such discrimination between signals may be very challenging. Female *Hyla ebreccata* (a species of tree frog) face considerable difficulty even detecting a signal in natural levels of background noise from the breeding chorus (Wollerman, 1999). It was estimated that from

any given location in the chorus, a female frog might only be able to detect one male when males were not aggregated. In this situation, females would need to move about the chorus in order to sample the calls of several males, thereby increasing energy expenditure and the increasing the risk of predation. Most interestingly, it seems that preferences between males with low frequency calls are lost when the receiver is faced with detecting and discriminating between call types (Wollerman & Wiley, 2002a). These results raise questions about effective signaling and mate choice strategies in natural situations, and how these may change among choruses with differing densities and species compositions.

Communication errors can also arise as a result of another kind of background noise: the signals of closely related taxa. In this case, a receiver may have a higher probability for committing an error when both species use similar signals that fall within the receiver's threshold for response (or contain features that tap hidden preferences) (Ryan et al., 2001). Where such crosses result in infertile or unviable offspring, they represent a costly communication error. In such cases, natural selection against hybrids (*reinforcement*) might lead to changes in reproductive signals and signal preferences in order to avoid such crosses (*reproductive character displacement*) (Dobzhansky, 1940; Noor, 1995a). Specifically, a receiver might be expected to evolve strict criteria for response that reduce the probability of false alarms (hybridizations) and consequently increase the number of missed detections (opportunities to mate with conspecifics). Pfennig (2000) found differences in female signal preferences in southern spadefoot toads (*Spea multiplicata*) between populations that bred in pools that contained only conspecific males and female signal preferences in ponds that contained heterospecific males of a similar species, the plains spadefoot toad (*Spea*

bombifrons) or not. Though the calls of these two species are distinct, variation in calling rates of both species overlap. Female *S. multiplicata* prefer male calls with fast call rates in areas without heterospecific males. Females mating with males with these preferred calls were found to result in a greater number of fertilized eggs. In areas of sympatry (where both species overlap in the same pond), female *S. multiplicata* preferred conspecific calling rates near the population mean, since conspecific males with fast call rates overlapped with the call rates of *S. bombifrons* calls. In this case, then, there is evidence for reproductive character displacement in female breeding behavior between habitats based on the community composition at different ponds. Thus females are choosing to have reduced fertility in order to avoid hybridization. For the purposes of this review, this result is also interesting in terms of the ramifications such changes might have when immigrant individuals from different *S. multiplicata* populations (those breeding in sympatry with *S. bombifrons*, and those not) meet in a new pond. Would females from sympatric sites retain the preference for the median call rates, or would they regain the preference for the high call rates preferred by females in ponds with little risk of hybridization?

Interspecific competition can create conditions that can also favor changes in signal structure. Males from closely related species may respond aggressively to heterospecific territorial signals that are similar in structure to those of conspecific signals. Great Tits (*Parus major*) have been shown to respond as aggressively to some Blue Tit (*Parus caeruleus*) calls as they do to conspecific calls (Doutrelant et al., 2000). Aggressive reactions were reduced, however, for Blue Tit calls that ended in a terminal trill (a feature not found in Great Tit songs). Subsequent study of tit populations in Europe, Africa, Corsica and

the Canary Islands found a significant correlation between the prevalence of Blue Tit calls incorporating a terminal trill and the relative density of Great Tits (Doutrelant & Lambrechts, 2001). In areas with low densities of Great Tits, the prevalence of the use of the terminal trill declined in Blue Tits, evidence that supports the hypothesis that interspecific competition may lead to changes in signal structure. How females might develop preferences for such territorial calls has not been explored, though males facing reduced confrontation could have obvious advantages, in terms of the time and energy that they could devote to reproductive behavior. Release from interspecific and intraspecific competition has been suggested as one factor contributing to signal differences in populations isolated on islands (Espmark, 1999; Naugler & Ratcliffe, 1994).

Finally, two other components of the biological community may conceivably impact signal design and communication behavior, though in ways that differ from other abiotic or biotic constraints described above. Predators and parasites in the biological community can change the potential costs associated with signaling and responding to signals (Endler, 1988; Zuk & Kolluru, 1998; Mougeot & Bretagnolle, 2000a; Zuk, 1994). In order to reduce the risks from these threats signals may evolve to reduce detectability (Bayly & Evans, 2003) or receivers may become more weary (Acharya & McNeil, 1998). Signalers and receivers may also change the timing or location of reproductive communication, such as the evolution of nocturnal activity and moonlight avoidance in many seabirds (Mougeot & Bretagnolle, 2000a; Mougeot & Bretagnolle, 2000b; McNeil et al., 1993).

DO LOCALLY ADAPTED SIGNALS LEAD TO REPRODUCTIVE ISOLATION?

The idea that reproductive isolation can evolve as a direct result of locally adapted reproductive signals is slightly controversial. Traditionally, sexual signals were thought to play a secondary role in the speciation process, changing arbitrarily through mutation or genetic drift, or as a consequence of other adaptations arising in geographically isolated (allopatric) populations (Dobzhansky, 1937). Changes in reproductive signals might also be favored through natural selection against unviable or infertile hybrid offspring. This “reinforcement” of the isolation that existed between populations before they came into secondary contact should be seen in reproductive signals in zones of overlap (reproductive character displacement), but not in areas of allopatry. There is theoretical (Servedio, 2004; Servedio & Noor, 2003; Sadedin & Littlejohn, 2003; Noor, 1999; Coyne & Orr, 1989) and empirical (Pfennig, 2003; Gabor & Ryan, 2001; Saetre et al., 1997; Noor, 1995b; Hobel & Gerhardt, 2003) evidence for reinforcement and character displacement.

There is also theoretical support for the development of reproductive isolation through sexual selection alone (Servedio, 2001; Lande, 1981). Assortative mating may arise in some circumstances without the requirement of post-mating genetic incompatibilities (Higashi et al., 1999; Dieckmann & Doebeli, 1999; Kondrashov & Shpak, 1998; West - Eberhard, 1983; Panhuis et al., 2001; Gray, 2005; Gray & Cade, 2000; Lande, 1982). This is possible when the trait under sexual selection is itself advantageous, or when it is linked genetically to other beneficial alleles. A change in a reproductive signal or in signaling behavior which increases detectability and discriminability under local conditions could allow receivers to reduce the probability of errors, and would be advantageous. As discussed

in the previous sections, advantageous adaptations may differ between environments. Populations inhabiting different environments may then evolve to meet different optima.

Studies of the evolution of reproductive isolation are difficult to conduct, especially with wild populations. These need to incorporate information about the biology, life history, ecology and evolutionary history of the species involved. A two-step process is required in order to investigate whether locally adapted reproductive signals can lead to reproductive isolation. First, differences in reproductive signals or behavior must be shown to be adaptive in terms of local environmental signaling constraints. Not all differences in signals represent adaptive solutions to the local challenges (Nemeth et al., 2001; Reeve & Sherman, 1993), and animals need not evolve signals that meet theoretical maximums for performance.

Communication signals are often optimized based on a variety of differing costs and benefits to the signaler and receiver (Nemeth et al., 2001; Lemon et al., 1981; Wiley & Richards, 1982b). Finally, plasticity in communication behavior may complicate the link between local signals and genetic isolation. In the 1970's, for example, interest in the potential role of signal variation in sexual isolation was aroused by the description of stable song dialects in White-crowned Sparrows (*Zonotrichia leucophrys*) in the northwestern U.S. (Baptista, 1975; Baptista & King, 1980; Harbison et al., 1999; MacDougall-Shackleton & MacDougall-Shackleton, 2001; Tomback & Baker, 1984). In a related species, dialects were found that showed evidence of adaptations to local signaling constraints (Handford & Loughheed, 1991; Nottebohm, 1975). Female preference for males singing the local song dialect seemed like an excellent mechanism for genetic isolation through cultural inheritance and sexual selection (Baker, 1975). A recent comprehensive study by Soha (2004), however, found no

evidence for genetic differentiation (using microsatellites from nuclear DNA) between White-crowned sparrows from areas with different song dialects. Song learning, it seems, allows both gene-flow and dialect retention.

When adaptive differences in sexual signals have been established, mate choice experiments may be carried out to determine levels of reproductive isolation related to these changes. Most research on reproductive isolation involves mate choice tests in the lab, or in a controlled area in the field (Hill, 1994; Saetre et al., 1997; Gabor & Ryan, 2001; Rundle & Schluter, 1998; Scott, 2004; Miller et al., 1998; Ryan & Rand, 2003; Gray, 2005). These tests may be impractical to carry out for some organisms. A receiver's actions during such experiments may be difficult to interpret given the difficulty of distinguishing between the many potential outcomes possible when tests involve both detection and discrimination between two types of signals (Wollerman & Wiley, 2002a).

In her 2002 review, Boughman provides several other examples of research related to the development of reproductive isolation due to locally adapted signals, including her work on visual signals in three-spine sticklebacks (*Gasterosteus spp.*). Some additional research related to this topic is shown in *Table 1.1*. Many studies cover only one aspect of topic: either reporting adaptive changes in communication behavior or showing the evolution of reproductive isolation without exploring the mechanisms behind such changes. Future studies should seek to address both types.

One study that addresses both the evolution of locally adapted signals and how these contribute to reproductive isolation between two sub-species of the Song Sparrow (*Melospiza melodia*) (Patten et al., 2004). They meet in a hybrid zone in southern California where *M. m. heermanni* occupies dense habitat with larger trees, while *M. m. fallax* inhabits more open habitat. The acoustic characteristic of their songs diverge in ways that fit predictions based on habitat characteristics, namely that *M. m. heermanni* has more widely spaced notes than *M. m. fallax* (which may help to avoid some effects of reverberation in their denser habitat). In mate choice tests, females of both subspecies responded weakly to heterospecific song, even when these were presented in concert with a model of a conspecific male. These two subspecies are thought to have evolved in isolated glacial refugia, and this study seems to implicate habitat specific changes to sexual signals in the development of reproductive isolation. Some question still remains, though, whether reproductive isolation developed as a direct result of signal changes, or in concert with other adaptations. More research should investigate whether the other sub-species in this group show similar behavioral adaptations, and the potentially confounding role of song learning should also be considered.

CONCLUSION

In conclusion, animals communicating in natural environments face a range of biotic and abiotic constraints that may reduce transmission and reception of signals, and change the potential costs and benefits of these interactions. Receivers should favor signals and communication behaviors that increase detectability under local signaling constraints. Indeed, many animal populations show evidence that they have signals adapted to local biotic

and abiotic signaling constraints. Local changes in the signals that mediate reproductive behavior might lead to reproductive isolation among populations inhabiting locations that impose different signaling constraints. There is evidence that predation, habitat structure, and co-occurring species communicating in the same channels have influenced signals and communication behavior differently among geographically isolated populations. More research is needed to learn how plastic these local behavioral changes are in different species, and to determine the relative importance of the various categories of communication constraints on adaptation in reproductive signals.

I end by highlighting a group of organisms that offers a number of opportunities for continuing research in this area: the order Procellariiformes. The order procellariiforms (the albatrosses, petrels, shearwaters, and similar) are a monophyletic taxon of seabirds, many of which are nocturnal at their breeding sites and rely primarily on acoustic signals for reproductive communication. These wide ranging species breed on isolated islands around the world. A good deal is known about the communication behavior of these birds (Bretagnolle, 1989; Bretagnolle & Robisson, 1991; Genevois & Bretagnolle, 1994; Bretagnolle, 1996; Mougeot & Bretagnolle, 2000a; James, 1985b). Most importantly, the family presents opportunities to study communication in species with innate (not learned) reproductive behavior under a wide variety of signaling constraints. This includes factors such as differing levels of background noise (con-specific, hetero-specific, and abiotic), differing habitat structures, co-occurrence of related species that produce similar reproductive signals, and the presence of a variety of different types of predators. Species (and different populations of species) sometimes breed on colonies that differ in one or more

of these factors (*Table 1.2*). There are a number of potential research opportunities for comparative study, and for experimental tests. Though it is often difficult to access the breeding sites of these species, many long-term studies are being conducted on a number of important seabird islands. Recording equipment is now light-weight and relatively inexpensive, making it easy to ship equipment to potential collaborators working in out-of-the-way places, and opening a range of opportunities for investigating locally adapted communication behavior.

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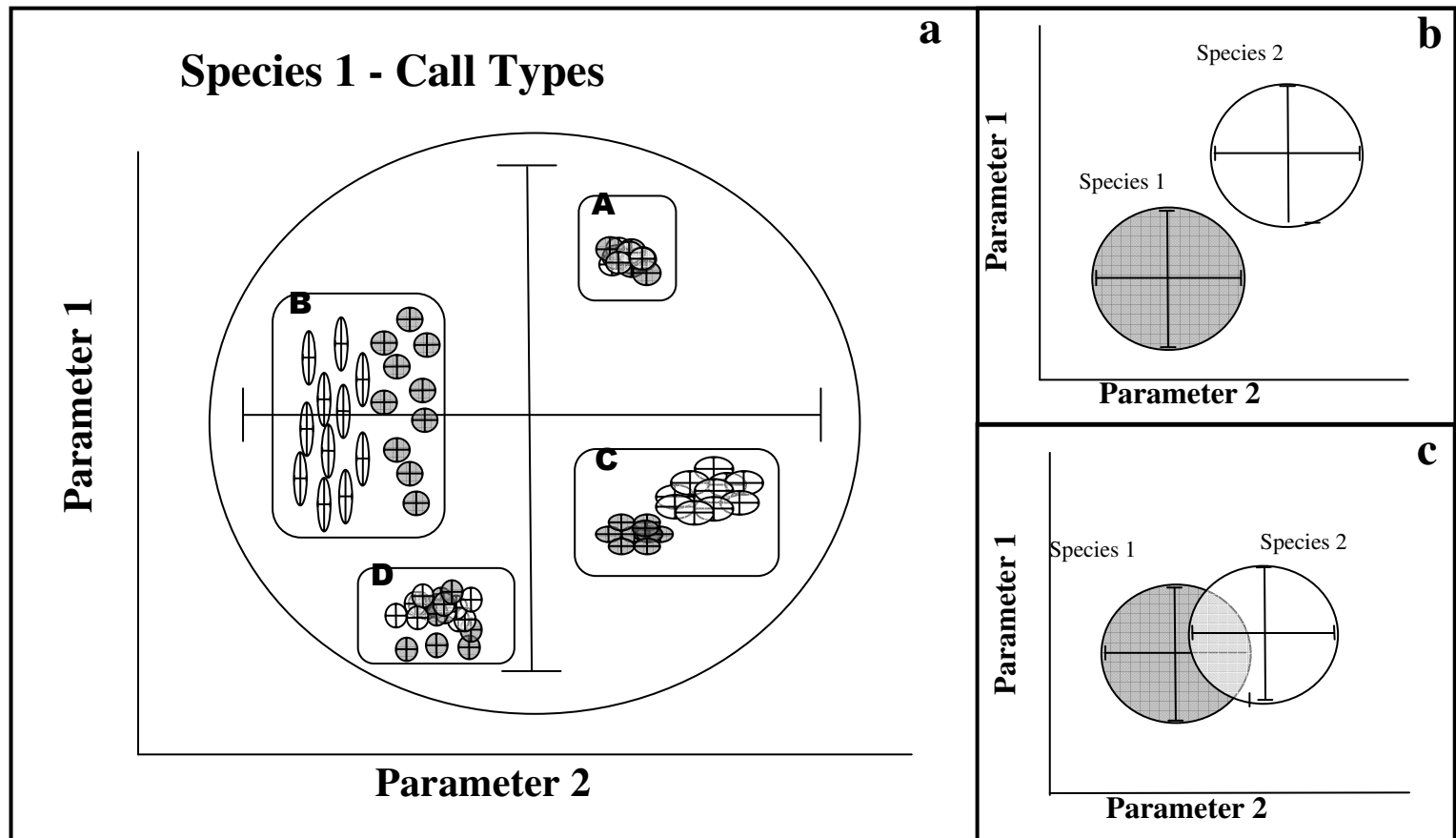
Table 1.1 Recent studies of breeding signal variation and reproductive isolation

<i>Species</i>	<i>Question</i>	<i>Signal adaptation to</i>			<i>Reference</i>
		<i>Abiotic const.</i>	<i>Biotic const.</i>	<i>Rep. Isolation ?</i>	
Field cricket calls <i>Gryllus texensis</i> & <i>Gryllus rubens</i>	Did pops. historically encounter differences in signaling environment?	?	?	Yes	(Gray & Cade, 2000; Fitzpatrick & Gray, 2001)
Fruit fly “song” <i>Drosophilla willistoni</i>	Do pops face differences in signaling env.?	?	?	Yes	(Gleason & Ritchie, 1998; Gleason, 2005)
Little Greenbul song <i>Andropadus virens</i>	Pops. in forest vs. ecotone habitat	Yes	?	?	(Slabbekoorn & Smith, 2002)
Anolis lizard dewlap <i>Anolis cristatellus</i>	Pops. from habitats differing in light intensity	Yes	?	?	(Leal & Fleishman, 2004)
Song Sparrow song <i>Melospiza melodia heermani</i> & <i>Melospiza m. fallax</i>	Pops. from forest vs. riparian habitat	Yes	?	Yes	(Patten et al., 2004)
Madeiran Storm Petrel calls <i>Oceanodroma castro</i>	Pops. breeding in the same location at different times of the year	?	?	Yes	(Smith & Friesen, 2007; Bolton, 2007)

Table 1.2 Examples of petrel species, sub species, and populations breeding in areas with differing signaling constraints

<i>Taxonomic comparison</i>	<i>Species</i>	<i>Colony</i>	<i>Breed. Hab.</i>	<i>Pop. Density</i>	<i>Other seabird sp.</i>	<i>Predator</i>
The Cookilaria Subgenus	<i>Pterodroma cookii</i>	Little Barrier Is. (Summer)	Forest	Medium	2, low density	Diurnal
	<i>P. defilippiana</i>	Santa Clara, Chile (Winter)	Boulder fields	Low	None	Nocturnal
	<i>P. longirostris</i>	Alejandro Selkirk, Chile (Summer)	Grassy ridgeline	High	1, high density	Diurnal
	<i>P. pycrofti</i>	Lady Alice I., NZ (Summer)	Forest	Medium	1, med. density	Diurnal
Shearwater Sister Species	<i>Puffinus creatopus</i>	Santa Clara, & Robinson Crusoe, Chile	Rock slope	Medium	2, low density	No
	<i>Puffinus creatopus</i>	Isla Mocha, Chile	Forest	High	None	?
	<i>Puffinus carneipes</i>	Lady Alice I., NZ	Forest	Medium	1, low density	?
Snow Petrel sub-sp. Secondary contact	<i>Pagodroma nivea major</i>	Sympatric & allopatric Pops., Antarctica	Rocky outcrops	-	-	Yes?
	<i>P. n. minor</i>					Yes?
Seasonal Pops	<i>Oceanodroma castro</i>	Winter – Azores	-	High	None	?
	<i>Oceanodroma castro</i>	Summer – Azores	-	Low	None	?

Figure 1.1 A representation of how the signals of individuals within species may encode information through patterns of variation in signal parameters, and the kinds of interactions that may occur as individuals and species compete for signal space



CHAPTER 2

Individual and sexual variation in the burrow calls of the Juan Fernandez Petrel *Pterodroma externa*

ABSTRACT

Recognition of individuals is an important component of many social interactions in animals. Individual variation in signals used in communication and individual recognition based on this variation has been reported for many organisms. Colonial seabirds often have individually distinctive calls that are known to identify the sex of the caller and to allow individual recognition of mates, young, and neighbors within their crowded colonies, but no previous study has investigated variation in the calls of petrels in the speciose genus *Pterodroma*. These birds breed in large colonies on remote oceanic islands and are highly pelagic when away from colonies. To assess sexual and individual variation in the calls of Juan Fernandez Petrels *Pterodroma externa*, I measured 12 features of calls made from the breeding burrow by marked birds in the large mixed species colony on Isla Alejandro Selkirk, Chile. Burrow calls were found to be sexually dimorphic, as confirmed by molecular tests of sex. Six measures varied significantly among individuals ($F_{9,10} > 16.88$, $p < 0.001$), and all 12 measures contained a total of 3.06 bits of individual information. Two multivariate classification techniques, linear discriminant function analysis and probabilistic neural networks correctly classified 77% and 71% of the calls from 14 individuals respectively. Correct classification rates generally improved as more explanatory variables were included in the analysis, but variables with high levels of information increased classification rates more than did randomly selected variables. Both classification techniques made more errors when classifying greater numbers of individuals and when fewer examples were used to train the classification functions. Different combinations of individuals led to different error rates, an indication that some individuals were more difficult to classify than others with these procedures. Finally, calls grouped into non-equivalent categories of individuals (mate, neighbors, strangers) were classified at rates better than that expected by chance. These results illustrate fundamental issues faced by receivers when discriminating between signals for discrimination between individuals or categories of individuals.

INTRODUCTION

Behavioral interactions such as courtship, cooperation among mates, territory defense, and recognition of young are mediated by communication between individuals. Important information for these interactions (such as species, sex, and identity) can be conveyed by signals in various sensory modalities (visual, olfactory, auditory, electrical or tactile) (Bradbury & Vehrencamp, 1998). Interactions that involve the recognition of individuals (mate recognition, tit-for-tat cooperation, chick provisioning, nest defense) require signals that vary predictably among individuals (Halliday, 1983; Falls, 1982; Beer, 1970).

Measurements of the variation in signals within and among individuals can therefore be used to calculate the amount of information available for recognition of individual or categories of individuals. Based on the theory developed by Shannon and Weaver (1949), information is measured by the number of binary choices allowed by a signal. A signal with one unit of information allows a choice between two equally probable options. Thus, information is measured in binary units or bits. Haldane and Spurway (1954) present a clear explanation of the relationship between bits of information in the waggle dance of honeybees *Apis mellifera* and the precision of directional cues in the dance. A hypothetical waggle dance that could only indicate food sources either in more northern or more southern directions from the hive would contain one bit of information, enough information for one binary choice. If the dance could also indicate more eastern or more western directions, it would contain 2 bits of information about direction, enough for bees observing the dance to

visit one of four equally probable compass quadrants. Based on variability in the dance, Haldane and Spurway calculated that the waggle dance contained enough information to designate any of 32 equivalent categories of direction (5 bits), equivalent to the compass headings North, North by East, North-North-East, North-east by North, etc., each indicating a sector of 11.25 degrees.

Measures of the information available for the recognition of other categories of equivalent elements can also be estimated. For example, acoustic signals with 5 bits of information about the individuals producing them would theoretically allow recognition of 32 individuals on average. The more the calls of each individual vary in relation to overall variation in the group, the fewer individuals can be recognized, on average. Individual information in signals has been reported in a variety of organisms and different sensory modalities (Falls, 1982; Sherman, 1997; Bradbury & Vehrencamp, 1998).

Careful study of the variation in signals of different species can help to clarify adaptations for communicating in different environments and the possibilities and consequences of errors in communication. Measures of information in signals can be used to test predictions about signal design in species that differ in life histories or that breed under different ecological conditions. For example, differences in the amount of information in the calls of nestling swallows correspond to differences in the recognition tasks faced by parents. The most colonial species, Bank Swallows *Riparia riparia* (nestling calls with 17.0 bits of information about individual identity), must recognize their young among hundreds of chicks in a colony. In contrast, Rough-winged Swallows *Stelgidopteryx ruficollis* (3.2 bits) nest solitarily and thus have no nearby nests to create confusion (Beecher 1982).

In some cases, it might be sufficient to distinguish between categories of individuals rather than between each individual. For example, Beecher (1989) suggested that instead of discriminating between hundreds of individuals when searching for their chicks, swallows might only distinguish between two categories “my chicks” and “all others.” Such a binary classification between categories might also suffice for animals defending territories. A male songbird, for example, might benefit from distinguishing between (and reacting differently to) the songs of strange and neighboring males (Fisher, 1954; Ydenberg et al., 1988; Godard, 1993). In addition, it must often be advantageous for individuals to distinguish between signals from males and females, even when individuals of each sex are not recognized. There is, however, no fundamental difference between distinguishing individuals and distinguishing categories of individuals. The calls or other signals produced by one individual are themselves just one category of signals. In all cases, if some categories are more variable than others (some individuals have more variable calls or some groups include more individuals than others), the estimate of the bits of information in the signals represents an average over multiple categories.

Petrels and their relatives have provided good subjects for studying many of these issues in communication. They form long-term pair bonds in which both sexes cooperate to incubate the egg and provision the chick each year. Breeding pairs re-establish pair bonds at the beginning of each breeding season, coordinate multiple incubation shifts with their breeding partner, defend their burrow against other individuals, and cooperate in gathering resources for their chick. Some return to a nest to feed their chicks, while others must find

their young among crèches of similarly aged chicks. Individual recognition is a basic component of these social interactions (Beer, 1970; Falls, 1982; Halliday, 1983; Bretagnolle, 1996).

Furthermore, the properties of individual recognition differ between species. In many procellariiform seabirds courting pairs, breeding partners, and territorial rivals calls at their underground nesting burrows. In these species, experiments have demonstrated that birds can recognize males and females, mates, and neighbors (Brooke, 1978b; Warham, 1990; Bretagnolle, 1996; Brooke, 2004a; Mackin, 2005). So far, however, there have been no studies of individual or sexual variation in the calls of any of the 32 or so species in the genus *Pterodroma*, aside from some suggestions of sexual variation in two species (Grant et al., 1983a; Tomkins & Milne, 1991). This speciose genus is remarkable for its highly pelagic distribution when feeding and its prolonged breeding cycles in dense colonies on isolated oceanic islands (Warham, 1996; Warham, 1990; Brooke, 2004a).

In this study I measure variation in the calls of the Juan Fernandez Petrel *Pterodroma externa* (JFPE), a petrel that nests in a large breeding colony that contains hundreds of thousands of individuals of 2 different *Pterodroma* species (Brooke, 1987). I focus on calls used at the nest site in order to measure variation from known individuals over multiple time scales. Previous research and my observations indicate the importance of these calls for communication between mates and the defense of burrows. I show that JFPE have sexually dimorphic burrow calls that meet predictions based on previous studies of sexual dimorphism in other petrels. I also measure variation within and among calls from 10 male JFPE in order

to measure the information in these signals. I then compare the accuracy of two multivariate techniques, linear discriminant analysis (LDA) and non-linear probabilistic neural networks (PNN), for classifying individuals based on the features of these calls, and show that features with the highest information content improve classification over randomly selected variables. Finally, I use PNNs to simulate classification tasks that involve distinguishing between non-equivalent categories, such as burrow calls from a hypothetical mate (one individual), hypothetical neighbors (~ 4-8 individuals), or unknown petrels (potentially thousands of individuals). Although neither multivariate analysis method closely resembles the neural processing of signals by a bird, analysis of real petrel calls with these procedures identifies some of the fundamental issues faced by all receivers.

METHODS

STUDY SITE AND STUDY SPECIES

The field work for this study was carried out on Isla Alejandro Selkirk (Lat. 33° 45' S, Long. 80° 45' W) in Chile's Juan Fernández Archipelago (*Figure 2.1*). Located 880 km west of Valparaíso, Chile, Alejandro Selkirk is an isolated island with only a seasonal human settlement. It is the only known breeding site for the Juan Fernandez Petrel. All of the recordings and observations for this study were made at the primary breeding colony for this species on Inocentes Bajos Ridge, 1200 m above sea level on the southwestern side of the island (*Figure 2.2*). This colony includes an estimated 1 million breeding pairs of Juan Fernandez Petrels and 131,000 breeding pairs of Stejneger's Petrel (*Pterodroma longirostris*), another endemic species (Brooke, 1987).

Like many other species in the order Procellariiformes, JFPE nest in underground burrows and are nocturnal at breeding colonies. Female JFPE lay one egg each breeding season and both sexes alternate incubation shifts (~14 days each) during the 60-day incubation period (Brooke, 1987). After the chick has hatched, both members of the pair help to provision the chick for an additional 40 days. JFPE and STPE are highly vocal in the air above the colony and on the ground during the night. Mates, courting pairs, and rivals also vocalize with a characteristic call from within, or at the entrance to breeding burrows.

STUDY POPULATION

Field work included the last few weeks of incubation and the beginning of hatching for JFPE during two breeding seasons (February-March 2004 and 2005). Active breeding burrows were identified with a flexible infrared camera (Peep-A-Roo, Sandpiper Technologies, Manteca, CA). A hatch was excavated above each nest chamber to permit access to the adult and chick. All burrows under study were within the same region of the breeding colony in an area devoid of tree-fern forest (*Dicksonia externa*). A total of 53 JFPE adults was banded in 2004 and an additional 28 individuals (18 adults and 10 fledglings) were banded in 2005, all with U.S. Fish and Wildlife Incoloy bands (size 3B). Breeding adults were banded after chicks had hatched to reduce the risk of nest abandonment. This study was conducted in cooperation with Joanna Smith (University of Washington) and Peter Hodum (California State University – Long Beach).

RECORDING AND ANALYSIS OF VOCALIZATIONS

Recordings sampled all aspects of vocal activity at the colony, including aerial activity, vocalizations on the colony surface, and calls from within the breeding burrow. Recordings were made with a Sony TC D5 Pro II tape recorder. Ambient acoustic activity at the colony (including birds calling above the colony and on the surface) was recorded with a Senheisser ME-20 omnidirectional microphone. For vocalizations of individual petrels on the surface and in breeding burrows, I used a Senheisser ME-80 directional microphone.

Recordings were digitized and analyzed with *WildSpectra 2* and *WildSpectra 1* respectively (Wiley and Wiley 2005, version 080125, www.unc.edu/~rhwiley/wildspectra) on an Apple MacMini computer (with Intel Core Duo II processors). Digitized sound files were saved at a sampling rate of 22.05 kHz. Measurements of frequencies in calls were made on spectrograms with a Fast Fourier Transform (FFT) size of 516 (frequency resolution = 86 Hz), and all temporal measurements were made with an FFT size of 256 (temporal resolution = 5.8 ms). Spectrograms presented in this paper were produced using *WildSpectra 1*.

STATISTICAL ANALYSIS

For statistical calculations I used R (version 2.4.1, GUI 1.18 (4038), R Development Core Team 2006) with the MASS (Venables, W. N. & Ripley, B. D. 2002) and Outliers (Komsta 2007) packages or JMP 6.0 (SAS Institute, Cary, NC, USA). Neural networks were built using MATLAB R2007a and the Neural Networks Toolbox v 3.0.

JFPE VOCALIZATIONS

Call Types

Aerial vocal activity was recorded at 4 separate locations roughly 500 m apart along the colony ridge. Calls were also recorded opportunistically in other parts of the colony and at all hours of the night. These recordings of individual petrels included vocalizations from breeding adults, unpaired adults, and chicks. I present the most common call types heard during incubation and chick-rearing periods (*Figure 2.3*). However, this paper focuses on calls made within the breeding burrows (*Figure 2.3c,d*).

Burrow calls are thought to be integral to intra-pair communication and nest defense, interactions where information about the identity and sex of the caller are important (Bretagnolle 1996). Recordings can be obtained from known individuals in marked burrows on different nights in a breeding season so that comparison of calls is possible within and among individuals over different time scales.

Recording and measuring burrow calls

These petrels used a specific call type (*Figure 2.3c,d*) from the burrow during intra-pair duets and in response to disturbances at the burrow entrance (the latter sometimes accompanied by physical attacks). Sounds observed to elicit burrow calls included vocalizations from breeding partners and/or potential breeding partners within the burrow, vocalizations or loud noises at the burrow entrance, and incursions into occupied burrows by

petrels other than the breeding partner. To elicit vocalizations from known individuals, I used recordings of burrow calls (*Figure 2.3c,d*) and ground calls (*Figure 2.3b*) played into the burrow tunnel with a Sony M-450 micro-cassette recorder. Exemplars from at least three different individuals were played on each night, and recordings were changed periodically throughout the season.

In order to describe variation within the calls of individuals, I attempted to record individuals on multiple nights. Individuals were identified by checking leg bands and by placing lattices of twigs across burrow entrances to monitor movements of individuals. As long as a lattice remained intact across a burrow entrance, the petrel incubating the egg within the burrow was assumed to be the same individual. Lattices that had been disturbed indicated possible change overs at the nest. Lattices across the entrances of burrows containing banded individuals were sometimes disturbed although the same individual remained within the burrow the following day. In these cases lattices might have been disturbed by prospecting individuals or by defensive behavior at burrow entrances. However, because the identity of unbanded individuals could not be confirmed in any other way, any disturbance of a lattice across a burrow containing unbanded birds was assumed to indicate a potential changeover within the burrow. Recordings were obtained on 128 occasions from 38 breeding burrows. Response rates to playbacks at burrow entrances varied considerably and differed between sexes (see below). Compared to observations of the behavior of many *Puffinus* shearwaters in their burrows (such as *P. lherminieri*, *P. creatopus*, and *P. pacificus*), JFPE respond much less frequently to noises and recordings played at the entrance to the breeding burrow.

Vocal responses from a burrow typically consisted of 1-2 burrow calls in succession. Each burrow call consisted of a series of 3-5 phrases also repeated at regular intervals (*Figure 2.4*). Phrases, in turn, contained 2-7 notes with a series of evenly spaced harmonics (integer multiples of the fundamental frequency of the note, *Figure 2.4*). Phrases started with a relatively high-pitched long note followed by a series of lower short notes. I used call phrases as the relevant unit for statistical comparison within and between individuals because JFPE often responded to the playback stimulus after the first phrase had been broadcast into the burrow. In fact, many responses started after only the first few notes of a phrase were played at the burrow entrance.

For measurements of the spectral and temporal properties of these call phrases, I took total of 12 measures of frequency and timing from spectrograms displayed by *WildSpectra2* (*Figure 2.4*). Six measures of temporal features included notes per phrase (*NPPH*), notes per second (*NPS*), phrase length (*PHL*), length of the first note (*N1L*), length of the second note (*N2L*), and inter-note distance between the first and second notes (*N1N2D*). Six measures of frequencies included the dominant frequency of the first note (*N1DF*), 6 dB bandwidth of the first note (*N16DB*), mean harmonic interval of the first note (*N1MHI*), dominant frequency of the second note (*N2DF*), 6 dB bandwidth of the second note (*N26DB*), and mean harmonic interval of the second note (*N2MHI*). The dominant frequency represents the frequency in the entire note with the greatest amplitude, and the 6 dB bandwidth measures the frequency range within 6 dB above and below the dominant frequency. The mean harmonic interval (MHI) was measured by taking a narrow frequency section in the middle of each note and

measuring the mean distance (Hz) between each of the harmonic overtones of the note (*Figure 2.4*). This measure estimates the fundamental frequency (FF) of each harmonic note, and the mean value was almost always equal to the frequency of the first harmonic in the note. I chose to measure only the first two notes of each phrase because these usually differed from each other considerably and because phrases from all individuals contained at least two notes (where as some did not). Focusing on the first notes seemed biologically relevant because individual JFPE often responded after only the first few notes of a playback stimulus. The 12 features measured allowed a basic characterization of these notes.

Sexual dimorphism in burrow calls

To assess sexually dimorphism in burrow calls I used measurements of 142 phrases from seven burrows where both individuals in the breeding pair had been recorded during the same breeding season. In six breeding burrows (102, 105, 106, 119, 126, and 136) calls had been recorded from both members of a breeding pair during the same breeding season. Recordings from a seventh burrow (124) were included after an initial analysis showed that calls recorded before and after an apparent change in burrow occupancy showed a concomitant change in the fundamental frequency. Overall results did not change when recordings from burrow 124 were included in the analysis.

Molecular tests of sex

Blood samples were collected from 38 breeding JFPE in order to determine the sex of at least one member in each of the breeding pairs in the study population. Twelve of these individuals were also recorded in their burrows.

Molecular classification of sex, performed by my collaborators (Smith 2008), followed the methods outlined in Fridolfson and Ellegren (1999), which has been shown to determine sex in a wide array of avian species, including other procellariiforms. PCR analysis of DNA from blood samples was used to amplify two sex specific markers binding with the primers 2550F (5'- GTTACTGATTCGTCTACGAGA-3') and 2718R (5'- ATTGAAATGATCCAGTGCTTG-3'). The test detects fragments on the sex-linked chromosomes in birds, W and Z. Unlike mammals, females are the heterogametic sex, with a W and a Z chromosome while males have two copies of the W chromosome. When the PCR products were separated by gel electrophoresis, the similarly sized W gene fragments formed one band (for males), while the differently sized W and Z fragments formed two bands for females. Analyses were conducted at several different MgCl₂ concentrations and double the DNA for samples that did not amplify the first time. To confirm that markers amplified males and females correctly, we used tissue samples from known male and female specimens (two of each) loaned from the Burke Museum of Natural History and Culture, Seattle, WA (*Pterodroma externa* UWBM 64594, 64595, 64597 and 64600).

Individual variation in burrow calls

To describe individual variation in burrow calls and to estimate the amount of information potentially available for individual identification, I analyzed 120 phrases from 10 male JFPE (determined by call characteristics). I measured the 12 features described above for the calls of each individual recorded on at least two different nights in the same breeding season. These measurements were replicated at three scales (call, night, and individual) in order to partition the variation within individuals and between individuals by including measurements from 12 phrases for each individual (3 phrases per call, 2 calls per night, 2

nights per individual). Each scale of measurement was used as a factor in a nested analysis of variance (ANOVA), with individual as the highest factor. Because all three factors represented random samples of the larger population of possible individuals, nights, and calls, I used Model II ANOVA (random effects) (Underwood 2002). A random effects model is appropriate for general questions about individual variation rather than variation in specific individuals (Underwood 2002). I used the expected mean square (EMS) ANOVA method in JMP 6.0 to calculate F-ratios and to estimate the variance components from the data.

Several of the variables measured were correlated with each other. To eliminate correlations of variables, 12 independent variables (principal components) were generated by Principal Component Analysis (PCA) on the correlation matrix. Principal components that explained a substantial amount of the total variance (eigenvalues ≥ 1) were analyzed with the same 3-factor nested ANOVA described above.

The information content of burrow call phrases

I followed Beecher's (1982; 1989) method for calculating the amount of information in burrow calls potentially available for individual identification. Developed from information theory (Shannon & Weaver, 1949), this method calculates the number of binary decisions (bits) required for an ideal receiver to discriminate between equally variant individuals (Beecher 1989). Information content is calculated from the variation among the calls of different individuals in relation to the variation within the calls of individuals (Beecher 1989 *Equation 8*):

$$H_s = \sum_{i=1}^N H_i = \log_2 \sqrt{\frac{\sigma_A^2 + \sigma_W^2}{\sigma_W^2}} \quad (1)$$

where H_s is a measure (in bits) of the total information in the calls, H_i is the amount of information in each variable measured in the calls, σ_A^2 is the among-individuals variance component, and σ_W^2 is the within-individual variance component for each variable respectively. Both σ_A^2 and σ_W^2 are estimated from the 3-factor nested ANOVA described above. The variance component among individuals was estimated as

$$\sigma_A^2 = \frac{MS_{individual} - MS_{night(individual)}}{nrq} \quad (2)$$

and the total within-individual variance component was estimated as

$$\sigma_W^2 = \frac{MS_{night(individual)} - MS_{call(night(individual))}}{nr} + \frac{MS_{call(night(individual))} - MS_{Residual}}{n} + MS_{Residual} \quad (3)$$

where $MS_{individual}$ is the mean square for among-individual variance, $MS_{night(individual)}$ is the mean square for night nested within individual, $MS_{call(nights(individual))}$ is the mean square for calls nested within nights nested within individual, $MS_{Residual}$ is the mean square for the residual, q is the number of nights measured, r is the number of calls measured, and n is the number of phrases measured per call (Quinn and Keough 2002).

Calculating H_s from raw variables could lead to inflated estimates of the amount of information in a signal as correlated variables would add redundant information (Beecher, 1982,1989; Medvin et al., 1993). Instead, information measures should be calculated using

orthogonal variables obtained from principal components analysis. Beecher (1989) proposed that PCs calculated from the variance-covariance matrix are preferred over calculations from the correlation matrix, as the former maintains the relative weights of each variable. However, that conclusion assumes that all variables are measured in the same units, and if not, one must convert variables to comparable units. Beecher suggests standardizing the variables by dividing each by the within-individual standard deviation before calculating PCs from the variance-covariance matrix. Because, in the end, calculations following this method produce results similar to those produced by calculating PCs of un-standardized variables from the correlation matrix, I chose the latter method, which is most straight-forward. However, I present calculations of H_s based on the raw (correlated) variables, on PCs calculated from the standardized covariance matrix (following Beecher), and on PCs calculated from the raw correlation matrix.

H_s is an estimate of the number of binary decisions that an ideal receiver would need to distinguish between individuals based on the measured variation in calls. Thus

$$2^{H_s} = \text{maximum number of equivalent individuals can be distinguished} \quad (4)$$

In natural systems the assumptions that all individuals have unique and equally variable signals and that receivers can always perceive all of the information available in a signal are suspect (Beecher, 1989; Wiley, 1994). *Equation 4* nevertheless provides an estimate for the theoretical upper limit of a group in which complete recognition is possible. Conversely, this equation also predicts the theoretical amount of information in calls required

for tasks a species might be expected to perform in a natural setting. For example, an incubating petrel might benefit (in terms of reproductive success) from the ability to discriminate between the burrow calls of their mates and the individuals breeding in the neighboring burrows (typically between 5-9 individuals in total). Therefore one might predict that the burrow calls of petrels would contain between 2.32 and 3.17 bits of information ($\log_2 5 = 2.32$ bits, $\log_2 9 = 3.17$ bits) to allow complete recognition among equivalent individuals in this group. If instead the recognition task only requires recognition of two equal categories (say for instance mate and stranger), an ideal receiver could perform this task with calls containing only 1 bit of information.

Classification of burrow calls in multivariate space

I compared 2 techniques for multivariate classification to assess the reliability with which individual petrels might be identifiable by the variation in burrow calls. Both linear discriminant function analysis (LDA) and probabilistic neural networks (PNN) have been used in other studies of variation in acoustic signals (Terry et al., 2001; Terry & McGregor, 2002; Bourgeois et al., 2007; Blumstein & Munos, 2005; Lovell & Lein, 2004; Parsons & Jones, 2000; Peake et al., 1998; Wollerman & Wiley, 2002b). These techniques involve a training phase, in which half the data is used to build functions that best classify the data into predefined classes, and a validation phase in which the other half of the data is used to test the effectiveness of these functions in classifying novel instances. To compare the classification success for LDA and PNN, I used a dataset of 168 phrases (6 from each of 14 individuals recorded on each of 2 different nights). I divided the dataset in half to form training and validation matrices that each included 3 phrases from each individual and night.

Comparisons between classification techniques

I tested the sensitivity of both LDA and PNN classifications to variations in three parameters that define any classification problem: the number of classes in the model (2, 3, 5, 10, and 13 individuals), the number of explanatory variables used for classification (either 6 or 12 variables), and the number of exemplars in the training set and the validation set (4 training and 4 validation or 8 training and 4 validation). Scripts in R and MATLAB classified calls into all possible combinations of 13 individuals ($N = 14$ possible combinations), 10 individuals ($N = 1001$ combinations), 5 individuals ($N = 2002$ combinations), and 2 individuals ($N = 91$ combinations) from the 14 individuals in the data set. In each case, a combination of individuals was drawn from the set of possible combinations (without replacement), a PNN (or LDA) was trained with phrases (4 or 8) from these individuals, and the classification network was then verified with 4 new phrases from these same individuals. I report error rates, the percent of total erroneous classifications at each validation stage ($\pm$ s.e.). The mean error rate for all possible combinations of 5 individuals is thus the mean error rate for all 2002 classifications by PNN (or LDA). I varied the other parameters (number of explanatory variables and number of training exemplars) in the same way.

Finally, I considered whether variables estimated to include more information improved classification rates or whether improved classification was merely a function of increased explanatory variables in LDAs. To do this comparison, I performed repeated LDAs, each trained and tested with calls from a grouping of 9 individuals selected at random

for each classification. To test different numbers of explanatory variables ($X = 2-12$), I ran 10,000 LDAs using X randomly selected explanatory variables, and 10,000 LDAs using the set of X explanatory variables with the greatest combined information value. Thus, I could compare classification results for 2-12 randomly selected variables with results for the 2-12 variables with the highest combined information content.

Classification of non-equivalent categories

I used PNNs to explore the challenges faced by ideal receivers when performing other potentially relevant recognition tasks. With the large dataset of call measurements from JFPE I tested 4 hypothetical scenarios in which an ideal receiver recognized classes of individuals as opposed to individuals themselves. These individuals had calls with different levels of variation, unlike the equivalent categories estimated by information theory.

The 4 hypothetical scenarios I simulated are relevant situations that might occur in animal populations, including large seabird colonies. In the first scenario “mate vs. stranger”, the receiver’s task is to classify calls into 2 categories, a category containing calls of one individual (say a mate), and a category containing calls from many individuals (say strangers investigating a burrow) (*Table 2.1*). The second hypothetical scenario “mate vs. neighbors vs. stranger” requires classification of a category with low levels of variation (mate), a category with slightly more variation (neighbor = calls from 4 individuals), and the widely varying category (strangers). Scenarios 3 and 4 are variations on these discriminatory tasks (*Table 2.1*). Differences between these categories were determined by the number of calls from one individual contained in the set of calls used to train the classification function,

on the one hand, and the set of calls used to test the classification success of these functions, on the other hand (*Table 2.2*). Although the total number of phrases was equal for the training sets for each category (8), the number of individuals represented in each training set differed between categories. For categories intended to represent “known” individuals (for instance mate, known neighbor, and known stranger) all 8 phrases in the training set were selected from the same individuals. For broader categories, the training sets contained more individuals and fewer exemplars per individual. The training set for the broader “neighbors” category, for example, contained 2 calls from 4 different individuals (N= 8 total) (*Table 2.2*). Strangers were modeled by building a training dataset without any replication (each of the 8 calls in the training set was drawn from a different individual), in order to simulate a situation in which the receiver has no previous knowledge of the caller (*Table 2.2*). Strangers are meant to represent unpaired individuals prospecting for breeding sites/partners throughout the colony that are unlikely to interact repeatedly with a given receiver. The “known strangers” category in the final classification scenario might represent a hypothetical situation where unpaired petrels prospect in specific areas of a colony and are recognized as individuals by breeders in burrows. In summary, while the training sets for each category contained the same total number of exemplars (8), the variability of signals within each category differed considerably.

The validation datasets for each category did not differ from each other in the same way. Instead test datasets for each simulation were composed of 4 different calls from the same individual. However, the identity of the individual chosen for the validation set varied for each category. Known categories (mate, known neighbor, and known stranger) were

validated with 4 new calls from the individual represented in the training set (*Table 2.2*). Validation calls representing the neighbor category were drawn from only 1 of the 4 individuals represented in the training set. Classification of unknown strangers was tested using a validation set with 4 calls from a novel individual not represented in any of the training sets (*Table 2.2*).

I tested each of these scenarios only with PNNs, as LDAs were unreliable when classifying JFPE calls from small numbers of individuals (See *Results*). For each of the 4 hypothetical scenarios for classification (*Table 2.1*), I wrote scripts in Matlab that randomized the individuals assigned to each category (without replacement), trained a PNN using calls from these individuals as described above, and tested classification rates with new calls as specified above. To account for differences in error rates in classification between different combinations of individuals, I repeated this randomization and classification process 20,000 times (after which error rates stabilized for each scenario). The mean (+/- s.e.) error rates for all 20,000 trials are reported.

I do not claim that these simulations reproduce the actual abilities of JFPE receivers to distinguish between groups of individuals or that these simulations identify a mechanism by which JFPE operate in the natural world. Instead, I use a balanced dataset of carefully analyzed natural signals to explore some general consequences of classification into categories with differing ranges of variation. In particular, this approach tests whether or not it is possible for an ideal receiver to classify these hypothetical categories at rates exceeding that expected by chance alone.

PERMITS AND INSTITUTIONAL OVERSIGHT

This study was approved by UNC's Institutional Animal Care and Use Committee (IACUC Protocol: 04-304.0-C). Work within the Juan Fernandez Islands National Park was conducted under CONAF – Juan Fernandez permit #021 and SAG permit #3419, and banding was carried out under USFWS banding sub-permit 08654-AH.

RESULTS

Vocal activity at the Inocentes Bajos breeding colony

Both petrel species at the Inocentes Bajos breeding colony (JFPE and STPE) were nocturnal, returning to the colony only after sunset and calling in the air and on the ground until about 60-30 minutes before sunrise. The mean arrival time during both the 2004 and 2005 field seasons was 20.5 (s.e. = 0.59, N=49) minutes after sunset for STPE and 27.7 (s.e.= 0.57, N=49) minutes after sunset for JFPE. The bulk of the JFPE did not arrive until about 1 hour after sunset when noise levels increased dramatically at the colony (see Chapter 3) as a result of calls on the ground, in the air, and in burrows (*Figure 2.3*).

Sexual dimorphism in burrow calls

The possibility of sexual dimorphism in JFPE burrow calls was first noted while recording breeding pairs as they vocalized to each other within the breeding burrow. In this situation two distinct call types were noted, one clear and the other slightly hoarse and high-pitched. In shearwaters, female calls are usually higher pitched and have a broad frequency

spectrum (Warham, 1990, Bretagnolle 1996, Brooke, 2004, Mackin 2004). Distinguishing between call types was more difficult in the field when only one bird was present in a burrow. Measurements of the mean harmonic interval in the first note of phrases showed significant differences between paired individuals in 5 burrows, and similar trends in the other 2 burrows (*Figure 2.5*). Based on these differences, calls from these individuals were divided into two call types. Type I calls had notes with a low fundamental frequency and clear harmonics (*Figure 2.3c*). Type II calls had notes with less well-defined harmonics, higher fundamental frequencies, and more broad-band components (*Figure 2.3d*). There were no intermediate or ambiguous phrases recorded. By analogy with vocalizations of *Puffinus*, I expected Type I calls were produced by males, and Type II calls by females.

The frequency and timing of male and female calls differed significantly in only one of the measured features, the mean harmonic interval of the first note (t-test, $N = 14$, $p < 0.05$ with Dunn-Sidak correction for multiple tests) (*Table 2.3*). The first two principal components (calculated from all 12 features) explained 46% of the total variation in the calls, and each differed significantly between call types. PC 1 loaded heavily (eigenvectors $\geq |0.30|$) on timing variables of the call, while PC 2 loaded heavily on frequency variables.

Of the 42 individuals whose burrow calls were measured, only 8 had call types of females. This preponderance of males probably resulted from the use of recordings made in the field to elicit calls from breeding burrows.

Molecular tests of sex

33 of the 38 blood samples from JFPE could be classified to sex by the molecular markers and techniques described by Fridolfson and Ellegren (1999). Of these, only 12 were birds that had been recorded on multiple nights (or mates of birds sexed by molecular methods). Based on characteristics of the calls of these birds and previous studies of sexual dimorphism in procellariiforms, I predicted that 7 of these 12 birds were male and 5 were female. The results of the PCR tests showed that 11 of these predictions matched the classifications of sex by molecular methods (Sign Test, 11+, N=12, $p < 0.05$, *Table 2.4*). The one error likely occurred when both members of the pair were present in the breeding burrow. In this case, I might have recorded calls of one but then confirmed the band of the other. Both members of this breeding pair (Burrow 136) had been present in the burrow at the same time the night before.

Individual variation in phrase variables

I examined each of the 12 features of phrases at 3 scales in a 3-factor nested ANOVA with random effects. All calls were male calls (Type I). Several of the variables violated assumptions of normality (significant Shapiro Wilks W tests in *Table 2.5*), homogeneity of variance (significant Cochran's C tests in *Table 2.5*), both assumptions of the parametric ANOVA method. Log and Box-Cox transformations improved the homogeneity of variance of five variables, *N1MHI*, *N1NL*, *N1N2*, *N2MHI* and *N2NL*. Only *PHL* and *N26DB* did not meet assumptions of homogeneity of variance after transformation. Seven variables, *NPPH*, *N1DF*, *N1MHI*, *N2DF*, *N26DB*, and *N2NL* did not meet assumptions of normality after

transformation. Because ANOVA is robust to violations of both assumptions when data are balanced (Underwood, 2002), I retained these variables in the analyses.

The nested ANOVA partitioned variance among phrases within a single call, between calls on a single night, between calls on different nights, and among the calls of different individuals (*Table 2.6*). Six variables (*PHL*, *NPPH*, *NPS*, *NIN2*, *N2MHI*, and *N2NL*) explained a significant amount of the variation between individuals ($F_{9,10} > 16.88$, $p < 0.001$, Dunn-Sidak correction for multiple tests). Of these, *N2MHI* is a measure of frequency while the other five variables are measures of timing in calls. Only one variable, *N16DB*, showed significant variation in the calls of individuals recorded on different nights ($F_{10,20} = 5.62$, $p < 0.05$, Dunn-Sidak correction for multiple tests). Examination of the variance components showed that the differences between individuals explained the majority of the total variance in seven variables (*Table 2.6*).

The correlation matrix of the data showed significant pair-wise correlations between many of the phrase variables. To generate independent variables and to reduce the dimensionality of the data, I performed principal component analysis (PCA) on the correlation matrix for all 12 variables. For comparison, I also did PCA on the covariance matrix.

The first four PC's were retained as variables in the nested ANOVA described above, as each explained more than 10 % of the total variance and had eigenvalues > 1 . Combined, these four PCs explained 76% of the total variation in these variables. Principal component

loadings indicate that PC's 1 and 3 were heavily influenced (loadings > |0.30|) by timing variables, while PC's 2 and 4 were heavily influenced by both frequency and timing variables. All four principal components met assumptions of homogeneity of variance ($p < 0.05$, Cochran's Test) and normality ($p < 0.05$, Shapiro Wilks Test Cochran's Test).

In the nested ANOVA of the first 4 PCs (*Table 2.7*), most of the variation in the first 3 PCs can be explained by differences between individuals ($F_{9,10} > 23.2$, $p < 0.001$, Dunn-Sidak correction). PC 4 varied significantly within the calls of individuals recorded on different nights ($F_{10,20} = 3.19$, $p < 0.05$, Dunn-Sidak correction).

While these results show individual variation in burrow call phrases, they do not imply that all individuals differ for any one variable. Significant F-ratios between individuals can result when only one individual differs significantly in one variable. For example, the lengths of note 2 vary significantly among individuals (ANOVA, $F_{9,110} = 38.2$, $p < 0.0001$). However, the values for the length of note 2 overlap between all individuals except one (Tukey's HSD, $q = 3.96$, $p > 0.05$, *Figure 2.6*). This, is important for two reasons. First, the variation from only one individual leads to a significant ANOVA result. Second, most individuals cannot be distinguished using this one variable. This pattern applies to all variables measured including composite variables produced by PCA. No single variable can distinguish all 10 individuals in the dataset. To test whether the combined pattern of variation in multiple variables might differentiate individuals, it is necessary to assess individual variation in multivariate space.

Information in burrow call phrases

When H_s is calculated from PC calculated on the correlation matrix of the raw variables (*see Methods*) JFPE burrow call phrases contain 3.06 bits of information (*Table 2.8*). If H_s is calculated directly from the raw variables without correcting for the correlation between variables the estimate of H_s is 5.77 bits of information. Thus estimates for the number of equivalent individuals that can be recognized corresponding to each of these methods are 8 and 55 individuals respectively (i.e. $2^{3.06} = 8$, $2^{5.77} = 55$).

The relatively large estimate of H_s calculated from the raw variables results from redundant measurements of variance from multiple pair-wise correlations between the variables. Thus PCA is an essential step when estimating the information content from signals with correlations between variables. Though the estimate of 5.77 bits of information based on raw variables is high, it is interesting to note that the 6 variables measuring timing parameters account for 4.10 bits of information, while the 6 variables measuring frequency components account for 1.67 bits of information. Thus, both frequency and timing components contain information about individuals, though timing variables account for more information. The combined variation between individuals suggests that roughly 8 equivalent individuals might be distinguished with the 12 variables I measured from burrow call phrases.

Individual variation in multivariate space

To determine whether or not the information and variation I measured in burrow calls can be used to classify the calls of individuals in multivariate space, I used a larger dataset containing measurements of 12 phrases from 14 different individuals (total number of phrases = 168). I tested the effects of 3 parameters on classification rates by LDAs and PNNs. If half of the data (6 phrases per individual) were used to train these functions, and the other half to test the effectiveness of the classification functions, an LDA with all 12 discriminatory variables correctly classified phrases from the 14 individuals 77% of the time (range from 33 - 100% per individual) while the correct classification rate for a PNN using the same data is 71% (ranging from 17 – 100% per individual). Both results are better than the expected classification rate of 7% for random classification of 14 individuals. Thus both classification methods were able to classify individual petrels reliably based on the combination of all 12 variables. It is important to note that both methods made errors in classification and that some individuals were more difficult to classify than others.

Four different parameters affected the accuracy of classification: the number of individuals to be distinguished (group size, 13, 10, 5 or 2 individuals), the number of discriminatory variables in the function (6 or 12 variables), the number of exemplars used for training (4 or 8 phrases), and finally, the classification method itself (LDA or PNN). In all cases, tests of classification used the same 4 phrases from each of the individuals included in the training set.

An ANOVA found that group size ($F_{3,24675} = 1220.56$, $p < 0.001$), number of discriminatory variables ($F_{1,24675} = 944.35$, $p < 0.001$), number of phrases in the training set ($F_{1,24675} = 26.73$, $p < 0.001$) and classification method ($F_{1,24675} = 53.13$, $p < 0.001$) each had a significant influence on classification error rates (*Table 2.9*). Post-hoc tests showed that error rates were significantly better when classifying smaller than larger groups (2 vs. 13 individuals) (Tukey HSD, $Q = 2.57$, $p < 0.05$). It is also apparent that error rates decreased for both LDA and PNN when more discriminatory variables (12 vs. 6) are used to build the classification functions ($t = -30.73$, $df = 24675$, $p < 0.05$), even when the 6 variables used were those that showed significant inter-individual variation. Not surprisingly, classification improved when the number of phrases in the training set doubled from 4 to 8 phrases ($t = -57.32$, $df = 24675$, $p < 0.05$), although both values are relatively low in comparison to those recommended for any training set (McGarigal et al., 2000).

Finally, although classification error rates were similar between LDA and PNN, the LDA method was significantly more effective overall at classifying JFPE phrases than was the PNN method ($t = -7.29$, $df = 24675$, $p < 0.05$). The LDA method, however, was not always the better classifying technique. When only 4 phrases were used to train the functions, LDA could not classify effectively between some combinations of 2 individuals because the technique encountered multiple collinearities between the discriminatory variables. The LDA method also had higher error rates than PNN in cases where these functions were classifying 5 individuals (*Table 2.9*). These increased error rates were a result of specific combinations of individuals that could not be distinguished effectively with linear

discriminant functions trained with only 4 exemplars. PNN was able to classify all possible combinations of 2 individuals in every case.

Information and Classification

Classification of burrow calls from the 10 individuals used to measure the information in burrow calls showed that explanatory variables with greater amounts of information improved LDA classification over randomly selected variables (*Figure 2.7*). As in the analysis described above, correct classification rates went up as more explanatory variables were used. However, variables with the most information peaked at 5 variables (91% correct classification), and remained fairly constant from there on (*Figure 2.7*). Randomly selected variables, on the other hand, did not achieve 91% correct classification until all 12 variables were included.

Classification by category

In the simplest of the 4 hypothetical classification scenarios of nonequivalent categories (M, S), the mean classification error rate was 20% over all 20,000 tests (*Figure 2.8*). This error rate is higher than the 4% mean error rate for all possible combinations of 2 individuals tested previously with both PNN and LDA (*Table 2.9*). Still, it is better than the 50% classification rate one would expect for random classification between two categories. The mean error rate for classifying the less variant category (mate) was 5%, while the error rate for classification of the more variant stranger category was 35%.

In the scenario with 3 hypothetical categories (M, N, and S), the mean error rate was 30%. Mean error rates were 8%, 23%, and 60% for the mate, neighbor, and stranger categories, respectively. The error rate expected at random for each category was 67%. Classification of the most variable category (strangers) thus approached the error rate expected for random classifications.

The classification of M, KN, and S involved 6 potential categories: mate, known neighbor-1, KN-2, KN-3, KN-4, and stranger. The mean error rate for this scenario was 23%. Based on previous tests, we would expect error rates to increase with the group size (*Table 2.9*). However, despite the large number of classes in this scenario (6), the limited variability within categories reduced overall error rates compared to the previous 3-category scenario (M, N, and S). As expected, the error rate for each category representing a hypothetically known individual (mate and neighbors 1-4) was the same (12%). The PNN classified calls from the stranger category incorrectly 78% of the time, slightly better than the 83% expected by chance.

Finally, the M-KN-KS scenario required classification between 9 categories: mate, known neighbors 1-4, and known strangers 1-4. The mean overall error rate was 16%, which was also the error rate for each category. This figure is close to the error rate for all combinations of 10 individuals (17%, *Table 2.9*). The expected error rate for random classification of 9 classes is 88%.

In these simulations, classification accuracy increased as the number of equally variant categories increased. In every case, however, the neural net was able to generalize and to classify highly variable categories (neighbor, stranger) at rates that were better than expected by chance alone. In addition, classification rates of the invariant groups (known individuals) were actually improved by the inclusion of highly variable categories.

DISCUSSION

Juan Fernandez Petrels at their primary breeding colony on Isla Alejandro Selkirk produce calls that contain information about the sex as well as the identity of the caller, the first such reports for any *Pterodroma*. From measurements of the acoustic properties of calls replicated at a number of temporal scales, I estimated that there are 3.06 bits of information available for individual recognition, sufficient to recognize 8 individuals on average. These calls have sufficient individual variation to be classified correctly by two multivariate classification techniques (LDA and PNN). Finally, through a series of simulations based on measurements of real vocalizations, I showed that an ideal receiver classifying burrow calls with PNNs can distinguish between non-equivalent categories of signals, but that accuracy of classification depends on the variability in each category. The inclusion of broadly varying categories of individuals (N & S) improved the accuracy of classifying those categories that were less variable.

Acoustic communication in petrels

For many nocturnal and burrow-nesting Procellariiforms, acoustic signals are often the primary means for long-range communication (Brooke, 1978, Bretagnolle 1996). Such signals in other birds often include information about species, sex, and individual identity (Falls, 1982; Dhondt & Lambrechts, 1992; Becker, 1982; Emlen, 1972). Observational and experimental studies have shown that the vocalizations of procellariiform species also contain information about the species (Bretagnolle & Robisson, 1991; Bolton, 2007; Bretagnolle, 1989), sex (Brooke, 1978b; Brooke, 1988; James & Robertson, 1985b; Bourgeois et al., 2007; Bretagnolle & Lequette, 1990b; Bretagnolle, 1996; Storey, 1984; James, 1985b), and identity of the caller (Brooke, 1978b; James, 1985b). This study documents sex- and individual-specificity of calls in the genus *Pterodroma* for the first time.

Sexual dimorphism in burrow calls

Many of the species in the family Procellariidae are monomorphic in their plumage and the sexes are not easily distinguished in the field (Warham, 1990; O'Dwyer et al., 2006). The burrow calls of JFPE breeding pairs in this study showed significant differences between individuals in a pair in the fundamental frequencies of notes. These sexual differences in burrow calls were confirmed by the PCR-based molecular test of sex (Fridolfsson & Ellegren, 1999).

Whether or not JFPE can distinguish between the sexes by burrow call alone remains to be tested experimentally, but the natural history of the species and results from previous

studies of sexual recognition in other petrel species suggest this possibility. The preponderance of males recorded during this study also supports this possibility. The recordings used to evoke vocalizations consisted mostly of male calls, so the prevalence of responses by males suggests that they can recognize the sex of the played-back calls and respond primarily to calls of their own sex.

Two other studies have suggested dimorphism in the vocalizations of species in the genus *Pterodroma*, burrow calls and duets for *P. hypoleuca* (Grant et al., 1983b) and aerial calls in *P. phaeopygia* (Tomkins & Milne, 1991), although neither study confirmed the sex of the vocalizing petrels.

Individual variation in burrow calls

Burrow calls recorded from marked individuals included significant variation among individuals in both timing and frequency components of calls. There were more individual differences in timing (phrase length, notes per phrase, notes per second, note 1 – note 2 interval, and note 2 note length) than in frequency variables (note 2 mean harmonic frequency interval). Individual variation in both frequency and timing variables was also apparent in all four principal components of these variables. Although PC's 1 and 3 (together explaining 43% of the total variation) loaded heavily on timing variables, PC's 2 and 4 (explaining an additional 33% of the variation) loaded heavily on both frequency and timing variables. This result differs from findings for other species of petrel in which only timing variables are important in separating individuals (Bretagnolle 1996). Experiments suggest that individual recognition of mates and neighbors is widespread within the

Procellariidae (Brooke, 1978b; Brooke, 1990; Mackin, 2005; Bretagnolle, 1996; Falls, 1982; Bretagnolle & Lequette, 1990b). Because both members of a breeding pair were seldom recorded during the same year, a consequence of the exceptionally long intervals between change-overs at the nest, it was not possible to conduct similar experiments as part of this study.

Other signals could also promote individual (and sexual) recognition at breeding burrows. Petrels have relatively large olfactory bulbs, and a number of experiments have shown that they can use olfactory cues to locate food at sea (Nevitt, 2000; Nevitt et al., 1995; Verheyden & Jouventin, 1994; Hutchison & Wenzel, 1980; Warham, 1996). Recent experiments have also shown that some petrels (and storm-petrels Hydrobatidae) can use their olfactory capabilities to locate breeding burrows within breeding colonies (Bonadonna et al., 2003; Bonadonna & Bretagnolle, 2002; Grubb, 1974) and to identify breeding partners (Bonadonna & Nevitt, 2004; Jouventin et al., 2007). It would be interesting to know whether or not response rates to the calls of mates increase when calls are accompanied by appropriate olfactory cues.

Bits of information in burrow call phrases

The estimate of 3.06 bits of individual information in JFPE burrow calls suggests an effective group size for this signal of 8 individuals. An ideal receiver using all of the measured frequency and timing cues in these calls could distinguish between 8 individuals with equally varying signals (Beecher 1982). This theoretical estimate of group size is probably high because the calls of JFPE individuals are not equally variable. This was

reflected in the results from multivariate classifications where some combinations of individuals are harder to classify than others. However, this estimate of effective group size is compatible with the relatively small number of individuals an incubating petrel is likely to hear repeatedly and the relatively few individuals likely to approach a burrow during a breeding season.

Variables with the greatest amount of information improved classification rates over randomly selected variables (*Figure 2.7*). Successive additions of these informative variables reached an asymptote for accuracy of classification after 5 variables, whereas accuracy with random variables continued to increase until all 12 variables were included. Although there is always the possibility that other variables in the phrases or calls of JFPE might have increased the estimate of information in these calls, the fact that correct classification between groups of 9 individuals reached 91% after inclusion of 5 variables and did not improve further suggests that additional informative variables would be difficult to identify.

My estimate of H_s in JFPE burrow calls is slightly larger than the 1.9 bits of information reported for burrow calls of Audubon's Shearwater (*Puffinus lherminieri*) (Mackin, 2004). It is, however, considerably lower than estimates reported for acoustic signals for parent-offspring recognition in penguins, another group of colonial seabirds. Searby and Jouventin (2005) reported estimates of 6.15 bits and 8.27 bits of information in the calls of adult Rockhopper Penguins (*Eudyptes chrysocome*) and Macaroni Penguins (*Eudyptes chrysolophus*) respectively. Both are species that breed in large colonies in which

chicks are known to recognize parents by their calls. The estimates of H_s reported for these two species were calculated directly from acoustic parameters as opposed to principal components and are therefore augmented to an unknown degree by correlations between the variables. H_s estimated directly from acoustic parameters of JFPE calls (5.77 bits) is comparable to that reported for the penguin species.

These four seabird species (JFPE, AUSH, and the two penguin species) might be expected to have similar amounts of individual information in their vocalizations based on their similar life histories. Breeding adults in each species return to a fixed nest within a large colony, a situation that greatly reduces the number of individuals to be discriminated. More complex signature calls occur in species that lack fixed nests, such as the King Penguin (*Aptenodytes patagonicus*) and Emperor Penguin (*A. forsteri*), though estimates of H_s have not been published for either species (Jouventin & Aubin, 2002; Jouventin et al., 1999). The complex double-voice calls produced by both King and Emperor Penguins might allow discrimination between large numbers of individuals, so that adults can recognize mates and chicks among many constantly shifting individuals. The calls of these species should be studied further to see if they confirm the prediction that species with nest sites have vocalizations with lower information content than species that must locate and feed chicks in crèches.

A similar prediction has been studied in swallows. The estimated information capacities of the calls of nestling Bank Swallow (*Riparia riparia*), Cliff Swallow (*Hirundo pyrrhonota*), Barn Swallow (*H. rustica*), and Rough-winged Swallow (*Stelgidopteryx*

ruficollis) chicks are 17.0, 9.0, 5.2, and 3.2 bits respectively (Beecher, 1982; Medvin & Beecher, 1986). The amount of information in the calls of swallow chicks corresponds to the difficulty of recognizing chicks faced by parents of these species (Beecher 1982).

The calls of nestling Rough-winged Swallows contain roughly the same amount of information as adult JFPE burrow calls. For these swallows, a nestling's calls presumably serve to distinguish between their own young and the chicks in nearby nests (Beecher, 1990), while JFPE burrow calls might allow individuals to discriminate between the individuals entering and/or interacting near the breeding burrow.

Classification of burrow calls in multivariate space

Two multivariate classification techniques, LDA and PNN, confirm that the variation among individuals' burrow calls can be used to classify calls. Both techniques could discriminate effectively between all 14 individuals in the sample when all 12 variables were included (77% correct detection for LDA and 71% correct for PNN). Whether or not JFPE can discriminate individuals by their calls as well as, or better than, these mathematical techniques remains to be tested. Experimental evidence of individual recognition in other petrel species has confirmed abilities to discriminate between mates (Brooke, 1978, 1986; Bretagnolle and Lequette, 1990, James 1985a) and individuals in neighboring burrows (Mackin, 2005).

Classifying JFPE burrow calls with LDA and PNN illustrate some of the fundamental issues facing receivers in natural environments. Not only do error rates for classification

increase as the number of individuals to be classified increases, but some combinations of individuals are more difficult to discriminate between than others. These errors might be a result of similarities between the calls of certain individuals, measurement errors during analysis, or the quality of the recordings. All three of these problems (similarities in signals, noise in receptors, and noisy channels) are also possible in natural communication (Wiley, 1994; Wiley, 2006).

Classification of non-equivalent categories

Animals might not distinguish between all of the individuals they encounter, but instead only classify them into categories such as “my chick” and “all other chicks.” However, this involves classification of signals from categories with different levels of variation, and increases the possibility that signals will overlap in key features.

I took advantage of the well-characterized set of JFPE calls obtained during this study to explore the problem of classifying non-equivalent categories. I created hypothetical categories of individuals that a petrel might differentiate between from within a burrow. These tests were not meant to prove that any of the scenarios was more likely or that petrels classify calls in ways that resemble the multivariate technique I employed or the categories I created. They do however use the natural calls of JFPE to illustrate general problems in any classification of individuals by means of vocalizations.

Classification of different categories of individuals with PNNs show the importance of well-characterized categories, with low variance in the training and validation sets. The

greater the number of training phrases from a single individual the lower the probability of classification errors. Groups that varied widely (few calls from many individuals) were classified at rates that exceeded that expected by chance, but only slightly. On the other hand, the classification accuracy in low variation categories (all calls from one individual) was increased when widely varying groups were included in the set of calls. Thus the PNN recognized “known individuals” well, but “stranger’s calls” at rates only slightly better than random.

For petrels, recognizing classes or individuals could have implications for reproductive success. Strangers entering a burrow might pose a threat to incubating petrels, whereas mates and nearby neighbors might not. Mackin (2005) showed that Audubon’s Shearwaters distinguish between the burrow calls of neighbors and strangers. Experiments are needed to test whether or not JFPE can recognize their neighbors or regular prospectors in their neighborhood individually.

Acoustic monitoring techniques for sensitive/secretive species

Burrow-nesting species are notoriously difficult to monitor. Often investigators must excavate access hatches to confirm the presence of marked individuals within burrows. Access hatches can reduce the structural integrity of burrows (Smith, Hodum and McKown, unpublished data) and some species increase rates of nest abandonment if handled during the incubation period (Davis, 1957; Boersma et al., 1980; Warham, 1990; Boersma et al., 2002). In addition, access hatches are not practical in colonies where burrows are situated among rocks or are located on cliffs. Acoustic monitoring, a less invasive yet effective tool for

checking occupancy of burrows, has been used to estimate occupancy rates in a number of seabird colonies (Ratcliffe et al., 1998; Berrow, 2000; Ambagis, 2004; Barbraud & DeLord, 2006; Insley et al., 2002).

Acoustic identification of individuals might be particularly useful for elusive or inaccessible species. Terry and McGregor (2002) explored vocal individuality as a tool for censusing Corncrakes (*Crex crex*), and others have suggested similar monitoring schemes (Gilbert et al., 1994; Holschuh & Otter, 2005; Tripp & Otter, 2006; Saunders & Wooller, 1988). Terry and McGregor (2002) recommended the use of PNN for monitoring programs because of their accuracy in classifying Corncrake calls, their ease of use, and their recognition of novel classes not included in the training set.

The results of this study, and of many previous studies of species in the order Procellariiformes, suggest that burrowing petrels can easily be identified to sex by vocal characteristics. This could facilitate studies of the division of incubation responsibilities and burrow attendance patterns among mates, while reducing the need for more intrusive methods. It is conceivable that the calls might be useful for identifying individuals in some threatened species, though the methods used to measure and classify calls for this study would probably not be practical for most monitoring programs. Other classification methods based on spectral-cross correlation or some other similar pattern recognition methodology might be more feasible (Chen & Maher, 2006; Mellinger & Clark, 2000; Fagerlund, 2007). However, the results of this study point out that monitoring projects based on individual variation in calls are bound to involve errors. For example, detecting changes in burrow

occupancy from year to year on the basis of acoustic signals alone would be fraught with difficulty, as new individuals could have calls similar to those of individuals that have left the population. The classification simulations in this paper found that certain combinations of individuals led to higher error rates in classification. Thus monitoring projects in the field might have different error rates in different subsets of a colony or between years. Without permanently marked individuals, it would be difficult to establish the true identity of individuals in a burrow and to estimate error rates for the monitoring technique.

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Table 2.1 Four scenarios used to test classification of non-equivalent categories

<i>Classification Scenario</i>	<i>Categories</i>
<i>Mate vs. Stranger</i> (M vs. S)	<i>Mate</i> <i>Stranger</i>
<i>Mate vs. Neighbor vs. Stranger</i> (M vs. N vs. S)	<i>Mate</i> <i>Neighbor</i> <i>Stranger</i>
<i>Mate vs. Known Neighbors vs. Stranger</i> (M vs. KN vs. S)	<i>Mate</i> <i>Neighbor 1</i> <i>Neighbor 2</i> <i>Neighbor 3</i> <i>Neighbor 4</i> <i>Stranger</i>
<i>Mate vs. Known Neighbor vs. Known Stranger</i> (M vs. KN vs. KS)	<i>Mate</i> <i>Neighbor 1</i> <i>Neighbor 2</i> <i>Neighbor 3</i> <i>Neighbor 4</i> <i>Stranger 1</i> <i>Stranger 2</i> <i>Stranger 3</i> <i>Stranger 4</i>

Table 2.2 **Number of individuals represented in each category and number of phrases per individual in the PNN training and validation data sets**

<i>Category</i>	<i>Individuals represented in Category</i>	<i><u>Phrases per individual</u></i>	
		<i>in Training Set</i>	<i>in Validation Set</i>
<i>Mate</i>	1	8	4
<i>Neighbor</i>	4	2	4*
<i>Stranger</i>	8	1	0 ^Ω
<u>Known Neighbors</u>			
<i>Neighbor 1</i>	1	8	4
<i>Neighbor 2</i>	1	8	4
<i>Neighbor 3</i>	1	8	4
<i>Neighbor 4</i>	1	8	4
<u>Known Strangers</u>			
<i>Stranger 1</i>	1	8	4
<i>Stranger 2</i>	1	8	4
<i>Stranger 3</i>	1	8	4
<i>Stranger 4</i>	1	8	4

* all from 1 of the 4 individuals in the training set

^Ω 4 phrases from a **new** individual not represented in the training set

Table 2.3 Acoustic measurements of male and female burrow calls

<i>Variable</i>	<u>Male burrow calls</u>			<u>Female burrow calls</u>			<u>t-Tests</u>			
	<i>Individuals</i>	<i>Mean</i>	<i>s.e.</i>	<i>Individuals</i>	<i>Mean</i>	<i>s.e.</i>	<i>t-ratio</i>	<i>df</i>	<i>p</i>	<i>Dunn-Sidak corrected p</i>
<u>Timing Variables</u>										
<i>Phrase length (ms)</i>	7	628.2	34.8	7	484.6	49.6	-2.4	12	0.04	
<i>Notes per phrase</i>	7	3.2	0.2	7	2.4	0.2	-2.8	12	0.02	
<i>Notes per second</i>	7	5.1	0.2	7	5.2	0.1	0.3	12	0.78	
<i>Note 1 note length (ms)</i>	7	157.1	7.5	7	143.4	6.0	-1.4	12	0.18	
<i>Note 2 note length (ms)</i>	7	111.6	4.7	7	98.9	7.6	-1.4	12	0.18	
<i>Note 1-Note 2 inter-note distance (ms)</i>	7	127.3	14.1	7	140.4	9.9	0.8	12	0.46	
<u>Frequency Variables</u>										
<i>Note 1 dominant frequency (Hz)</i>	7	2172.1	388.4	7	2772.5	191.4	1.4	12	0.19	
<i>Note 2 dominant frequency (Hz)</i>	7	768.9	208.2	7	1206.7	198.9	1.5	12	0.15	
<i>Note 1 6 dB bandwidth (Hz)</i>	7	5143.5	257.2	7	4852.8	280.3	-0.4	12	0.71	
<i>Note 2 6 dB bandwidth (Hz)</i>	7	2861.2	303.9	7	2663.4	415.0	-0.4	12	0.71	
<i>Note 1 Mean harmonic interval (Hz)</i>	7	880.4	19.1	7	1925.9	214.0	4.9	12	0.00	<0.05
<i>Note 2 Mean harmonic interval (Hz)</i>	7	578.9	9.0	7	1031.9	160.7	2.8	12	0.02	

Table 2.4 Sex of individuals predicted from burrow vocalizations (Mean harmonic interval) and determined through molecular analysis (PCR results) (Sign Test, 11+, N=12, P<0.05).

		<u>Prediction based on the</u> <u>Note-1 Mean harmonic interval</u>	
		<i>Male?</i> <i>< 1000 Hz</i>	<i>Female?</i> <i>> 1,000 Hz</i>
<u>PCR results</u>	<i>Male (WW)</i>	7	0
	<i>Female (WZ)</i>	1	4

Table 2.5 Summary statistics for 12 parameters of burrow calls measured from 10 individuals

<i>Variable</i>	<i>Mean</i>	<i>SD</i>	<i>N</i>	<i>Cochran's C</i>	<i>Shapiro-Wilks W</i>
<u>Timing Variables</u>					
<i>Phrase Length (ms)</i>	676.03	176.82	120	0.22	0.98^
<i>Notes per Phrase</i>	3.41	0.80	120	0.18	0.86^
<i>Notes per second</i>	5.12	0.67	120	0.22	0.98
<i>Note 1 Length (ms)</i>	136.12	26.69	120	0.17	0.98
<i>Note 2 Length (ms)</i>	105.93	14.74	120	0.23*	0.98
<i>Internote (N1 to N2) (ms)</i>	148.48	51.64	120	0.30*	0.95^
<u>Frequency Variables</u>					
<i>Note 1 Dominant Frequency (Hz)</i>	2289.31	1363.57	120	0.20	0.84^
<i>Note 2 Dominant Frequency (Hz)</i>	1165.03	1157.75	120	0.23	0.65^
<i>Note 1 6dB Bandwidth (Hz)</i>	5065.40	1308.99	120	0.21	0.99
<i>Note 2 6dB Bandwidth (Hz)</i>	3401.13	1495.08	120	0.25*	0.98^
<i>Note 1 Mean Harmonic Interval (Hz)</i>	838.56	78.16	120	0.22	0.95^
<i>Note 2 Mean Harmonic interval (Hz)</i>	577.44	100.91	120	0.29*	0.98

* p < 0.05, Cochran's C test, indicates heterogeneous variance between groups

^ p < 0.05, Shapiro-Wilks W, data are not normally distributed

Table 2.6 **Nested ANOVA (random effects) of 12 parameters of burrow calls**

<i>Phrase Variable</i>	<i>Source</i>	<i>SS</i>	<i>df</i>	<i>F Ratio</i>	<i>p</i>	<i>corrected p¹</i>	<i>Estimated Variance Component</i>	<i>Percent Of Total Variance²</i>
Phrase length	Individual	2338587	9	17.75	<0.001	<0.001	20555	60%
	Night(Individual)	146399	10	1.30	0.296		562	2%
	Call(Night(Individual))	225700	20	0.87	0.629		-586	0%
	Phrase = Residual	1042785	80				13034	38%
Notes per phrase	Individual	50	9	16.88	<0.001	<0.001	0.44	63%
	Night(Individual)	3.34	10	1.87	0.113		0.03	4%
	Call(Night(Individual))	3.58	20	0.74	0.768		-0.02	0%
	Phrase = Residual	19.25	80				0.24	34%
Notes per second	Individual	31.97	9	29.12	<0.001	<0.001	0.29	59%
	Night(Individual)	1.22	10	0.59	0.801		-0.01	0%
	Call(Night(Individual))	4.11	20	1.05	0.421		0.00	1%
	Phrase = Residual	15.71	80				0.20	40%
Note 1 dominant frequency	Individual	50201679	9	2.40	0.095		272688	15%
	Night(Individual)	23250989	10	2.24	0.060		215505	12%
	Call(Night(Individual))	20791220	20	0.75	0.761		-115396	0%
	Phrase = Residual	110706259	80				1383828	74%
Note 1 6dB band	Individual	36939241	9	1.22	0.378		62190	3%
	Night(Individual)	33625656	10	5.62	0.001	<0.05	463494	26%
	Call(Night(Individual))	11954784	20	0.47	0.970		-224609	0%
	Phrase = Residual	101426015	80				1267825	71%
Note 1 mean harmonic interval (BoxCox)	Individual	301898	9	5.34	0.008		2285	41%
	Night(Individual)	62801	10	2.80	0.024		677	12%
	Call(Night(Individual))	44780	20	0.88	0.615		-105	0%
	Phrase = Residual	204212	80				2552	46%
N1 note length (BoxCox)	Individual	50204	9	6.19	0.004		392	52%
	Night(Individual)	9015	10	3.60	0.007		109	15%
	Call(Night(Individual))	5002	20	1.03	0.443		2.13	0%
	Phrase = Residual	19501	80				243	33%

Table 2.6 (cont'd) Nested ANOVA (random effects) of 12 parameters of burrow calls

<i>Phrase Variable</i>	<i>Source</i>	<i>SS</i>	<i>df</i>	<i>F Ratio</i>	<i>P</i>	<i>corrected p¹</i>	<i>Estimated Variance Component</i>	<i>Percent Of Total Variance²</i>
Log(Note 1-Note 2 inter-note distance)	Individual	8.25	9	33.95	0.000	<0.001	0.07	57%
	Night(Individual)	0.27	10	0.49	0.875		0.00	0%
	Call(Night(Individual))	1.09	20	0.96	0.522		0.00	0%
	Phrase = Residual	4.58	80				0.06	43%
Note 2 dominant frequency	Individual	57666514	9	1.71	0.207		223254	15%
	Night(Individual)	37443010	10	3.75	0.006		460319	31%
	Call(Night(Individual))	19974687	20	1.45	0.126		103162	7%
	Phrase = Residual	55277392	80				690967	47%
Note 2 6dB band	Individual	99963513	9	3.68	0.027		678158	35%
	Night(Individual)	30173911	10	2.22	0.062		278078	14%
	Call(Night(Individual))	27178407	20	1.73	0.046		191676	10%
	Phrase = Residual	62966828	80				787085	41%
Note 2 mean harmonic interval (BoxCox)	Individual	589310	9	25.57	<0.001	<0.001	5274	63%
	Night(Individual)	25611	10	0.97	0.500		-15.11	0%
	Call(Night(Individual))	53023	20	0.85	0.647		-156.68	0%
	Phrase = Residual	249485	80				3118.57	37%
Note 2 note length (BoxCox)	Individual	35979	9	22.30	<0.001	<0.001	320.10	73%
	Night(Individual)	1792	10	1.04	0.450		1.05	0%
	Call(Night(Individual))	3460	20	1.92	0.022		27.80	6%
	Phrase = Residual	7209	80				90.11	21%

¹ Dunn-Sidak correction for multiple tests (Gotelli and Ellison 2004)² Negative variance component estimates converted to 0 (Quinn and Keough 2002).

Table 2.7 ANOVA (random effects) of the first 4 principal components of acoustic parameters of burrow calls

<i>Principal Component</i>	<i>Source</i>	<i>SS</i>	<i>df</i>	<i>F Ratio</i>	<i>p</i>	<i>Corrected p¹</i>	<i>Variance Component</i>	<i>Percent Of Total Variance²</i>
1	Individual	588.58	9	23.2	<0.001	<0.001	5.25	75%
	Night(Individual)	28.19	10	1.6	0.168		0.18	3%
	Call(Night(Individual))	34.51	20	1.2	0.265		0.10	1%
	Phrase = Residual	113.70	80				1.42	20%
2	Individual	463.57	9	29.9	<0.001	<0.001	4.17	75%
	Night(Individual)	17.25	10	0.9	0.573		-0.04	0%
	Call(Night(Individual))	39.61	20	1.8	0.033		0.30	5%
	Phrase = Residual	87.43	80				1.09	20%
3	Individual	263.39	9	43.7	<0.001	<0.001	2.40	61%
	Night(Individual)	6.70	10	0.5	0.857		-0.10	0%
	Call(Night(Individual))	25.82	20	0.8	0.656		-0.08	0%
	Phrase = Residual	122.51	80				1.53	39%
4	Individual	109.41	9	3.8	0.024		0.75	28%
	Night(Individual)	31.93	10	4.1	0.004	<0.05	0.40	15%
	Call(Night(Individual))	15.66	20	0.5	0.960		-0.26	0%
	Phrase = Residual	125.69	80				1.57	58%

¹Dunn-Sidak correction for multiple tests (Gotelli and Ellison 2004)

²Negative variance component estimates converted to 0 (Quinn and Keough 2002).

Table 2.8 Information content (H_S) of burrow call phrases estimated from, 12 principal components (calculated from the raw variable correlation matrix), 12 principal components (calculated from the standardized variable covariance matrix), and 12 raw phrase variables

<i>Principal Components (Correlation)</i>	<i>H_i (bits)</i>	<i>Principal Components (Covariance)*</i>	<i>H_i (bits)</i>	<i>Raw Phrase Variables</i>	<i>H_i (bits)</i>
				<u>Timing Variables</u>	
PC 1	0.89	PC 1	1.14	Phrase Length	0.61
PC 2	0.67	PC 2	0.68	Notes per Phrase	0.66
PC 3	0.73	PC 3	0.70	Notes per Second	0.73
PC 4	0.18	PC 4	0.19	Note 1 Length	0.45
PC 5	0.06	PC 5	0.00	Note 2 Length	0.46
PC 6	0.17	PC 6	0.23	N1-N2 interval	0.62
PC 7	0.03	PC 7	0.00	<u>Frequency Variables</u>	
				Note 1	
PC 8	0.06	PC 8	0.05	Dominant Frequency	0.21
				Note 2	
PC 9	0.10	PC 9	0.09	Dominant Frequency	0.23
PC 10	0.03	PC 10	0.06	Note 1 6dB Bandwidth	0.07
PC 11	0.03	PC 11	0.02	Note 2 6dB Bandwidth	0.46
				Note 1	
PC 12	0.23	PC 12	0.23	Mean Harmonic Interval	0.33
				Note 2	
				Mean Harmonic Interval	0.90
$H_S =$	3.06	$H_S =$	3.33	$H_S =$	5.77
				$H_{(timing)} =$	4.10
				$H_{(frequency)} =$	1.67

* following Beecher (1982)

Table 2.9 Effects of group size (*13,10,5 or 2 individuals*), number of discriminatory variables (*6 or 12*), and number of phrases in the training set (*4 or 8 phrases per individual*) on mean PNN and LDA classification error rates

<i>Group Size</i>	N	<i>Number of Discriminatory Variables</i>	<i>Phrases in Training Set</i>	<i>Phrases in Test Set</i>	<i>Mean Error Rate (+/- s.e.)</i>	
					PNN	LDA
2	91	6	4	4	6% (1.0)	-
5	1001	6	4	4	18% (0.2)	20% (0.2)
10	2002	6	4	4	27% (0.1)	28% (0.2)
13	14	6	4	4	31% (0.6)	32% (0.2)
2	91	12	4	4	7% (1.0)	-
5	1001	12	4	4	17% (0.2)	28% (0.3)
10	2002	12	4	4	25% (0.1)	24% (0.2)
13	14	12	4	4	28% (0.4)	25% (0.7)
2	91	6	8	4	6% (1.0)	6% (0.8)
5	1001	6	8	4	18% (0.2)	16% (0.2)
10	2002	6	8	4	29% (0.2)	24% (0.2)
13	14	6	8	4	34% (0.9)	28% (0.7)
2	91	12	8	4	4% (0.7)	10% (1.4)
5	1001	12	8	4	11% (0.2)	9% (0.1)
10	2002	12	8	4	17% (0.1)	12% (0.1)
13	14	12	8	4	19% (0.6)	15% (0.8)

Figure 2.1 The Juan Fernandez Petrel breeds on Isla Alejandro Selkirk (arrow) in the Juan Fernández archipelago of Chile

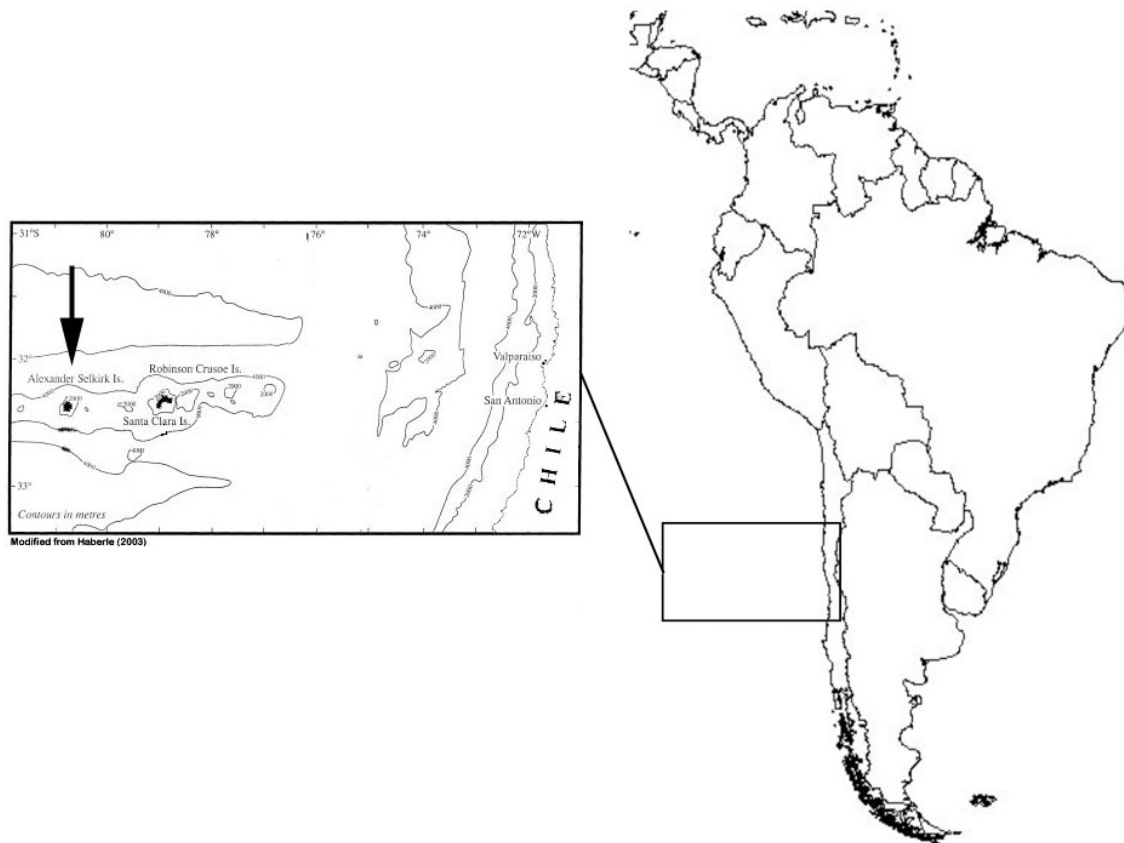


Figure 2.2 The Inocentes Bajos breeding colony is located at 1,200 m of elevation on the southwest side of Isla Alejandro Selkirk, Chile

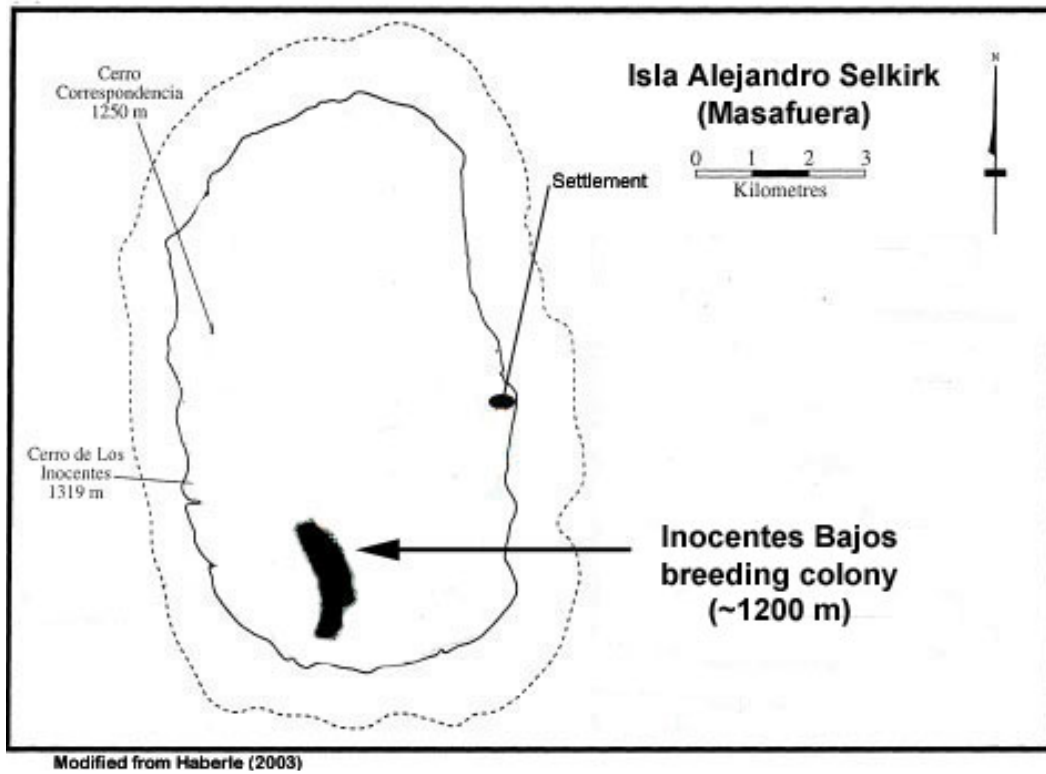


Figure 2.3 Common call types of the Juan Fernandez Petrel

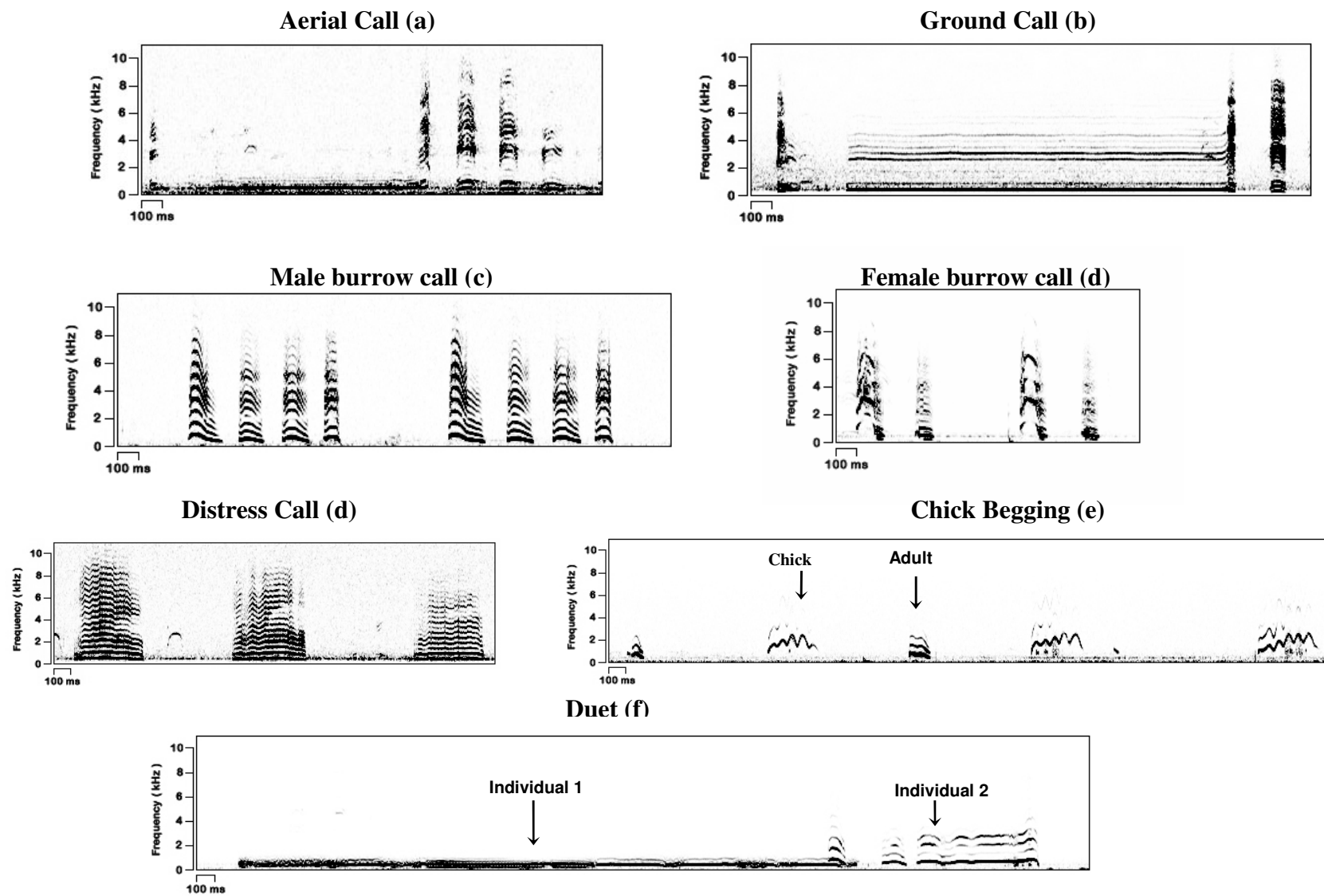


Figure 2.4 Acoustic measurements of JFPE burrow calls (numbers indicate how each variable was measured)

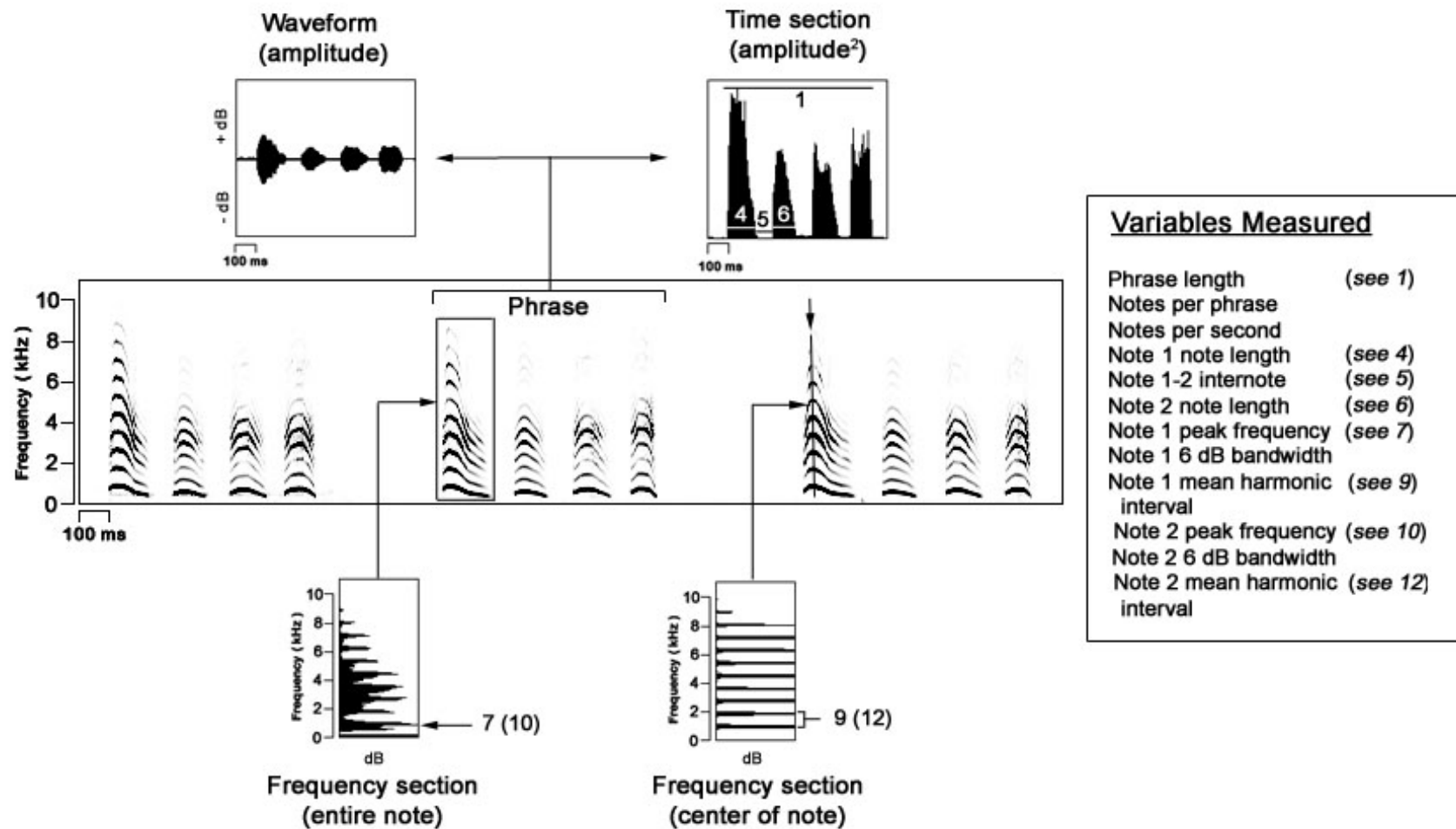


Figure 2.5 Mean harmonic interval (Hz) of the first note of call phrases from each individual (A and B) in a breeding pair (t-tests, Dunn-Sidak correction for multiple tests)

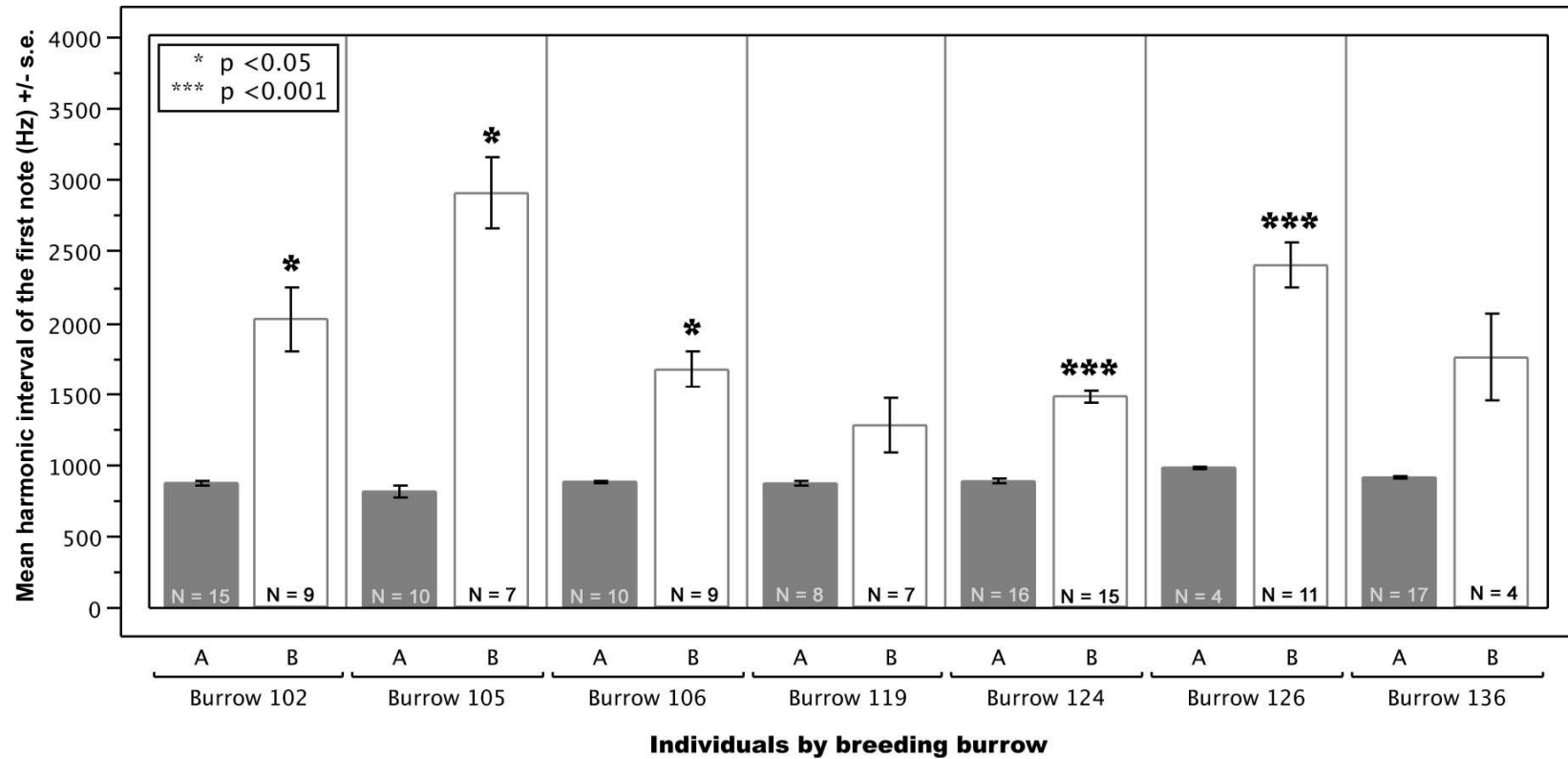


Figure 2.6 Length of note-2 (ms) by individual. Individuals not sharing a letter are significantly different from one another in this parameter (Tukey's HSD, $q = 3.23$, $p < 0.05$)

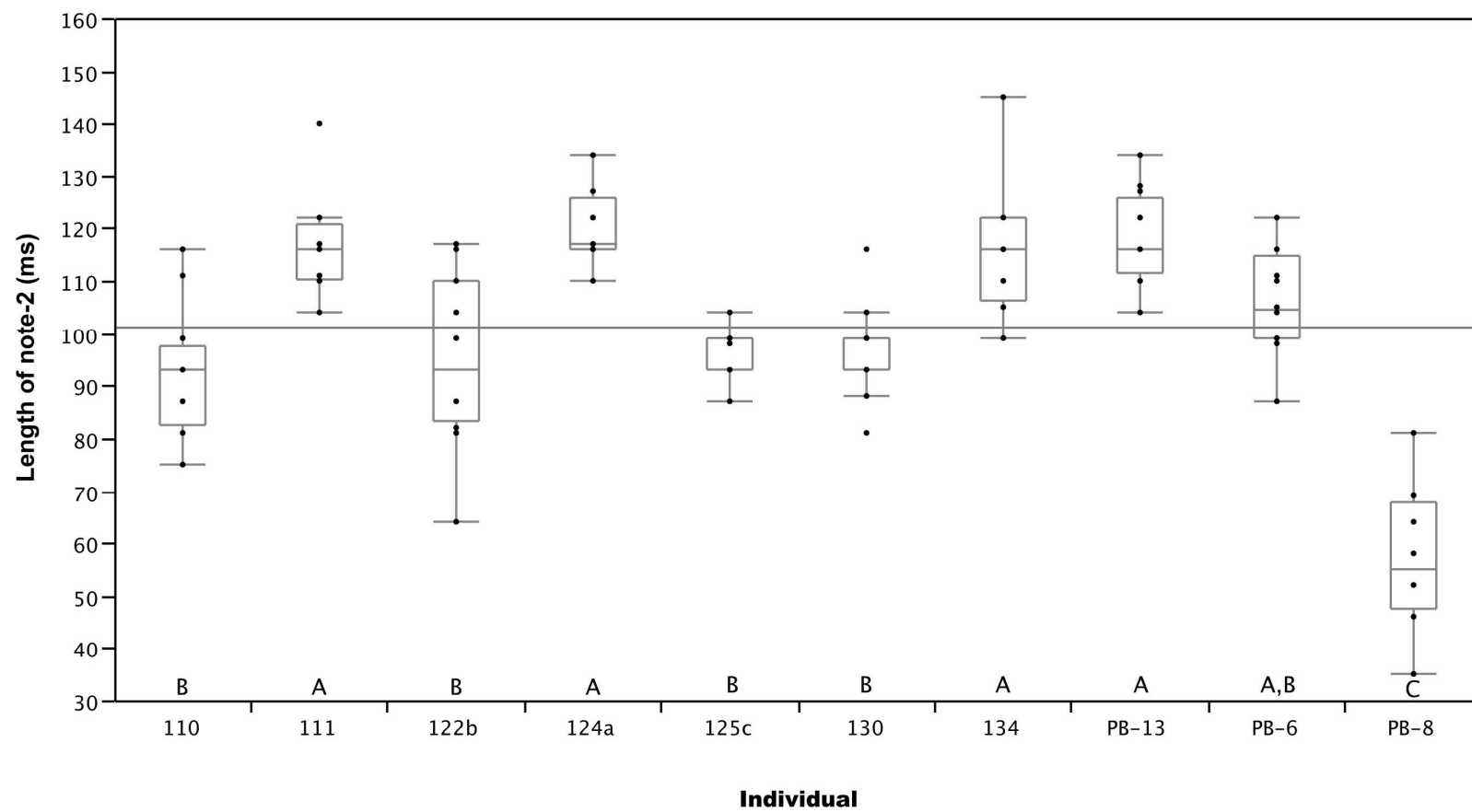


Figure 2.7 Correct classification rates from LDAs of 9 randomly selected individuals using different numbers of explanatory variables (2-12). Values represent the mean of 10,000 LDAs at each level (2-12). *Dashed line* - variables randomly selected from all 12 measured variables. *Solid line* - successive addition of variables with the next highest level of information content (H_s)

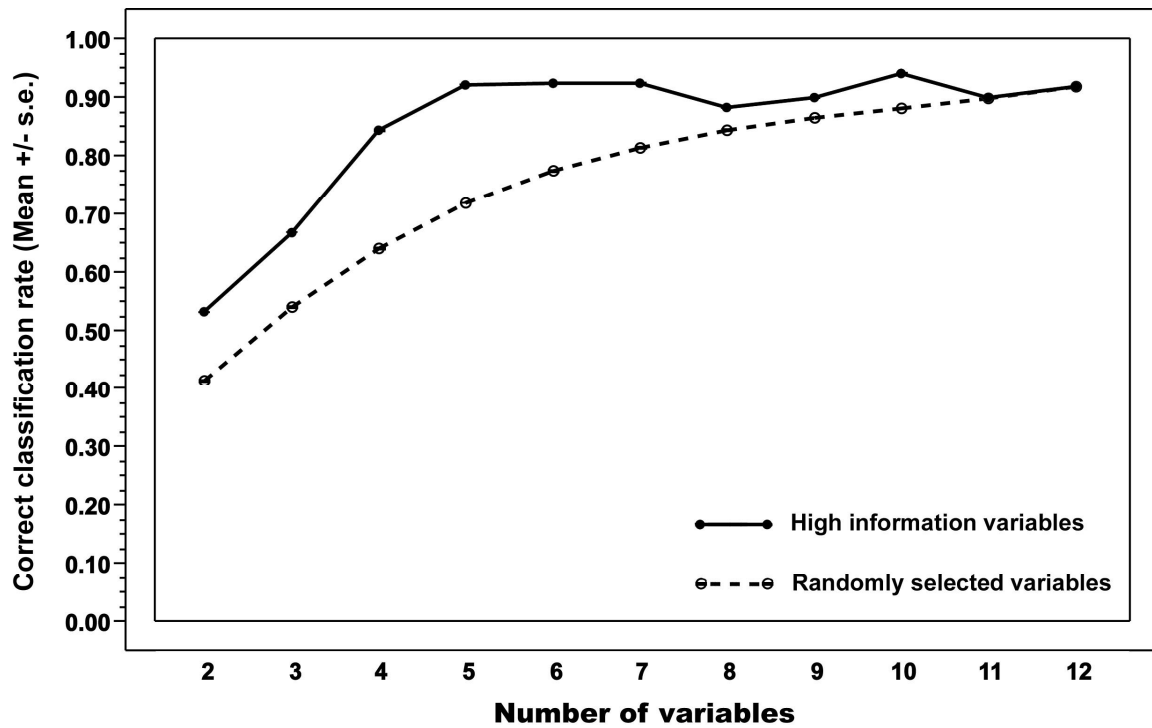
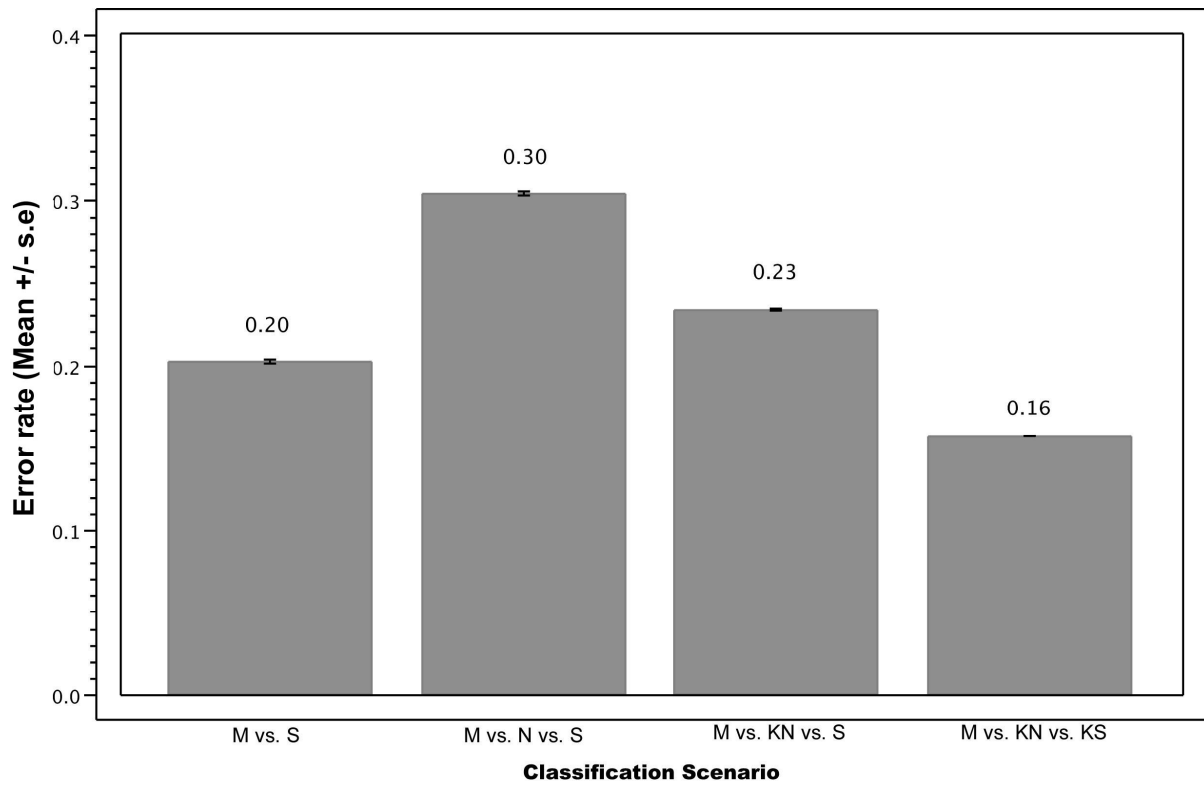


Figure 2.8 Classification error rates for four classification scenarios with non-equivalent categories: (1) Mate, Stranger (M vs. S), (2) Mate, Neighbor, Stranger (M vs. N vs. S), (3) Mate, Known Neighbor, Stranger (M vs. KN vs. S), and (4) Mate, Known Neighbor, Known Stranger (M vs. KN vs. KS)



CHAPTER 3

Vocal activity at a multispecies petrel colony: effects of predators and aerial collision on the costs of nocturnal behavior

ABSTRACT

Three lines of evidence suggest that predators influence the daily patterns of activity at seabird colonies. First, many seabirds are nocturnally active at breeding colonies with diurnal predators. Second, in colonies where diurnal predators can hunt by moonlight, nocturnal seabirds often reduce activity when the moon is visible. Finally, several populations of nocturnal seabirds are diurnal at colonies where daytime predation is reduced. No previous study has examined patterns of nocturnal behavior in moonlight when nocturnal predation is absent. I recorded the vocal behavior of two nocturnal petrel species, the Juan Fernandez Petrel (*Pterodroma externa*) and Stejneger's Petrel (*P. longirostris*), in a colony with a single strictly diurnal predator (Red-backed Hawk *Buteo polyosoma exsul*). Counts of aerial vocalizations during the breeding season (2004, 2005) showed that both Stejneger's Petrels and Juan Fernandez Petrels have distinct activity periods after sunset, and that both species increased vocal activity as the fraction of the moon illuminated increased over the lunar cycle. These findings add further support to the hypothesis that daily patterns of behavior in seabirds have evolved in response to predation and emphasize that the activity patterns of predators are important in determining the activity of seabirds. My observations also suggest that a risk of nocturnal behavior in seabirds is aerial collision. Differences in the risks of predation and collision for these two petrels species can account for the differences in their nightly patterns of activity. Whether or not immigrant individuals can learn to make the necessary adjustments in activity at colonies with differing risks remains an important open question.

INTRODUCTION

Like other patterns of behavior, daily activity should evolve in response to biotic and abiotic environmental factors that affect the survival and reproductive success of individuals (Kronfeld-Schor & Dayan, 2003). Biotic environmental factors include such things as resource availability, competitive interactions within and among species, and the risks associated with predation and parasitism. Abiotic factors include weather, temperature, day length, lunar/tidal cycles, and habitat. Previous research on daily patterns of activity have primarily focused on temporal partitioning of limited resources among the species in a community (Kronfeld-Schor & Dayan, 1999; Jones et al., 2001; Cotton, 1998). Diel patterns, however, can also be influenced by the conditions for successful reproduction, such as the distribution and availability of potential mates (Cooley et al., 2003; Welling et al., 1995), interactions within and between species that reduce the effectiveness of sexual signaling (Chek et al., 2003; Nelson & Marler, 1990; Paez et al., 1993; Sueur, 2002; Luther, 2008), physical constraints on signaling (Brown & Handford, 2003; Endler, 1993a; Henwood & Fabrick, 1979; Wiley & Richards, 1982a), and the costs of signaling from the risk of predation or parasitism (Burk, 1982; Belwood & Morris, 1987; Endler, 1987; Endler, 1988; Lima & Dill, 1990; Magnhagen, 1991; Acharya & McNeil, 1998; Zuk & Kolluru, 1998; Stoddard, 2002; Lima & Bednekoff, 1999; Ryan et al., 1982).

Diel patterns of attendance at colonies by many seabirds are good examples of activity behavior subject to these complex biotic and abiotic constraints. Species in the family Alcidae (puffins, auks, murre, guillemots and relatives) and the orders Procellariiformes (albatrosses, shearwaters, petrels, storm-petrels, and relatives) and

Sphenisciformes (penguins) are all colonial breeders. Many nest on isolated islands that are, or were once, devoid of mammalian predators. To reduce mortality and reproductive failure from avian predators, they often breed in dense concentrations and in protected nest cavities. Because individuals of these species forage over large areas of the ocean, behavior that precedes mating is concentrated at these colonies, where individuals gather in large vocal aggregations to court and establish nest sites. Colony attendance is highly synchronized, especially for un-paired individuals displaying at colony sites. Most seabirds do not breed in the first years of their lives, and young unpaired individuals visit colonies for a number of years before breeding for the first time (Warham, 1996; Brooke, 1990; Brooke, 2004a; Gaston & Jones, 1998). Non-breeders often outnumber breeding birds during some stages of the breeding season (Gaston & Jones, 1998; Warham, 1996; Brooke, 2004a). As a result, seabird colonies are often loud and chaotic places during the breeding season, with busy breeders and rambunctious non-breeders interacting in the same location. Here I explore some of the environmental factors thought to influence the diel patterns of colony attendance & vocal activity at colonies.

Three lines of evidence suggest that one of the most important influences on the daily patterns of vocal behavior by non-breeders at colony sites is the risk of predation and parasitism (in the form of kleptoparasitism). First, many small alcid and petrel species (as well as the smallest penguin species Little Penguin *Eudyptula minor*) are strictly nocturnal at breeding sites, apparently to reduce the risk of predation from diurnal species (gulls, skuas, and various raptors) (Lack, 1968; Watanuki, 1986a; Brooke & Prince, 1991; McNeil et al., 1993; Gaston & Jones, 1998; Warham, 1990; Warham, 1996; Klomp & Wooller, 1991).

Where species breed in areas without the potential protection of darkness (e.g. high latitude colonies with continuous daylight) several small alcid species return to colonies only in large well-synchronized flocks (Gaston & Jones, 1998).

The second line of evidence that predation risk influences colony attendance and vocal behavior is that in colonies where the risk of predation during daylight is reduced, some populations of nocturnal seabirds are diurnally active (*Table 3.1*). Audubon's Shearwaters *Puffinus lherminieri* are active in daylight when breeding on islands in the Galapagos archipelago that have nocturnal predators (Short-eared Owls *Asio flammeus galapagoensis*) but no diurnal predators (Galapagos Hawks *Buteo galapagoensis*). However, individuals are strictly nocturnal when roosting on another island in the archipelago (Fernandina) where hawks are present (Harris, 1969b).

Finally, many nocturnal seabirds reduce activity at colonies around the full moon, when diurnal predators can hunt by moonlight (*Table 3.2*). Typically, the effect of moonlight is most pronounced on the vocal activity of non-breeders, while breeders return to burrows silently to take over incubation responsibilities or feed their young (Mougeot & Bretagnolle, 2000a; Keitt et al., 2004; Watanuki, 1986a; Storey & Grimmer, 1986; Bretagnolle, 1990; Richdale, 1965a; Richdale, 1965b; Lockley, 1942).

Still, some have suggested that predators may not be the only factor influencing activity levels at seabird colonies. Imber (1973; 1975) has suggested that moonlight avoidance in seabirds may result from reduced foraging success on nights when increased

light levels dampen the vertical migration of prey. Foraging ecology may also explain differences activity patterns of some species in mixed species colonies. Although Wedge-rumped Storm Petrels *Oceanodroma tethys* and Madeiran Storm Petrels *O. castro* on the Genovesa Island in the Galapagos face the same owl predator, the *O. tethys* is active during the day while *O. castro* is active only at night. Harris (1969a) suggested these differences may be attributed to the foraging strategies of these species, and Brooke(2004) has suggested that similar differences may explain the differences in activity patterns observed in other mixed species colonies. Aggressive interactions between species (Harris, 1974), differences in the attendance patterns of non-breeders during different stages of the breeding season (Richdale, 1965a; Warham, 1996), and meteorological conditions such as wind speed and cloud can also influence activity at seabird colonies (Bourgeois et al., 2008; Bretagnolle, 1990; Jones et al., 1990). Thus the possibility exists that the activity patterns of un-paired individuals may vary among the species in a colony and by colony location according to local environmental factors such as predator identity, resource availability, co-occurring species, and meteorological conditions.

Here I describe the patterns of vocal behavior of two seabirds, the Juan Fernandez Petrel *Pterodroma externa* and Stejneger's Petrel *P. longirostris*, at a large colony with a strictly diurnal predator. I compare the timing of aerial activity for these two species in order to learn more about the factors that might influence activity patterns in seabirds. I evaluate whether variation in activity is correlated with moonlight, meteorological conditions, and the progression of the breeding season. In the absence of nocturnal predation pressure I predicted that there would be no relationship between vocal activity and the lunar

cycle. As shown here, I found the unexpected result that both petrel species are more active in moonlight, and that both species have largely exclusive activity periods during each night. These two results, and observations of frequent aerial collisions at the colony raise interesting possibilities about the influence of colony specific predation risks and species-specific costs of collisions on the timing of aerial activity at densely populated seabird colonies.

METHODS

Study Site and Species

The only breeding site for Juan Fernandez Petrels (JFPE) and Stejneger's Petrels (STPE) is Isla Alejandro Selkirk (Lat. 33° 45' S, Long. 80° 46' W) in the Juan Fernández Archipelago of Chile. These two petrels differ in mass by a factor of almost 3 (JFPE ~ 480 g, STPE ~170 g). Brooke (1987) estimated that the colony contained 1 million breeding pairs of JFPE and 130,000 breeding pairs of STPE, although the estimate for STPE may be high (*see below*). At the large breeding colony on Inocentes Bajos Ridge, JFPE breed from about 700 m on the slopes to the ridgeline at 1,200 m elevation. Burrows are found in tree fern forest (predominantly *Dicksonia externa*, see Haberle (2003) for description of vegetation) on both sides of the ridge and on the exposed ridge itself (Hodum & Wainstein, 2003; Hodum et al., 2002). STPE burrows are restricted to shallow peaty soil in open areas with rocky outcrops along the ridgeline (Hodum & Wainstein, 2003; Hodum et al., 2002). These aggregations (sub-colonies) of STPE breeding burrows may be restricted to areas where the larger JFPE cannot dig adequate burrows in the shallow rocky soils (Hodum & Wainstein, 2003; Hodum et al., 2002).

Both species are nocturnal at the breeding colony and are highly vocal in the air above the colony and on the ground. As in other seabird colonies, much of the vocal activity appears to be from non-breeding (unpaired) individuals (Simons, 1985; Bretagnolle, 1996; Brooke, 1990; Warham, 1996; Richdale, 1965a; Richdale, 1965b; Harris, 1966).

Observations of JFPE and STPE breeding burrows agreed with previous observations - breeding birds flew silently as they approached their burrows, landed relatively close to their burrow entrance, and moved inside relatively quickly. Though I could not account for the aerial activity of the apparently silent breeding birds before their approach and landing, the behavior of these birds differed markedly from that of vocally active birds landing on the ground. The latter type typically engaged in noisy group flights (where petrels chase and vocalize to each other on the wing) before pausing or ending these interactions by alighting and calling from the ground. These presumably unpaired individuals would not enter a burrow, but instead investigated a number of potential breeding burrows and were often involved in aggressive interactions with established occupants of burrows or other prospecting individuals. Throughout the breeding season, non-breeding pairs were found duetting and sleeping, usually for no more than one night, in previously unoccupied burrows. Whether such pairs go on to breed in these burrows in future years is not yet known.

The only native predator on the island is an endemic subspecies of the Red-backed Hawk (*Buteo polyosoma exsul*), locally known as the Blindado. The remains of both petrel species were found near Blindado roosting sites on the southwestern cliffs of the island, and individual hawks have been observed with live petrels of both species in their talons (Brooke, 1987). Individual petrels flying near the colony in daylight are quickly chased by multiple

Blindados, and any injured JFPE on the ground during the day is soon caught. Blindados are found throughout the island from sea level to the ridgeline. The species is active during daylight hours and into twilight (earliest observed activity 35 min before sunset, latest activity 36 min after sunset). Blindados were never seen or heard at night (>1 hr before sunrise or after sunset)

Introduced predators include domestic cats, brown rats *Rattus norvegicus*, and the house mouse *Mus musculus*. Domestic dogs are also found on the island, although unaccompanied dogs have not been observed at the colony during the incubation or chick-rearing periods.

Acoustic Recording

Ambient acoustic activity at the Inocentes Bajos colony (including birds calling above the colony and on the colony surface) was recorded with a Shure omnidirectional dynamic microphone (Radio Shack Model # 33-3006) and a Sony TC D5 Pro II tape recorder (2004) or a Sony MZ-NH900 minidisk recorder (2005).

Recordings of acoustic behavior at the colony were made from February 9 to March 5, 2004 (total = 13), and from February 7 to March 15, 2005 (total = 16). These dates corresponded with the incubation and chick-rearing periods for both species.

Vocal activity was recorded at 4 separate locations spaced roughly 500 m apart along the ridge running through the colony. I chose two recording locations (Point Break and

Canelo Crest) where > 60% of the burrows within 10 m of the count site were JFPE burrows, and two sites (Far Side and Stonehenge) where > 60% of the burrows within 10 m of the count site were STPE burrows. In 2004, 10-min recordings of ambient activity were made 30, 60, 90, 120, and 150 min after sunset at one location per night. In 2005, I recorded activity for the first 95 min after sunset with the minidisk recorder, as data from 2004 showed that peak activity levels for both species occurred within this time period. I conducted two all-night counts (10-min recordings every 30 min after sunset) and three dawn counts (10 min recordings every 30 min starting 1.5 hours before sunrise) in 2004, and 5 all-night recordings in 2005 using the HI-MD compression rate on the minidisk recorder. The earliest recordings started 30 min after sunset when the first birds started to arrive on each night. The time of the first vocalization heard for each species was noted on each night.

Times of sunrise, sunset, moonrise, moonset, and fraction of the moon illuminated for Isla Alejandro Selkirk were obtained from the website of the U.S. Naval Observatory (USNO), Astronomical Applications Department website (<http://aa.usno.navy.mil/index.php>). Observations of behavior were performed over two full moons and a new moon in 2004, and one full moon and a new moon in 2005. Watches used in the field were set to GMT -3 according to the USNO Time Services Department (<http://tycho.usno.navy.mil/>).

Measures of Vocal Activity and Sound Analysis

To compare vocal activity at the colony, I counted distinctive notes in the calls of the two species. The most common aerial calls for both species consist of an introductory tone

followed by a series of evenly spaced harmonic notes (*Figure 3.1a,b*). Many petrels in the genus *Pterodroma* have similar sounding vocalizations with a long introductory tone followed by a series of evenly spaced harmonic notes (Warham 1996). The former have been dubbed “Moan” notes, while the latter are known as “Ti” notes, roughly onomatopoeic (Warham, 1996). For consistency I will call the harmonic notes in JFPE and STPE aerial vocalizations Ti notes, although the notes of these species sound quite different from each other. JFPE aerial calls typically contain 1-5 Ti notes while STPE aerial vocalizations include 4-20 Ti notes. Both species also produce other types of aerial calls much less frequently (*Figure 3.1c and d*). Finally, JFPE also vocalize with the same call while on the ground (STPE do not). I did not make an effort to distinguish between ground and aerial calls for this analysis, although the majority of JFPE calls counted were from the air.

I quantified vocal activity by classifying and counting Ti notes for each species at half-hour intervals after sunset (e.g. *Count period 1* = 30–40 min after sunset, *Count period 2* = 60–70, *Count period 3* = 90–100, *Count period 4* = 120–130, and *Count period 5* = 150–160 min after sunset). I tallied Ti notes as opposed to Moan notes or whole calls because the large numbers of petrels calling at any moment precluded identification of individual moan notes and calls (*Figure 3.2*). Counting Ti notes in the field was not feasible. Instead, I made spectrograms from 1-minute samples of point-count recordings to count Ti notes in the lab. Spectrograms were produced by *WildSpectra 1* with a Fast Fourier Transform (FFT) size of 256 and a standard gain (Wiley and Wiley 2005, version 080125, www.unc.edu/~rhwiley/wildspectra). Ti notes could easily be classified to species and counted reliably despite considerable overlap.

I counted the mean number of Ti notes from five separate minute-long samples during each count period (sampled at 0, 2, 4, 6 and 8 min from the beginning of the count period). I calculated the mean number of Ti notes/min for each Count period from these five samples. Counts were made without knowledge of the lunar phase, day of the year, or meteorological conditions during the recording to avoid the potential for biasing counts.

Several sources of error might influence Ti note counts conducted in this manner. For example, within years, point-counts were all recorded at the same recording level, whereas recordings levels may have differed slightly between years (In 2004 recordings were made with a tape-recorder while 2005 recordings were made with a minidisk recorder). However, there was no indication that counts differed significantly between years (*see Results*). Detection errors resulting from the masking of Ti notes on recordings due to background noise are another potential source of error. Activity levels (conspecific and heterospecific) and wind could have influenced the effective size of the sampling area during each recording, and might lead to reduced estimates of activity. To account for the potential effect of wind (either due to changes in petrel behavior, or due to reduced Ti note detections in noise) measurements of wind speed from each night were included as an explanatory variable in the linear model describing the variation in Ti note counts. I did not attempt to correct for potential decreases in Ti note counts resulting from increased vocal activity. Extremely low call counts resulting from saturated recordings (spectrograms) would be easily distinguishable from low counts resulting from minimal activity. At no time in this study were my samples saturated with Ti-notes so that I could not have counted more.

Finally, though STPE Ti notes were harder to count during periods of JFPE peak activity, the higher pitched STPE calls could still be easily heard by observers in the field and on recordings even when JFPE activity was at its loudest. Therefore I am confident that the distinct activity periods for STPE and JFPE reported in this study (*see Results*) are not an artifact of the counting method.

Visual Counts of Aerial Activity During Point-counts

Visual counts of activity were conducted during portions of recording periods on 13 nights in 2004. Counts were performed using a 10-watt dive-light (Princeton Tech) pointed into the air so that the beam was perpendicular to the ground. Any bird that flew through the light during the minute-long sampling period was counted. The beam illuminated a circle with a diameter of ~5 m at 20 m. I could not identify birds to species, as the petrels flew through the light at high speed and at various altitudes. While white light from flashlights can attract petrels to a light source, the dive-light used to make visual counts was equipped with a red filter and did not attract petrels. The same light was used to navigate through the colony at night without disturbing birds on the ground, or inviting collisions with birds flying over the colony.

Vocal Activity and the Lunar Cycle

The study period contained observations during one lunar cycle in 2004 and 2005. In 2004, recordings began on a waning moon that was 85% illuminated, continued through the new moon, and ended near a full moon on a night when 98% of the moon was illuminated (*Figure 3.6*). In 2005, observation began just before a new moon, continued through the full

moon, and ended after the next new moon. I analyzed variation in vocal activity (Mean Ti notes/min) over the lunar cycle in a linear model with 6 explanatory variables: breeding season (*Year*), recording location (*Location*), the progression of the breeding season (*Julian Date*), top wind speed (*WindHi*), cloud cover (*PercCloud*), and the fraction (percentage) of the lunar face illuminated (*VisMoon*). On nights where the moon had not risen or had set before the count period, I corrected the percentage of the moon illuminated during the count period to “0” regardless of lunar phase. Wind and other meteorological data were collected from the same location before sunset on each night with a Kestrel 4000 handheld weather instrument. I used measurements of the highest wind speed to account for blustery weather that might affect recordings (and/or petrel behavior). Cloud cover on above the colony on each night was expressed as a percentage for analysis.

Residuals from all linear models were tested for normality using the Shapiro-Wilks W Test, and when necessary, the count data were transformed to meet this parametric assumption. All statistics were computed with JMP 6.0 (SAS Institute, Cary, NC, USA).

RESULTS

Nightly Arrival Times

Individual STPE were the first to call on 47 of 49 nights. On two nights the first STPE and JFPE were heard at the same time. Arrival times did not differ between years within species but did differ significantly between species (Tukey’s HSD, $Q = 2.62$, $p < 0.05$) (*Figure 3.3*). When data from both years were combined, the mean arrival time for STPE

was 20 min after sunset (± 0.6 s.e., $N = 49$) and 27 min after sunset (± 0.6 , $N = 49$) for JFPE. Therefore STPE arrived 4 ± 0.60 min before the end of civil twilight, and JFPE arrived 3 ± 0.6 min after the end of civil twilight ($t = -8.42$, $p < 0.001$, $N = 49$).

A linear regression of arrival times on the fraction of the moon illuminated (corrected to 0 when moon not above horizon) showed that JFPE arrived slightly later as the fraction of the moon illuminated increased ($r^2 = 0.09$, $F_{(1,47)} = 4.52$, $p = 0.04$). There was no significant difference in the arrival times of STPE related to the lunar cycle ($r^2 = 0.00$, $F_{(1,47)} = 0.06$, $p = 0.80$).

Activity Patterns at Dusk and Dawn

STPE aerial activity peaked in the first 30 – 40 minutes after sunset with a mean count of 327 Ti notes/min (± 19 , $N = 134$). Activity for this species declined dramatically in the second count period (60 – 70 min after sunset) to a mean of 5 Ti notes/min (± 0.8 , $n = 125$), and remained low for the rest of the evening (*Figure 3.4*).

In contrast JFPE vocal activity was generally lowest during the first count period (78.1, ± 8.9 Ti notes/min, $n = 134$) and peaked 60-70 min after sunset at 701 Ti notes/min (± 12.4 , $n = 125$). JFPE vocal activity declined in subsequent count periods, but remained vocally active in the air throughout most of the night. JFPE vocal activity ceased $32 (\pm 6, n = 13)$ min before sunrise. STPE were only recorded on two mornings, once 64 min before sunrise and another 35 min before sunrise.

Thus aerial vocal activity differed considerably for the two study species. STPE arrived first at the colony, reached peak vocal activity 30-40 minutes after sunset, and in essence ceased when JFPE vocal activity reached its peak 60 – 70 minutes after sunset (*Figure 3.4*). Individual STPE were heard sporadically throughout the night, but aerial vocal activity never again reached the levels observed in the first count period. This difference was not a result of STPE calls on the recordings being masked by the more numerous JFPE calls. Though some STPE vocalizations are doubtless missed, STPE calls could be heard and recognized on recordings, and to observers in the field. A linear regression of STPE calls on JFPE calls found no significant correlation between JFPE and STPE Ti note counts during the second Count period ($r^2 = 0.03$, $F_{1,26} = 0.7$, $p > 0.05$) as would be expected if STPE activity were being masked by JFPE activity.

Visual counts of birds flying through a flashlight beam during the 2004 point-counts showed similar trends in aerial activity to these from acoustic counts, though visual observations could not be separated by species (*Figure 3.5*).

Vocal Activity and the Lunar Cycle

Patterns of variation in nightly vocal activity were analyzed using data from the first count period (30-40 min after sunset) for STPE and second count period (60-70 min after sunset) for JFPE, as these corresponded with periods of peak activity for each species. Linear models included 6 variables that might influence vocal activity and/or measurements of vocal activity (see *Methods*).

The linear model explained a significant amount of the variation during the peak activity periods for each species; the first 30-40 min after sunset for STPE ($r^2 = 0.57$, $F_{8,17} = 2.85$, $p < 0.05$, *Table 3.3*), and 60-70 min after sunset for JFPE ($r^2 = 0.77$, $F_{8,15} = 54.54$, $p < 0.0001$, *Table 3.3*). Residuals from the model of JFPE activity during the second count period were not normally distributed (Shapiro-Wilks W Test, $W = 0.91$, $P < 0.05$). A linear model using a square transformed response variable (mean JFPE Ti notes/min²) met the assumption of normally distributed residuals (Shapiro-Wilks W Test, $W = 0.94$, $P = 0.15$), but did not change the results. Therefore only untransformed data are presented here.

During peak activity, STPE activity varied significantly among recording locations in the breeding colony (ANOVA, $F_{3,17} = 4.58$, $p = 0.02$, *Table 3.3*), and increased with the brightness of the visible moon (ANOVA, $F_{1,17} = 6.87$, $p = 0.02$, *Table 3.3*). Recording locations in predominantly STPE areas (Far Side and Stonehenge) had significantly higher STPE vocal activity than areas dominated by JFPE breeding burrows (Point Break and Canelo Crest) (independent contrast, $F_{1,17} = 8.04$, $p = 0.01$).

JFPE vocal activity increased as the illumination of the visible moon increased ($F_{1,15} = 54.54$, $p < 0.0001$) (*Figure 3.6*). Wind speed and cloud cover did not explain a significant portion of the variation in JFPE vocal activity. Neither did year, count location, or progression of the breeding season, at least during the incubation and early chick rearing stages of the breeding season.

Linear models for data from non-peak periods (Count period 2 for STPE, and Count period 1 for JFPE) did not explain a significant amount of the variation in acoustic activity for either species (*Table 3.3*). Mean Ti note counts for both species during these non-peak periods were quite variable, and included many 0 counts and residuals from the linear models were not normally distributed. Square transformation of the response variables (Mean Ti notes/min ²) resulted in normally distributed residuals, but did not change the results for JFPE activity in the first count period. Residuals from the model of STPE activity during the second count period could not be improved by transforming the data. Only results from untransformed data are presented in *Table 3.3*.

Visual counts from 2004 also showed increased aerial activity (mean individuals per min) as the fraction of the moon illuminated increased ($r^2=0.13$, $F_{1,61}=8.97$, $p<0.05$). This represents counts of activity for both species, as STPE and JFPE could not be distinguished using this method.

Injuries From Mid-air Collisions

Aerial collisions were common above the breeding colony although most collisions do not seem to cause permanent injury. Typically birds collided, crashed to the ground, and quickly returned to the air. Nevertheless at least 20 living JFPE with broken wings (or other injuries) were observed on the colony surface in daylight. I found only 2 STPE with similar injuries, presumably caused by mid-air collisions. Working in the colony at night frequently involved first-hand experience with such collisions, as JFPE would often fly into researchers,

sometimes at great speed. Petrels were also observed colliding with stationary tree ferns and tents.

Activity of Predators

Blindados quickly preyed upon injured petrels during daylight hours. These hawks were also a threat to petrels flying in the colony during the day (observed on three occasions), to petrels en route from the sea to the colony in the evening (an elevation gain of over 1,000 m), and when petrels departed the colony at dawn. Blindados were observed and heard above the colony as late as 36 min after sunset and as early as 35 minutes before dawn. On 6 different occasions, I observed groups of STPE mobbing Blindados soaring above the colony at dusk.

DISCUSSION

Acoustic monitoring of the petrel species breeding at Isla Alejandro Selkirk, Chile found that STPE and JFPE have distinct aerial activity periods. Recordings over two lunar cycles in different years showed that STPE and JFPE increased acoustic activity as moonlight increased. This was an unexpected result, and to my knowledge, is the first time that nocturnal seabird species have been found to increase activity in moonlight (*Table 3.2*).

Predation

These observations are consistent with predictions based on the hypothesis that seabird colony attendance and activity patterns are largely shaped by predation risk

(Watanuki, 1986a; Mougeot & Bretagnolle, 2000a; Mougeot & Bretagnolle, 2000b; Brooke & Prince, 1991). Both petrels arrive after sunset at a colony where they face a predation threat from a diurnal hawk (the Blindado). In the absence of nocturnal predation pressure, neither species reduced activity on moonlit nights. In addition, my results raise questions about other patterns of colony attendance. Why do STPE arrive when predators are still active in twilight? Why are STPE only active for a brief period before the arrival of most of the JFPE? And, why do both species increase vocal activity in moonlight at Isla Alejandro Selkirk?

Nocturnal Foraging

Several hypotheses have suggested that foraging strategies, and foraging success can influence activity patterns at seabird colonies. Harris (1969b; 1969a) and Brooke (2004) raised the possibility that the differences in breeding periods, arrival times, and activity periods reflect differences in the availability of resources, and the foraging strategies of different species. Imber (1973, 1975) has suggested that reduced vertical migration of prey species on moonlit nights might reduce colony activity by increasing the amount of time required for foraging. It is not known if STPE or JFPE feed at night.

My results do not support Imber's hypothesis as both species at the Selkirk colony increased vocal activity around the full moon. Differences in foraging strategies, however, might help to explain the brief activity period of STPE. If STPE are nocturnal foragers, while JFPE are not, one might expect a pattern similar to that found in this study. Limited observation of chick provisioning in STPE burrows appear to indicate that breeding birds

returned throughout the night to feed chicks. If un-paired birds leave the colony after a brief 30 minutes of activity in order to take advantage of the rich foraging opportunities, breeding birds, feeding both themselves and a chick, should show the same pattern.

Observations at the breeding colonies of species that do show moonlight avoidance do not seem to provide any evidence for the foraging hypothesis either. Notably, Keitt et al. (2004) found that radio tagged Black-vented Shearwaters *Puffinus opisthomelas* waited just offshore on moonlit nights (sometimes for hours), and only returned to the colony itself when light levels had been reduced to a threshold where predation risk was reduced. Others have reported that even though vocal activity at colonies declined around the new moon, breeders, and even non-breeders continued to visit the colony (Bretagnolle, 1990; Storey & Grimmer, 1986; Mougeot & Bretagnolle, 2000a; Mougeot & Bretagnolle, 2000b)

Sampling errors

It is unlikely that the observed decline in STPE activity resulted from reduced detection of STPE calls during peak JFPE activity. Although the nightly arrival of JFPE is certainly a spectacular phenomenon, the distinct high-pitched Ti notes of STPE could be heard by observers in the field as well as on recordings analyzed in the lab despite the chorus of JFPE in the background. Some STPE calls were doubtlessly missed during analysis, but these detection errors alone would not account for the 99% decrease in Ti notes. Also measures of STPE activity did not increase in subsequent count periods (90, 120, and 150 min after sunset) when JFPE activity declined, as might be expected if STPE calls were being masked on recordings.

If the activity of un-paired individuals increased during the incubation and early chick rearing stages of the breeding season, and the stage of the moon were confounded by the stage of the breeding season, one might obtain a spurious result of increased activity in moonlight. The activity of non-breeders is known to change in many seabird colonies at different stages of the breeding season (Warham 1996). However, because the lunar cycle is not synchronized to the calendar year, the lunar cycles during the 2004 and 2005 differed considerably. In 2004, the new moon occurred around the middle of the field season, while in 2005 there was a full moon halfway through the season (*Figure 3.6*).

Wind speed, cloud cover and differences between years have also been thought to influence activity levels at seabird colonies (Simons, 1985; Jones et al., 1990; Warham, 1996). None of these variables explained a significant amount of the variation in activity of STPE and JFPE. Given that cloud cover can influence moonlight levels, it might seem surprising that cloud cover did not explain more of the variation in vocal activity. Cloud cover measurements were made on each night before sunset. However, cloud cover could change rapidly throughout the night and by location along the ridgeline. Petrels returning to the colony, and flying above the colony might also encounter different levels of cloud cover depending on their elevation and location. This variation might account for the lack of correlation between cloud cover and vocal activity.

The risk of predation and costs of aerial collisions

The previous discussion leaves unexplained the early and brief activity of STPE and the increased activity of both species in moonlight. One possibility is that these patterns are

the result of a trade-off for each species between the risks of predation and aerial collision and the benefits of aerial display. The potential costs of aerial collision are different for STPE than for JFPE.

Aerial collisions are common in the Inocentes Bajos petrel colony. Typically such collisions are inconsequential, but sometimes they result in fatal injuries to one or both individuals. Aerial collisions have even been reported in a number of seabird colonies, including diurnal Wedge-rumped Storm Petrels colonies in the Galapagos (Warham, 1990; Harris, 1969a). If these nocturnal foraging seabirds collide when flying over dense colonies in daylight conditions, the risks for other petrels flying at night are presumably at least as great. How well adapted are nocturnal seabirds to low-light conditions?

An investigation of the eye of the Manx Shearwater (Martin & Brooke, 1991) and measurement of the visual threshold of Common Diving Petrels *Pelecanoides urinatrix* (1989) provide some evidence that procellariiform seabirds cannot see as well in low-light conditions as can other nocturnal birds such as owls. Instead, both petrels have visual capabilities closer to that of two diurnal birds, the Rock Dove *Columba livia* and European Starling *Sturnus vulgaris*. Humans have a lower visual threshold and thus better night vision than diving petrels (Brooke, 1990).

These results suggest that navigation under low-light conditions is a challenge for many seabirds (Warham, 1996; Brooke, 1978a; James, 1986; Brooke, 1990). Many species have been observed colliding with trees, rocks, and researchers that they presumably do not

see at night. Watanuki (1990) hung obstacles in a Rhinoceros Auklet colony, and found that more birds hit these obstacles 60– 90 minutes after sunset than they did in twilight 30-60 minutes after sunset (although the narrow dark “obstacles” may have been difficult for the birds to observe even under the best conditions). Manx shearwaters have even been observed to land at the nests of predatory gulls on really dark nights, ironically encountering the predator they were presumably trying to avoid by coming ashore under the cover of darkness (Corkhill, 1973). Storey and Grimmer (1986) and Manuwal (1974) have even suggested that the risks of encountering predators in such a manner might explain the reduced activity of Cassin’s Auklets and Leach’s Storm Petrels on extremely dark nights.

Because of the lack of specialization for night vision in petrels, nocturnal species with aerial displays presumably face higher risks of collision and injury on dark nights. One explanation for the increase activity of STPE and JFPE in moonlight, as observed in this study, is that moonlight reduces the risks of collision without increasing the risks of predation. Furthermore, the early arrival and brief activity of STPE might be explained by a difference in the risks of predation and collision for STPE and JFPE. The risk of predation in twilight for the small agile STPE is probably less than for the larger JFPE, but the costs of collision during the peak of JFPE activity are presumably greater. Not only are STPE nearly 1/3 the size of JFPE, but they are at least 1/10 as numerous. For STPE there is thus only a brief window when the risk of both predation and collision are low (*Figure 3.7*).

Conclusion

These findings strengthen the argument that nocturnal behavior in seabirds has evolved in response to risks of predation and emphasize that the activity patterns of potential predators are important in determining the timing of activity by seabirds. Many seabirds are nocturnal where there are diurnal predators, avoid moonlight where visual predators hunt by moonlight, and are diurnal in the presence of nocturnal predators. The increased activity of STPE and JFPE on moonlit nights, not reported for any other nocturnal seabird, emphasizes the advantages of avoiding a diurnal predator through nocturnal behavior. The brief period of activity by STPE each night suggests a trade-off between the risks of predation and collision in the dark. Furthermore, the difference in activity of the two species appears to depend on differences in the magnitude of these risks.

One implication of these findings is that each colony and species of seabird might have an optimal activity pattern that differs from those elsewhere. Whether or not immigrant individuals can learn to make the necessary adjustments in activity remains an important open question.

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Table 3.1 Colony attendance patterns for populations of species and species of similar size breeding on islands with either diurnal or nocturnal predators

<i>Species</i>	<i>Colony Location</i>	<i>Colony Attend.*</i>	<i>Diurnal Predator</i>	<i>Nocturnal Predator</i>	<i>Reference</i>
<i>Pterodroma defilippiana</i>	Santa Clara, J.F. Is., Chile	D	-	<i>Asio flammeus</i>	McKown, Ch. 4
<i>Pterodroma longirostris</i>	Alejandro Selkirk, J.F. Is., Chile	N	<i>Buteo polyosoma exsul</i>	-	This study
<i>Pterodroma neglecta</i>	Robinson Crusoe, J.F. Is., Chile	D	-	-	McKown pers. obs.
<i>Pterodroma externa</i>	Alejandro Selkirk, J.F. Is., Chile	N	<i>Buteo polyosoma exsul</i>	-	This study
<i>Puffinus lherminieri</i>	Genovesa, Galapagos, Ecu.	D	-	<i>Asio f. galapagoensis</i>	Harris 1969b
<i>Puffinus lherminieri</i>	Floreana, Galapagos, Ecu.	N	<i>Buteo galapagoensis</i>	-	Harris 1969b
<i>Puffinus lherminieri</i>	Réunion	N	<i>Circus maillardi</i>	?	Bretagnolle et al. 2000
<i>Pterodroma solandri</i>	Lord Howe I., Aus.	D	-	-	Medway 2002
<i>Pterodroma solandri</i>	Norfolk I., Aus.	N	<i>Extinct raptor</i>	-	Medway 2002
<i>Pterodroma nigripennis</i>	Lord Howe, Aus.	D	-	-	Medway 2002
<i>Pterodroma nigripennis</i>	Muttonbird I. NSW, Aus.	N	<i>Haliaeetus leucogaster</i> , <i>Falco peregrinus</i>	-	Medway 2002
<i>Puffinus pacificus</i>	Lord Howe I., Aus.	D	-	-	Medway 2002
<i>Puffinus pacificus</i>	Muttonbird I. NSW, Aus.	N	<i>Haliaeetus leucogaster</i> , <i>Falco peregrinus</i>	-	Medway 2002
<i>Oceanodroma castro</i>	Genovesa, Galapagos, Ecu.	N	-	<i>Asio f. galapagoensis</i>	Harris 1969a
<i>Oceanodroma tethys</i>	Genovesa, Galapagos, Ecu.	D	-	<i>Asio f. galapagoensis</i>	Harris 1969a
<i>Oceanodroma tethys</i>	Ferrol I., Peru	N	?	?	Ayala & Sanchez-Scaglioni 2007
<i>Cerorhinca monocerata</i>	Sea Lion Caves, OR, US	D	?	?	Wehle, 1980; Thoresen 1980
<i>Cerorhinca monocerata</i>	Teuri I. and Daikoku I., Jap.	C/N	<i>Larus crassirostris</i> (kleptoparasite)	-	Thoresen 1983; Watanuki 1990
<i>Calonectris diomedea</i>	Salvages, Por.	D/C/N	?	?	Bretagnolle 1990; Hamer and Read 1987
<i>Calonectris diomedea</i>	Berlenga I., Por.	N	?	?	Granadeiro et al. 1998

* Volony attendance: D = Diurnal, N = Nocturnal, C = Crepuscular

Table 3.2 **Effect of moonlight on colony attendance and vocal activity in seabird species**

<i>Species</i>	<i>Location</i>	<i>Moonlight effect on activity?</i>	<i>Predator</i>	<i>Reference</i>
Family – Alcidae				
<i>Synthliboramphus antiquus</i>	Reef I., BC, Can.	Yes / -	<i>Haliaeetus leucocephalus</i>	Jones et al. 1990
<i>Cerorhinca monocerata</i>	Teuri I. & Daikoku I., Jap.	Yes / -	<i>Falco peregrinus</i>	Watanuki 1990
<i>Ptychoramphus aleuticus</i>	Southeast Farallon I., US	Yes / -	<i>Larus crassirostris</i>	Manuwal 1974
Family – Procellariidae				
<i>Halobaena caerulea</i>	Mayes I., Kerguelen Arch.	Yes / -	<i>Catharacta skua lönnbergi</i>	Mougeot & Bretagnolle 2000
<i>Pachyptila vittata</i>	Whero I., NZ	Yes / -	<i>Catharacta skua lönnbergi</i>	Richdale 1965b
<i>P. belcheri</i>	Mayes I., Kerguelen Arch.	Yes / -	<i>Catharacta skua lönnbergi</i>	Mougeot & Bretagnolle 2000
<i>P. turtur</i>	Whero I., NZ	Yes / -	<i>Catharacta skua lönnbergi</i>	Richdale 1965b
<i>Calonectris diomedea</i>	Salvage I.	No	?	Bretagnolle 1990
<i>C. diomedea</i>	Berlenga I, Por.	No	?	Granadeiro et al. 1998
<i>C. diomedea</i>	Azores	Yes / -	?	Klomp & Furness 1992
<i>Puffinus bulwerii</i>	Salvage I.	Yes / -	<i>Larus michahellis</i>	Bretagnolle 1990
<i>P. carneipes</i>	Eclipse I., Aus.	Yes / -	<i>Circus approximans</i>	Warham 1958
			<i>Haliaeetus leucogaster</i>	
			<i>Falco berigora</i>	
			<i>Accipiter fasciatus</i>	
<i>P. creatopus</i>	Santa Clara, J.F. Is., Chile	Yes? / -	<i>No known avian predator</i>	Hodum et al. 2003
<i>P. tenuirostris</i>	Cat I., Tas., Aus.	Yes / -	<i>Circus approximans</i>	Warham 1960
			<i>Falco peregrinus</i>	
<i>P. puffinus</i>	Skokholm and Skomer, UK	Yes / -	<i>Larus marinus,</i>	Lockley 1942; Harris 1966;
			<i>L. argentatus.</i>	Corkhill 1973; Brooke 1990
			<i>L. fuscus</i>	
<i>P. puffinus</i>	Middle Lawn Is., Can.	Yes / -	<i>Larus marinus,</i>	Storey & Grimmer 1986
			<i>L. argentatus</i>	
<i>P. yelkouan</i>	Hyères, Fr.	Yes / -	<i>Larus michahellis</i>	Bourgeois et al. 2008
<i>P. newelli</i>	Kauai, US	No?	?	Day & Cooper 1995

Table 3.2 (cont'd) Effect of moonlight on colony attendance and vocal activity in seabird species

<i>Species</i>	<i>Location</i>	<i>Moonlight effect on activity?</i>	<i>Predator</i>	<i>Reference</i>
<i>Family – Procellariidae</i>				
<i>P. opisthomelas</i>	Natividad I., Mex	Yes / -	<i>Larus occidentalis</i>	Keitt, et al. 2004
<i>P. huttoni</i>	Mt. Uterau, NZ	Yes / -	<i>Falco novaeseelandiae</i> <i>Circus approximans</i>	Harrow 1976
<i>P. lherminieri</i>	Réunion I.	Yes / -	<i>Circus maillardi</i>	Bretagnolle et al. 2000
<i>P. assimilis</i>	Salvages I., Por.	Yes / -	<i>Larus michahellis</i>	Bretagnolle 1990
<i>Pterodroma externa</i>	Alejandro Selkirk, J.F. Is., Chile	Yes / +	<i>Buteo polyosoma exsul</i>	This study
<i>P. sandwichensis</i>	Kauai, US	No?	?	Day and Cooper 1995
<i>P. hasitata</i>	Haiti	Yes / -	?	Wingate, 1964
<i>P. lessonii</i>	Mayes I., Kerguelen Arch.	Yes / -	<i>Catharacta skua lönnbergi</i>	Mougeot & Bretagnolle 2000
<i>P. longirostris</i>	Alejandro Selkirk, J.F. Is., Chile	Yes / +	<i>Buteo polyosoma exsul</i>	This study
<i>Family – Hydrobatidae</i>				
<i>Pelagodroma marina</i>	Salvage I.	Yes / -	<i>Larus michahellis</i>	Bretagnolle 1990
<i>Pelagodroma marina</i>	Whero I., NZ	Yes / -	<i>Catharacta skua lönnbergi</i>	Richdale 1965a
<i>Oceanodroma castro</i>	Salvage I.	Yes / -	<i>Larus michahellis</i>	Bretagnolle 1990
<i>O. castro</i>	Plaza I., Galapagos, Ecu.	Yes / -	<i>Asio flammeus galapagoensis</i>	Harris 1969a
<i>O. leucorhoa</i>	Little River Rock, CA, US	Yes / -	<i>Larus occidentalis</i> , <i>Bubo virginianus</i> , <i>Falco peregrinus</i>	Harris 1974

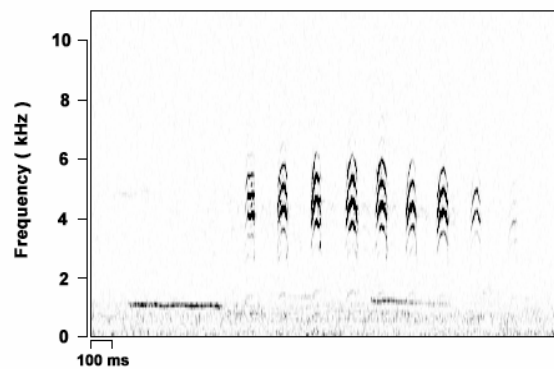
Table 3.2 (cont'd) Effect of moonlight on colony attendance and vocal activity in seabird species

<i>Species</i>	<i>Location</i>	<i>Moonlight effect on activity?</i>	<i>Predator</i>	<i>Reference</i>
<i>Family – Hydrobatidae</i>				
<i>O. leucorhoa</i>	Daikoku I. Jap.	Yes / -	<i>Larus schistisagus</i>	Watanuki 1986
<i>O. leucorhoa</i>	Green I., Bay of Fundy, Can	Yes / -	<i>Larus marinus</i> , <i>L. argentatus</i>	Gross 1935
<i>O. homochroa</i>	SE Farallon Is., CA, US	Yes / -		Ainley et al. 1990
<i>O. furcata</i>	Barren I., AK, US	Yes / -	<i>Larus glaucescens</i> , <i>Corvus corax</i> , <i>Haliaeetus leucocephalus</i> <i>Falco peregrinus</i>	Boersma et al. 1980
<i>O. furcata</i>	Little River Rock, CA, US	Yes / -	<i>Larus occidentalis</i> , <i>Bubo virginianus</i> , <i>Falco peregrinus</i>	Harris 1974
<i>Family – Pelecanoididae</i>				
<i>Pelecanoides georgicus</i>	South Georgia I.	Yes / -	<i>Catharacta antarctica</i>	Payne & Prince 1979
<i>P. urinatrix exsul</i>	South Georgia I.	Yes / -	<i>Catharacta antarctica</i>	Payne & Prince 1979
<i>P. urinatrix</i>	Mayes I., Kerguelen Arch.	Yes / -	<i>Catharacta skua lönnbergi</i>	Mougeot & Bretagnolle 2000

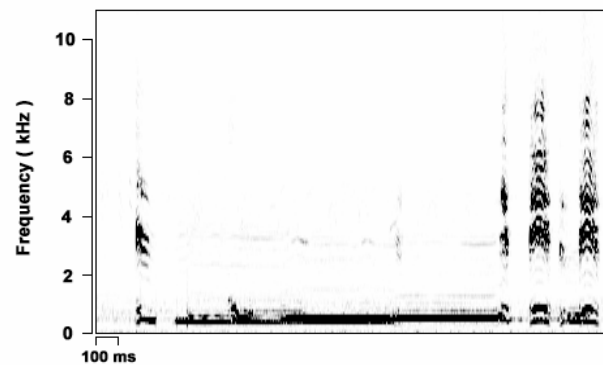
Table 3.3 Variation in STPE and JFPE vocal activity (Mean Ti notes/min) during the first and second count periods

Species		30-40 min after sunset				60-70 min after sunset				
STPE	Whole Model	r^2 = 0.57				Whole Model	r^2 = 0.31			
	Source	df	SS	F Ratio	Prob>F	Source	df	SS	F Ratio	Prob>F
	Model	8	122.02	2.85	0.03*	Model	8	0.08	0.84	0.583
	Error	17	90.95			Error	15	0.19		
	Total	25	212.96			Total	23	0.27		
	Source	df	SS	F Ratio	Prob>F	Source	df	SS	F Ratio	Prob>F
	Year	1	12918	0.67	0.42	Year	1	9.71	0.21	0.65
	DayofYear	1	3769	0.20	0.66	DayofYear	1	20.73	0.46	0.51
	Location	3	264672	4.58	0.02*	Location	3	75.53	0.55	0.65
	WindHi	1	15293	0.79	0.39	WindHi	1	60.32	1.32	0.27
PercCloud	1	6691	0.35	0.56	PercCloud	1	1.39	0.03	0.86	
VisMoon	1	132221	6.87	0.02*	VisMoon	1	62.48	1.37	0.26	
JFPE	Whole Model	r^2 = 0.29				Whole Model	r^2 = 0.77			
	Source	df	SS	F Ratio	Prob>F	Source	df	SS	F Ratio	Prob>F
	Model	8	16.19	0.87	0.56	Model	8	92.24	6.16	0.001***
	Error	17	39.39			Error	15	28.10		
	Total	25	55.58			Total	23	120.34		
	Source	df	SS	F Ratio	Prob>F	Source	df	SS	F Ratio	Prob>F
	Year	1	1792	0.21	0.65	Year	1	3813	0.57	0.46
	DayofYear	1	19136	2.29	0.15	DayofYear	1	13111	1.94	0.18
	Location	3	5129	0.20	0.89	Location	3	3113	0.15	0.93
	WindHi	1	2791	0.33	0.57	WindHi	1	1582	0.23	0.64
PercCloud	1	6311	0.76	0.40	PercCloud	1	1156	0.17	0.68	
VisMoon	1	1889	0.23	0.64	VisMoon	1	196328	29.11	<.0001***	

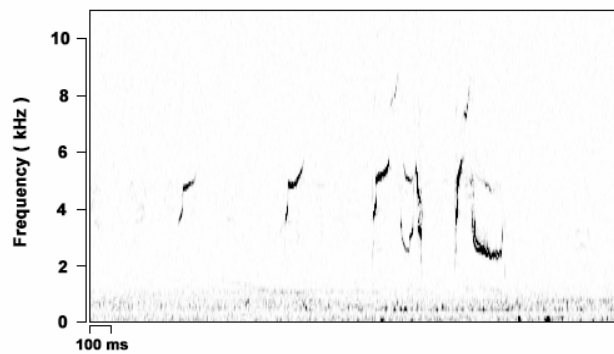
Figure 3.1 Aerial vocalizations of STPE and JFPE



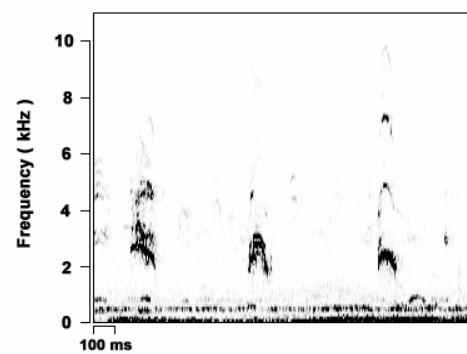
a) STPE aerial call (moan note followed by Ti notes)



b) JFPE aerial call (Ti note, moan, 3 Ti notes)

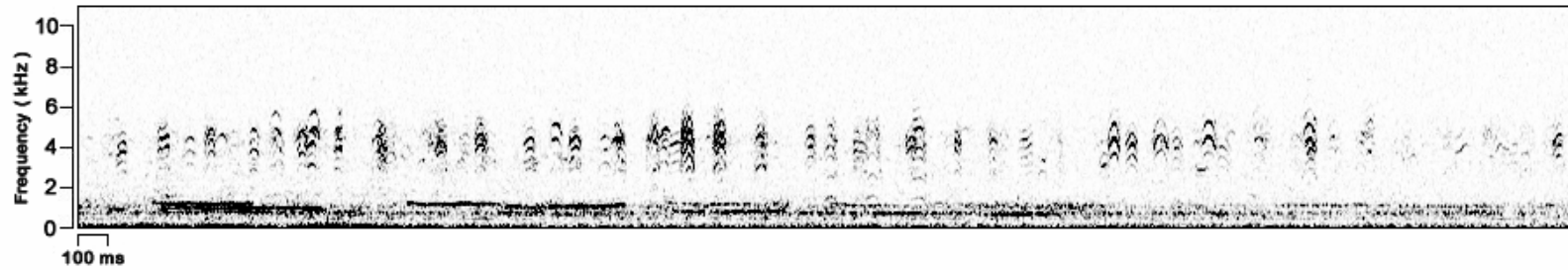


c) STPE secondary aerial call type

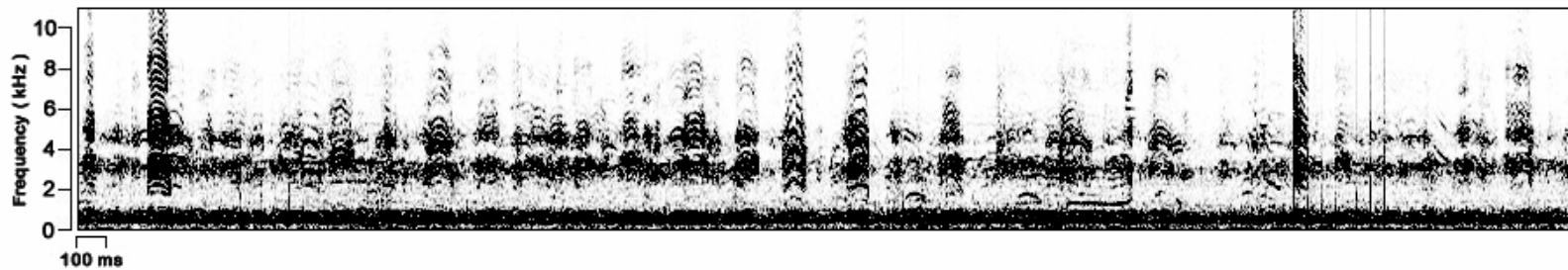


d) JFPE secondary aerial call type

Figure 3.2 Maximal STPE and JFPE vocal activity at the colony (Feb 18, 2005, 5-s spectrogram frame)



a) Example of maximal STPE vocal activity (36 minutes after sunset)



b) Example of maximal JFPE vocal activity (68 minutes after sunset)

Figure 3.3 Arrival times for JFPE and STPE by year (Tukey HSD, $Q = 2.62$, $p < 0.05$)

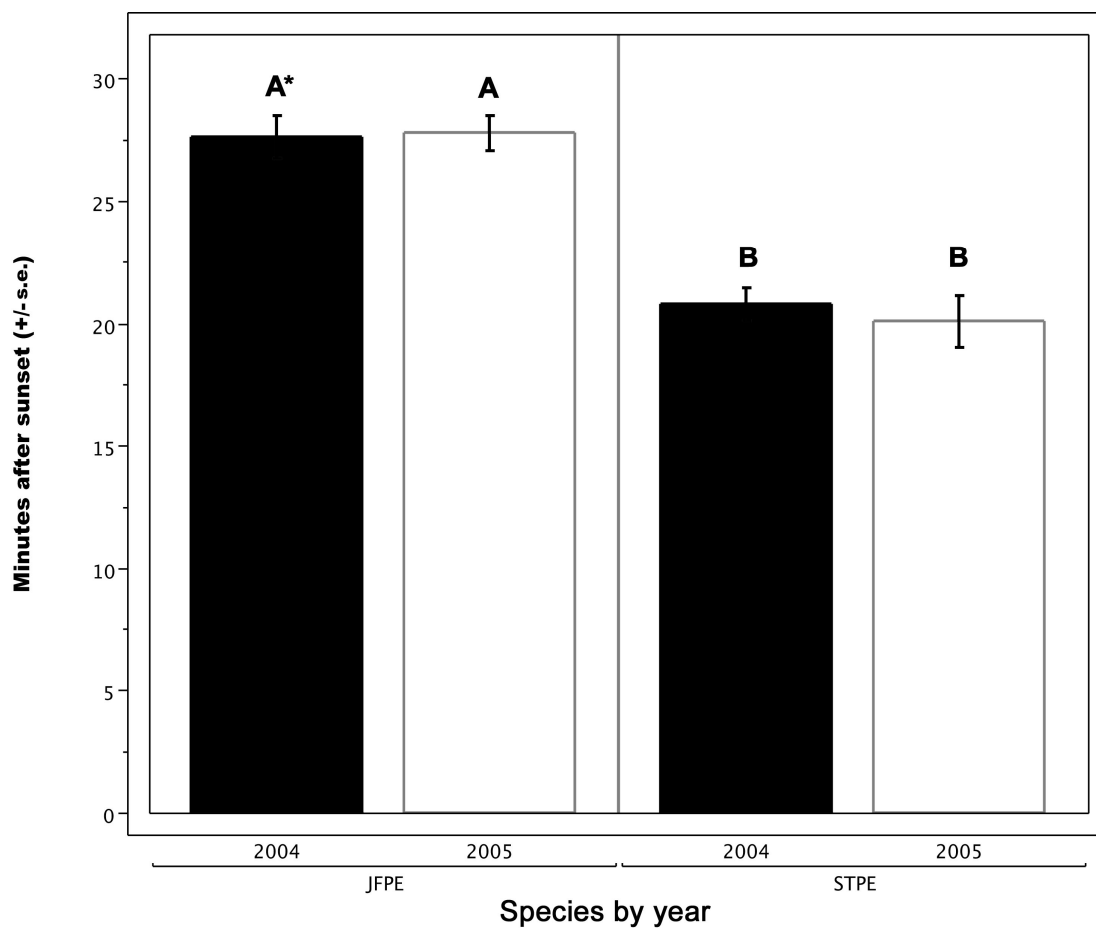


Figure 3.4 Mean number of Ti notes per minute for JFPE and STPE by minute after sunset

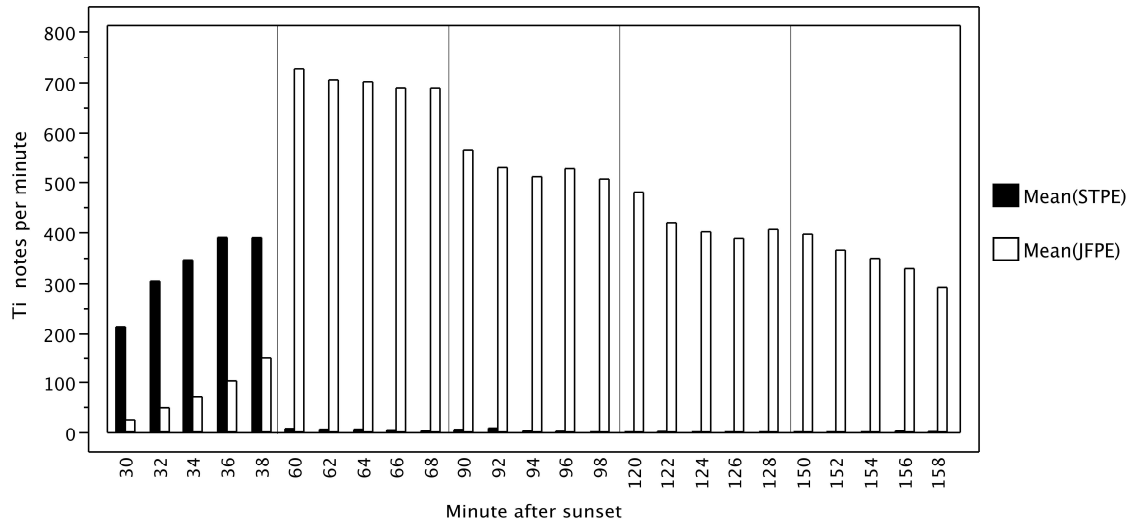


Figure 3.5 Mean acoustic (Ti notes/min) and visual (individuals/min) activity

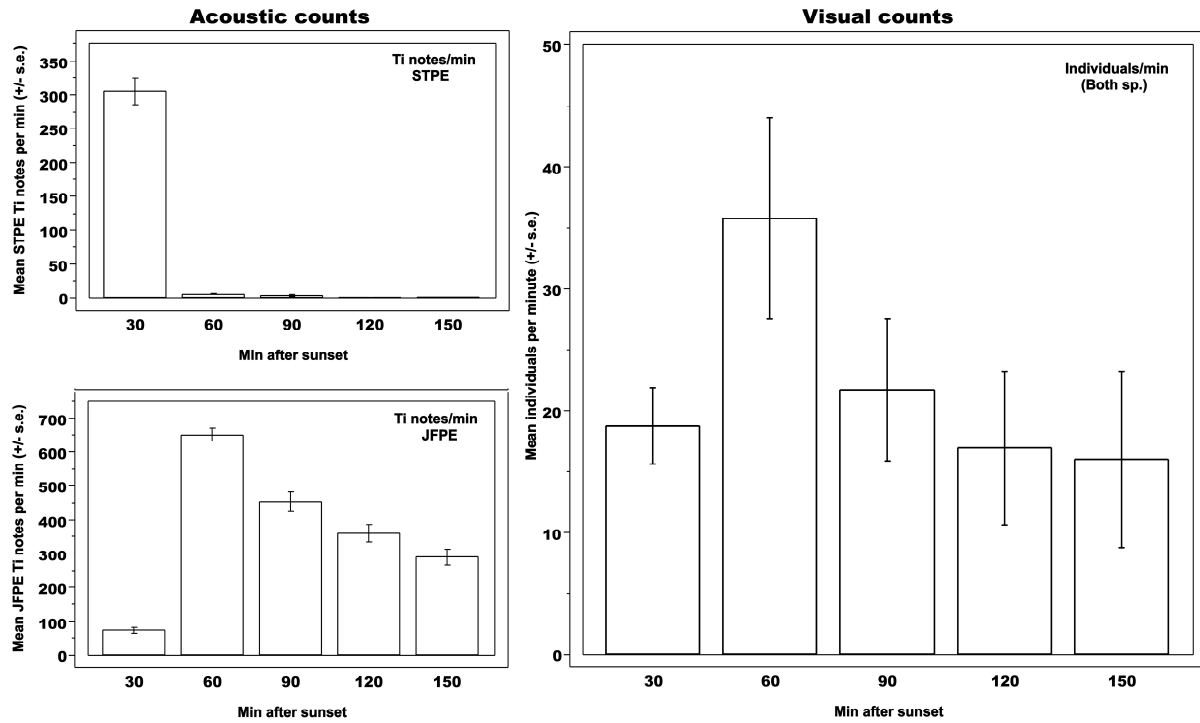


Figure 3.6 JFPE vocal activity through the lunar cycle (2004 and 2005)

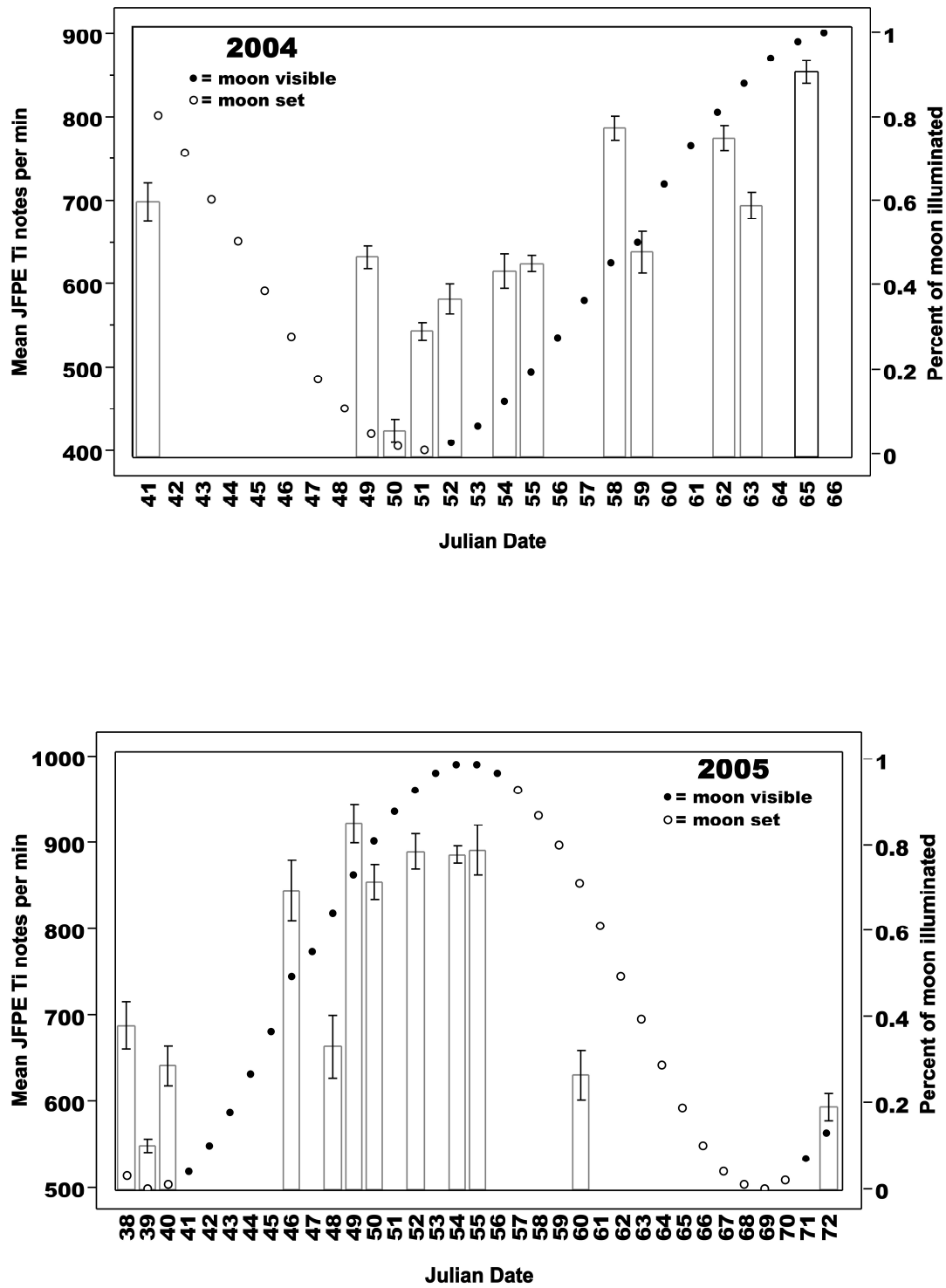
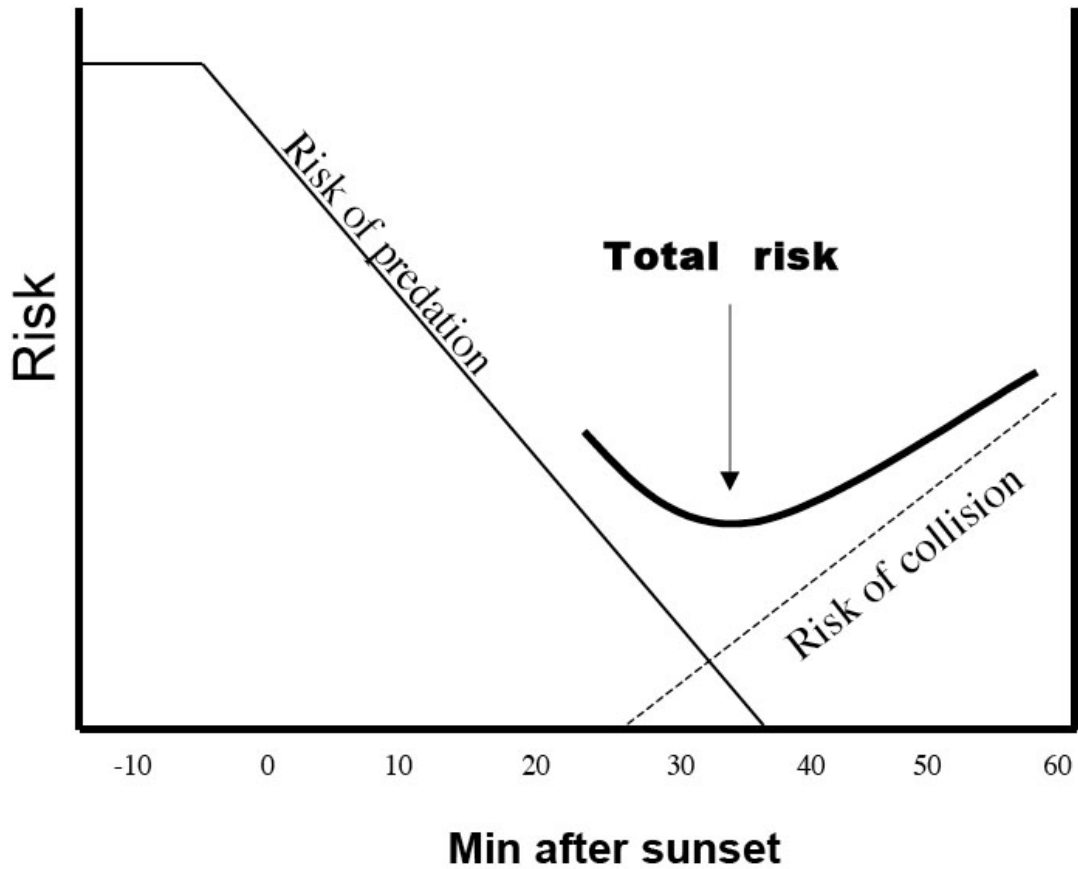


Figure 3.7 Simplified illustration of potential tradeoffs faced by STPE flying over the colony (risk of predation solid line; risk of collision with JFPE, dashed line; total risk, heavy line). The theoretical total risk reaches a minimum early in the night.



CHAPTER 4

A comparison of acoustic communication in *Cookilaria* petrels: phylogeny and environmental constraints

ABSTRACT

The species of petrels in the subgenus *Cookilaria* (genus *Pterodroma*) have similar vocalizations that allow comparisons of homologous characters between species. The vocalizations of 7 petrels in this group were compared in order to address three environmental factors that could affect communication: predators, coexisting species, and habitat. A relationship between predators and activity patterns is suggested by the only diurnal species in this group, *P. defilippiana*, which breeds on an island with only nocturnal predators. This diurnal species is also the only species that lacks vocal features that would make a signal easily locatable. The vocalizations of two species (*P. cookii* and *P. pycrofti*) that breed in close proximity to each another differ strikingly in dominant frequencies and intervals between notes. However, these differences are not easily explained by selection for greater species distinctiveness. First the frequency differences are correlated with differences in body mass. Furthermore, vocalizations of a *P. cookii* population breeding in proximity to *P. pycrofti* colonies did not differ from those in a population isolated from *P. pycrofti*. There was also no support for the prediction that species breeding in forests should have longer intervals between notes in order to counteract degradation by reverberation in closed habitats. The similarities in their vocalizations support the hypothesis that these species are closely related. Furthermore, the two *Cookilaria* species breeding in the Juan Fernández Islands share a unique feature of their aerial calls, and ground calls with similar structures, a suggestion that these species might be more closely related than currently thought. This study emphasizes the need for a molecular phylogeny of *Pterodroma* and for comparisons of the vocalizations of a larger number of species.

INTRODUCTION

The *Pterodroma* petrels are the most speciose genus in the order Procellariiformes. The 32 recognized species of *Pterodroma* represent 25% of the 125 species in the order. These pelagic predators breed on isolated islands in mid and low latitudes of the Pacific, Atlantic, and Indian Oceans, though no species breeds in the North Pacific (Brooke 2004). Though wide ranging, individuals of many species of *Pterodroma* return to breed at the colony where they were born (natal philopatry). Nearly a third (10) of the species breed on only one island or archipelago. For comparison, the genus with the next highest number of species and island endemics, the *Puffinus* shearwaters, contains 19 species, only 2 of which are single-island endemics (Brooke 2004).

The high degree of natal philopatry observed in many seabirds can lead to genetic and phylogenetic structuring within species, including reproductive isolation and speciation. Friesen et al. (2007a) reviewed genetic structuring in the auks (Charadriiformes, Alcidae), penguins (Sphenisciformes), gulls (Charadriiformes, Laridae), and petrels (Procellariiformes) to test theories about the causes of genetic differentiation among seabird colonies. They concluded that the strongest influences on genetic structuring within geographic regions affected the range of movement of potential dispersers between colonies (the presence of land and ice barriers between colonies, foraging ranges from colonies, and mixing of individuals from different colonies in non-breeding ranges). However, their study did not explore factors that influence the fate of immigrants following dispersal between colonies.

The primary evidence that dispersal does occur in philopatric species is, of course, the current presence of seabird colonies on islands throughout the world. Why individuals of highly philopatric seabirds like the *Pterodroma* petrels would choose to disperse to another colony is not understood, nor is it clear whether dispersal rates are influenced by factors at the natal colony (such as population density and resource availability) or changing conditions in remote locations (newly available breeding habitat or foraging habitat). Many immigrants are probably non-breeding individuals wandering in the years before their first return to their natal colony. Numerous records of seabirds found in colonies outside of their normal range indicate the potential for dispersal among distant colonies. For example, *Pterodroma externa*, and *P. longirostris*, two species breeding exclusively in the Juan Fernández Islands of Chile, have been found in the Chatham Islands and the North Island of New Zealand respectively, locations where neither species is known to breed (Falla, 1961; Imber et al., 1991). Prospecting *P. externa* are also heard on most nights of the breeding season in Pink-footed Shearwater *Puffinus creatopus* colonies on Isla Robinson Crusoe, and Isla Santa Clara, located almost 80 miles from their breeding colony on Isla Alejandro Selkirk (Hodum et al., 2002). On Midway atoll, individual Short-tailed Albatrosses *Phoebastria albatrus* have returned over repeated breeding seasons, despite the lack of potential conspecific mates on that island (Cousins et al., 2000). Presumably these *P. albatrus* will not breed with any of the local Black-footed Albatrosses *P. nigripes* or Laysan Albatrosses *P. immutabilis* at that location. These different species have evolved species-specific visual and acoustic signals important for pair formation and (usually) for reproductive isolation. Might signals also differ among populations of a species breeding in distant colonies?

Among the Procellariidae, many of the species are nocturnal at colonies (Warham 1996) and thus rely mostly on acoustic signals for communication in the dark. Vocal differences among populations have been described in at least 7 procellariids (James, 1985a; Bretagnolle, 1989; Bretagnolle, 1995; Bretagnolle & Genevois, 1997; Thibault & Bretagnolle, 1998; Bretagnolle & Lequette, 1990a; Tomkins & Milne, 1991). Breeding signals (and preferences for those breeding signals) are normally under strong stabilizing selection, because individuals with signals not recognized by potential mates (or preferences for signals not present in a population) would presumably have reduced reproductive success (Coyne & Orr, 2004). In contrast, between isolated populations, variation in signals, and preferences could result from genetic drift, mutation, and natural and sexual selection of signals and preferences (Kirkpatrick & Ryan, 1991). Environmental factors can favor the evolution of different signals and preferences in different habitats (Endler, 1988; Endler, 1992a; Endler, 1992b). These factors can include the presence and behavior of predators or parasites, the presence of closely related species, and abiotic factors that influence the transmission and perception of signals (Wiley & Richards, 1978; Wiley & Richards, 1982b; Wiley, 1991) (see Chapter 1).

The species of petrels in the subgenus *Cookilaria* provide an opportunity to study the reproductive signals of a group of closely related seabirds breeding in colonies that differ in habitat, predators, and coexisting species, all of which can influence the transmission and reception of acoustic signals (Wiley & Richards, 1982b; Wiley & Richards, 1978) (*Table 4.1*).

The Cookilaria

The *Cookilaria* species have long been recognized as a taxonomic group because of their comparatively small size, skull structure, plumage patterns, and blue legs (Bourne, 1983;

Murphy, 1929; Warham, 1990). There are currently 6 species recognized in the subgenus *Cookilaria* (Brooke, 2004a) (*Figure 4.1, Table 4.1*). In this analysis I also include recordings from the New Caledonian Petrel *P. leucoptera caledonica*, currently considered a subspecies of Gould's Petrel *P. l. leucoptera*. In the past, at least three other species have been proposed for inclusion in this group: Black-winged Petrel *P. nigripennis*, Bonin Petrel *P. hypoleuca*, and Chatham Island Petrel *P. axillaris* (Warham, 1990).

In this paper I describe the vocalizations of two species in the group (Stejneger's Petrel *P. longirostris* and DeFilippi's Petrel *P. defilippiana*) for the first time. I also compare calls of two species breeding in New Zealand (Cook's Petrel *P. cookii* and Pycroft's Petrel *P. pycrofti*). I then compare the aerial calls of all six taxa in the *Cookilaria* group (*Table 4.1*). I use published descriptions of the aerial calls of the three additional species sometimes grouped with *Cookilaria* to evaluate whether the calls of these species support their inclusion in this subgenus. Finally, the islands on which these species breed differ in a number of environmental features that can affect acoustic communication: predators, overlapping species, and habitat, and I explore the potential influence of these factors on the vocalizations and vocal behavior of these species.

Predators

The species of *Cookilaria* breed in colonies with a variety of potential avian predators. Predators and parasites can increase the costs of signaling and thus can influence both the evolution of signals and signaling activity patterns (Ryan, 1986; Ryan et al., 1982; Tuttle & Ryan, 1981; Zuk & Kolluru, 1998; Wagner & Basolo, 2007). In many seabirds, diurnal predators and kleptoparasites have resulted in the evolution of nocturnal activity at colonies

(Brooke & Prince, 1991; Mougeot & Bretagnolle, 2000a; McNeil et al., 1993). While the potential avian predators are not known in every colony location, I present one contrast between Stejneger's Petrel *P. longirostris* and Defilippi's Petrel *P. defilippiana*. Both species breed on separate islands in the Juan Fernández archipelago of Chile and face different predator types; *P. longirostris* breeds on Isla Alejandro Selkirk in the austral summer and is preyed upon by the diurnal Red-backed Hawk *Buteo polyosoma exsul*, while *P. defilippiana* breeds on Isla Santa Clara during the austral winter, and is preyed upon by the nocturnal Short-eared Owl *Asio flammeus*.

Overlapping species

Where members of the same genus (congeners) with similar reproductive signals occur in the same location, individuals discriminating between calls (receivers) face the risk of responding to the signals of inappropriate mates. If hybridization reduces reproductive success, species face selection for breeding signals that reduce overlap and decrease the probability of hybridization (known as reproductive character displacement) (Pfennig & Simovich, 2002; Brown & Wilson, 1956). A classic test of this reproductive character displacement is to compare the reproductive signals of populations that overlap with congeners to those from populations that do not overlap with congeners. If reproductive character displacement has occurred overlapping populations show differences in breeding behavior that reduces the possibility of mating with congeners, while non-overlapping populations will not.

In this study 2 species, Cook's Petrel *P. cookii* and Pycroft's Petrel *P. pycrofti* breed on islands in the Hauraki Gulf of New Zealand that are close enough (~30 miles) that prospecting

individuals are likely to encounter breeding individuals of the other species. I also measured calls of *P. cookii* recorded in a second colony (Codfish Island) over 800 miles to the south, where *P. pycrofti* is not likely to occur. Here I test whether there is evidence of reproductive character displacement in the calls of COPE breeding in proximity to PYPE .

Habitat

Five of the *Cookilaria* species breed in forests, the other two in open habitats (*Table 4.1*). Vocalizations in forests are degraded and attenuated by the vegetation. Leaves, trunks, and branches in the forest reflect and scatter the energy in acoustic signals. These reverberations obscure intervals between elements of a signal at any one frequency (Morton, 1975; Richards & Wiley, 1980; Wiley & Richards, 1982b). In order to minimize the effects of reverberation of the temporal structure of signals, species communicating in forests should produce signals with long intervals between elements at any one frequency.

Scattering also attenuates acoustic signals in forests, an effect that increases monotonically with frequency (Wiley, 1991; Morton, 1975; Wiley & Richards, 1982b). Marten and Marler (1977) found that frequencies above 1000 - 2000 Hz are attenuated more rapidly in dense vegetation than in open habitat and more in deciduous forests than in coniferous forests. However, lower frequencies should attenuate less in all habitats (Wiley 1991). Therefore, although a number of studies have tested predictions that dominant frequencies should differ between habitats (sometimes referred to as the Acoustic Adaptation Hypothesis), it is not clear from basic principles what the basis for these predictions might be. A number of studies have reported differences in dominant frequencies between species inhabiting open and closed

habitats, but other factors, such as body mass, phylogeny, and patterns of ambient noise might also explain these differences (Wiley, 1991; Ryan & Brenowitz, 1985).

Here I test whether the aerial calls of *Cookilaria* species breeding on forested islands have notes that are spaced farther apart, as predicted if the vocalizations of these species have evolved to reduce the effects of reverberation.

METHODS

Recordings and Acoustic Analysis

I obtained recordings of the vocalizations from all 6 species considered part of the *Cookilaria* group, Stejneger's Petrel (STPE), DeFillipe's Petrel (DFPE), Pycroft's Petrel (PYPE), Cook's Petrel (COPE), Gould's Petrel (GOPE), and Collared Petrel (CLPE) (Warham, 1996; Warham, 1990; Bourne, 1983; Roberson & Bailey, 1991; Brooke, 2004a; Imber, 1985). I also included recordings of the New Caledonian Petrel (NCPE), currently considered a subspecies of GOPE (Imber & Jenkins, 1981). In each case, my recordings come from a single population on one island, except COPE, for which I have recordings from two populations (COPE, COPE2, *Table 4.1*).

I recorded the vocalizations of STPE (January-March 2004, 2005), DFPE (August-September 2005), COPE (December 2005), and PYPE (January 2006) at 4 separate breeding colonies for these species (*Table 4.1*). These include recordings of aerial calls, ground calls, and calls from within breeding burrows. All were recorded with a Sony TC D5 Pro II tape recorder

or a Sony MZ-NH900 minidisk recorder (in the linear PCM/un-compressed setting). Ambient acoustic activity at breeding colonies (including birds calling above the colony and on the surface) was recorded with a Senheisser ME-20 omnidirectional microphone and a Shure omnidirectional dynamic microphone (Radio Shack 33-3006). Calls from individuals on the surface and in breeding burrows were recorded with a Senheisser ME-80 directional microphone.

Aerial activity in a second colony of COPE (COPE2) on Codfish Island, New Zealand, was recorded by Matt Rayner (University of Auckland) with the same minidisk recorder and Shure omnidirectional microphone described above. Recordings of the aerial vocalizations of three other taxa were obtained from the McPherson Natural History Unit Sound Archive (GOPE, NCPE) and from Dick Watling of Environmental Consultant's (Fiji) Ltd. (CLPE). Information was not available about the equipment used to make these recordings. Because different microphones (parabolic, directional, and omnidirectional) sample different aspects of ambient noise, background noise in these recordings cannot be easily compared with that in the previously described recordings.

Recordings were digitized and analyzed with *WildSpectra2* and *WildSpectral* respectively (Wiley and Wiley 2005, version 080125, www.unc.edu/~rhwiley/wildspectra) on an Apple MacMini computer (with Intel Core Duo II processors). Digitized sound files were saved at a sampling rate of 22.05 kHz. Measurements of frequencies were made on spectrograms with a Fast Fourier Transform (FFT) size of 516 (frequency resolution = 86 Hz), and all temporal measurements were made with an FFT size of 256 (temporal resolution = 5.8 ms). Spectrograms presented in this paper were produced using *WildSpectral*.

I measured 8 features from spectrograms of the aerial calls displayed by *WildSpectra2* (Figure 4.2). Except for DFPE, the aerial calls of all of the species in this study consisted of calls with two types of notes, a “Moan” note followed by a series of harmonic “Ti” notes (Figure 4.2, Figure 4.3). Three measures of the temporal features of these calls included the interval between notes (*NN*), the length of the Moan note (*LMO*), length of the Ti notes (*LTI*). Five measures of frequencies included the dominant frequency of the Moan note (*DFMO*), the 6-dB bandwidth of the Moan note (*6DBMO*), the dominant frequency of each Ti note (*DFTI*), the 6-dB bandwidth of each Ti note (*6DBTI*), and the mean harmonic interval of each TI note (*MHITI*). The dominant frequency of any note is the frequency with the greatest amplitude in a power spectrum. The 6-dB bandwidth is the frequency range with amplitudes within 6 dB above and below the dominant frequency. The mean harmonic interval was measured on a narrow frequency section in the middle of each Ti note as the mean difference in Hz between each of the harmonic overtones of the note (Figure 4.2). *MHITI* estimates the fundamental frequency of each Ti note, almost always equal to the frequency of the first harmonic in the note, although for some species the lower harmonics were absent in spectrograms. I focused on the aerial calls for these species because of their presumed homology, the availability of recordings for each species, and their importance in courtship behavior.

Individual Ti notes in an aerial call were presumably not independent statistically, so I averaged the measurements from the Ti note bouts for 5 different calls and used these mean values for comparison ($N = 5$ Ti note mean values per species). Calls analyzed were selected haphazardly from recordings on different nights or at widely different times for STPE, DFPE,

COPE, PYPE, and COPE2. The calls of GOPE, NCPE, and CLPE sampled for measurements could not be so carefully separated. I limited the number of calls measured for each species to 5, the largest number that could be measured from recordings of CLPE.

Statistical Analysis

All statistics were computed with JMP 6.0 (SAS Institute, Cary, NC, USA) with $\alpha = 0.05$.

Permits and Institutional Oversight

This study was approved by the Institutional Animal Care and Use Committee of the University of North Carolina at Chapel Hill (IACUC Protocol: 04-304.0-C). Work within the Juan Fernández Islands National Park was conducted under the Corporación Nacional Forestal (CONAF) research permit for the Juan Fernández Islands #021 and the Servicio Agrícola y Ganadero (SAG) permit #3419. Field work in New Zealand was carried out under Department of Conservation National Permit NO-17676-RES and Landing Permit NO-17622-LND. Work on Hauturu (Little Barrier Island) was carried out in collaboration with Matt Rayner (The University of Auckland) under Research Permit Number AK/14677/RES.

RESULTS

Vocalizations of STPE, DFPE, COPE and PYPE

STPE, DFPE, COPE and PYPE were each recorded on one island where it was the only *Cookilaria* breeding (although COPE and PYPE were on islands only about 30 miles apart in the northern Hauraki Gulf of New Zealand's North Island). All 4 species were recorded during approximately the same period of the breeding cycle (end of incubation and beginning of chick

rearing). Three types of calls were heard and recorded at each location: aerial calls, ground calls, and burrow calls (*Figures 3, 4 and 5*).

Aerial calls of STPE, COPE, and PYPE consisted of an introductory tonal note (Moan note) followed by a series of harmonic notes (Ti notes). The aerial calls of DFPE did not include Ti notes. A second type of aerial call was recorded from STPE, DFPE, and COPE, but these were heard much less frequently and were not measured (*Figure 4.3*).

Ground calls were recorded for all 4 species. These consisted of low-frequency harmonic notes (*Figure 4.4*). The ground calls of STPE, PYPE, and DFPE were structurally similar to one another. COPE ground calls consisted of a rapid series of pulsed notes with a wider frequency range than those of the other 3 species, sounding much like purring. At a distance, all 4 calls sounded qualitatively similar, but, when heard close by (< 5 m), the calls of COPE were noticeably different. All 4 species responded to human imitations of their ground calls by approaching and repeating the same call. COPE individuals attracted to within about ~ 1m changed to a cackling call, similar to the Ti notes of their aerial call (*Figure 4.4b*).

Burrow calls were recorded from all 4 species, although only one COPE individual was recorded (*Figure 4.5*). Burrow calls were produced by individuals in underground burrows (STPE, COPE, PYPE) or in crevices in rocks (DFPE) where these species nested. STPE, DFPE, and PYPE responded to recordings of their calls played near the burrow. COPE was quiet within its burrows, and calls could not be elicited from burrows known to be occupied by incubating individuals, even with recordings from the 1 COPE burrow call recorded. Three COPE

individuals emerged from the burrow in response to whistles and playbacks but none called (all of these individuals subsequently re-entered the breeding burrow from which they had emerged). On two occasions, I observed individual COPE as they put their heads into occupied burrows and uttered the ground call. These individuals had been wandering on the surface and uttering the ground call prior to investigating the occupied breeding burrows. The burrow occupants did not respond in either case.

Similarities within the Cookilaria

In summary, the *Cookilaria* species share distinctive aerial, ground, and burrow calls. Aerial calls from all seven taxa in the group (including recordings of GOPE, NCPE, and CLPE obtained from other sources) are very similar in structure, except for DFPE. All begin with similar introductory Moan notes, and (for the majority of species) broadband, short, and highly repeated Ti notes. Three (STPE, DFPE, PYPE) of the four species recorded as part of this study had burrow calls that were also similar to each other in structure and frequency. These species called readily in response to noises at the burrow entrance, while COPE did not. The only burrow recording from COPE presented here might not be representative of the calls of this species. At least five species in the group (COPE, PYPE, STPE, DFPE, this study; GOPE, Warham 1996) shared the low frequency “purring call recorded from birds on the ground.

In aerial calls, the dominant frequency of the Moan notes varied significantly among the *Cookilaria* taxa (Table 4.2) (ANOVA, $F_{7,32} = 56.3$, $P < 0.05$, Dunn-Sidak correction). The dominant frequencies of the Moan notes of STPE and DFPE were significantly higher in frequency than those of the other *Cookilaria* petrels but were not significantly different from

each other (Tukey's HSD, $\alpha = 0.05$, $q = 3.2$, $p < 0.05$) (Figure 4.6). The other taxa overlapped significantly in dominant frequency of the moan note. Lengths of Moan notes (ANOVA, $F_{7,32} = 1.98$, $P > 0.05$) and 6-dB bandwidths ($F_{7,32} = 1.87$, $P > 0.05$) did not differ between taxa.

The Ti notes of the seven *Cookilaria* with Ti notes in their calls differed significantly in dominant frequencies, 6-dB bandwidths, and mean harmonic intervals (Table 4.2) (ANOVA, all $F_{6,28} > 8.6$, $P < 0.05$). PYPE Ti notes had the highest dominant frequency (5274 Hz), although the Ti notes of PYPE and STPE did not differ significantly from each other (Tukey's HSD, $\alpha = 0.05$, $q = 3.17$) (Figure 4.7a). The dominant frequencies of Ti notes did not differ significantly between GOPE and NCPE, currently listed as sub-species, nor between COPE populations (COPE and COPE2). PYPE Ti notes had longer intervals between notes than all other species (Tukey's HSD, $\alpha = 0.05$, $q = 3.17$) (Figure 4.7b).

Body mass from colony sites was available for six taxa (STPE, DFPE, COPE, COPE2, PYPE, and GOPE) (Table 4.2). Ti note dominant frequencies were correlated with body mass, while Moan note frequencies were not (Ti: $r^2 = 0.88$, $F_{1,4} = 22.7$, $P < 0.05$; Moan: $r^2 = 0.31$, $F_{1,4} = 1.8$, $P > 0.05$).

Aerial calls of other Pterodroma species proposed as Cookilaria species

A visual comparison between published spectrograms of the aerial calls the three other *Pterodroma* species sometimes included in the subgenus *Cookilaria* (*P. nigripennis*, *P. hypoleuca*, *P. axillaris*) showed that these three species include longer “chevron-shaped” Ti notes in their calls, features not observed in any of the recordings of *Cookilaria* species that I measured (Grant et al., 1983a; Warham, 1996).

Predation

DFPE were the only species to breed on an island with a nocturnal predator (*Asio flammeus*) and no diurnal predators. STPE breed on an island in the same archipelago with a diurnal predator (Red-backed Hawk *Buteo polyosoma exsul*) and no nocturnal predators. The PYPE and COPE colonies visited for this study were on islands with Morpork Owls *Ninox novaeseelandiae*, a small species not thought to prey on petrels (but see Anderson, 1992). The risk of diurnal predation is not known, but at least one raptor *Circus approximans* was observed on Lady Alice Island on multiple occasions. Specific information about predators in the other colonies (GOPE, NCPE, and CLPE) was not available.

DFPE were diurnally active at the breeding colonies on Santa Clara. Visual counts of activity reached a peak 60 minutes after sunrise and declined after that. Individuals were observed and heard calling at the colony throughout the day and at dusk. No DFPE were observed on the colony surface at night, or recorded vocalizing from the air during three all-night counts.

The only diurnal species, DFPE did not produce Ti notes in their aerial calls. Although individuals of the other taxa sometimes produced only the Moan note in flight, all of these species also produced Ti notes. The dominant frequency of PYPE Ti notes was significantly higher than that of COPE Ti notes.

Co-occurring species

The mean dominant frequency of PYPE and COPE moan notes did not differ significantly from each other, or from any of the other *Cookilaria* except STPE and DFPE (*Figure 4.6*).

PYPE Ti notes had the highest dominant frequency (5274 Hz $\pm$ 191, N=5) and COPE Ti notes the lowest (3114 Hz $\pm$ 102, N=5; Tukey's HSD, α = 0.05, q = 3.17) (*Figure 4.7a*). COPE2 and COPE were the heaviest taxa in the group, and PYPE the lightest (*Table 4.1*).

PYPE aerial calls had the longest note-to-note interval between Ti notes (227 ms $\pm$ 18, N=5), while COPE2 and COPE had the shortest note-to-note intervals (118 ms $\pm$ 5, N=5 and 125 ms $\pm$ 12, N=5; Tukey's HSD, α = 0.05, q = 3.17). PYPE differed significantly from all other species in mean note-to-note length, while COPE overlapped with all other species except one (CLPE) in this measure.

COPE and COPE2 (3351 Hz, $\pm$ 134, N=5) did not differ significantly in any measure (*Figure 4.6 & 7a,b*).

Habitat

Only one of the species breeding in open habitat had Ti notes in its call (STPE). Of the species with Ti notes, PYPE had the longest inter-note intervals (*Figure 4.7b*). PYPE, a forest-breeding species, also had Ti notes with the highest dominant frequencies, which overlapped with the dominant frequencies of STPE, an open-habitat species (*Figure 4.7a*). Again, Ti note frequency is correlated with body mass in these species.

The mean dominant frequency of Moan notes differed significantly between the 2 species breeding in open habitat (STPE and DFPE), and the 6 taxa breeding in forest habitat (COPE, PYPE, GOPE, NCPE, CLPE) (Tukey's HSD, $\alpha = 0.05$, $q = 3.23$). Moan note frequency is not correlated with body mass.

Several sources of background noise were apparent in recordings from the different breeding colonies (*Table 4.3*). This noise included broad-band, low-frequency noise generated by waves breaking on a rocky shoreline, various bands of insect noise, and the calls of coexisting petrel species.

DISCUSSION

This study shows that the call structures of the aerial, ground, and burrow vocalizations within the *Cookilaria* subgenus appear to be highly conserved and support the idea that these species are a closely related group within the *Pterodroma*. At the same time, I present several prominent differences in the aerial calls of these species. First, STPE and DFPE, both breeding in the Juan Fernández Archipelago, have Moan notes with almost twice the frequencies of the other *Cookilaria*. Second, DFPE was strictly diurnal at its colonies and had the only aerial calls without Ti notes. Third, COPE and PYPE were at opposite extremes of the *Cookilaria* group in the dominant frequencies of their Ti notes and time between Ti notes. COPE and PYPE were also at opposite extremes of the group in terms of mass, which might explain the differences in dominant frequencies. There were no significant differences in these features between COPE populations. Finally, there was little support for the hypothesis that habitat affected the time

between notes in the calls of these species. The species with the longest note-to-note intervals breeds on a forested island (PYPE), but the 5 other forest-dwelling species overlapped with the one open-habitat species (STPE).

Vocalizations and phylogeny

The *Cookilaria* species share distinctive aerial calls, with similar introductory Moan notes, and (for the majority of species) broad-band, short, and highly repeated Ti notes. At least five species in the group (COPE, PYPE, STPE, DFPE, this study; GOPE, Warham 1996) also shared the low frequency “Purr” call recorded from birds on the ground. Finally each species had complex high frequency vocalizations produced by individuals at the nest site. Of the group, COPE had the most distinct vocalizations. First, this species seemed to have the most variable Ti notes of any species when heard in the field, something not be apparent in the small sample sizes available for this study. Second, the species had two ground calls, a “Purr” call, and a cackling call used in agonistic interactions. The COPE “Purr” call was distinctive among the *Cookilaria* for its slow, pronounced pulses.

A visual comparison between spectrograms of the aerial calls of the *Cookilaria* species with published spectrograms of the aerial calls from three other *Pterodroma* species sometimes proposed as members of the *Cookilaria* subgenus (*P. nigripennis*, *P. hypoleuca*, *P. axillaris*) showed that each of these species include longer “chevron-shaped” Ti notes not observed in any of the species in this study (Grant et al., 1983a; Warham, 1996). However, the moan notes, and Ti notes from vocalizations of these three species appear more similar to those of the *Cookilaria* group than they do to the calls of other species currently grouped in the *Hallstroma* and

Pterodroma subgenera (*P. externa*, *P. sandwichensis*, *P. phaeopygia*, *P. hasitata*, *P. neglecta*, *P. lessonii*, and *P. mollis*) (Warham, 1996; Bretagnolle, 1995; Bretagnolle, 1996; Tomkins & Milne, 1991; Simons, 1985). These comparisons could be improved for the entire group if more and longer recordings could be obtained.

Comparisons of the vocalizations within other subgenera proposed by Imber (1985) show some interesting mismatches. For example, under Imber's phylogeny, *P. externa* and *P. neglecta* are considered sister species, but the aerial calls of these species (recorded on different islands in the Juan Fernández Islands), are markedly different from one another in frequency and structure (Figure 4.8). On the other hand, *P. externa* calls are strikingly similar to the published sonograms of calls from two supposedly more distant cousins in the *Hallstroma* subgenus, *P. phaeopygia* and *P. sandwichensis* (Simons, 1985; Tomkins & Milne, 1991; Imber, 1985). These discrepancies suggest some potential problems with the existing phylogeny for the *Pterodroma*. A wider comparative study could provide useful information about agreement between the existing phylogeny and homologous vocal characters. A more robust phylogeny based on molecular characters would provide a firmer basis for these and other comparisons.

Cookilaria on Islas Juan Fernández

One unexpected finding was that STPE and DFPE had Moan notes with dominant frequencies that were roughly double that of the other *Cookilaria* species. Dominant frequencies of songs and calls have been shown to be correlated with body mass in many avian species, with heavier species producing lower frequency sounds (Ryan & Brenowitz, 1985; Wiley, 1991). This seems to hold true for the dominant frequencies of the Ti notes in the *Cookilaria* species, as these were highly correlated with body mass. However, the dominant frequencies of the moan

notes were not correlated with body mass and the two species breeding in the Juan Fernández are not the lightest *Cookilaria*. These two species do nest in open habitats, while the other species breed in forested habitats. Previous studies have found a correlation between forest species and low frequencies, but again, low frequencies should propagate with less attenuation in any habitat, so high frequencies should not be preferred in open habitat (Wiley 1991). Background noise can also influence the frequencies of avian vocalizations (Ryan and Brenowitz, 1985). The two *Cookilaria* in the Juan Fernández breed in areas with low-frequency background noise: waves breaking on a rocky shore for DFPE and calls of tens of thousands of coexisting *P. externa* for STPE (Table 4.3). More detailed studies of the background noise at colonies could address this possibility further.

It is also possible that the two *Cookilaria* species in the Juan Fernández Islands are more closely related to each other than they are to any of the other *Cookilaria*. Besides the novel moan notes in the calls of STPE and DFPE, these two species also share similar ground calls (Figure 4.4). The currently accepted phylogeny (Imber 1985, Brooke 2004) shows DFPE and STPE as sister species to COPE and PYPE respectively; in this phylogeny each of these species has its closest relative on the opposite side of the Pacific. Instead, it seems possible that the summer-breeding STPE and the winter-breeding DFPE evolved from a common ancestor in the Juan Fernández Archipelago. Madeiran Storm Petrels *Oceanodroma castro* have evolved separate winter- and summer-breeding populations from one ancestral population in at least five archipelagos (Friesen et al., 2007b). A more robust phylogeny for *Cookilaria* and *Pterodroma* could test this hypothesis.

Predation

As reviewed in Chapter 3, the evidence is strong that predators can affect the patterns of vocal activity at seabird colonies (Mougeot & Bretagnolle, 2000b; Watanuki, 1986b; Bretagnolle, 1990; Keitt et al., 2004). The only diurnal species of *Cookilaria* (DFPE) breeds on Isla Santa Clara, an island with a nocturnal predator (*Asio flammeus*) and no diurnal predators. This situation resembles that in the Galapagos, where the only known diurnal populations of Audubon's Shearwater *Puffinus lherminieri* and the only known diurnal storm-petrel (Wedge-rumped Storm-Petrel *Oceanodroma tethys*) breed on islands with Short-eared Owls and no diurnal predators (Harris, 1969b; Harris, 1969a; Snow, 1965; Snow & Snow, 1966). While Short-eared Owls do hunt at twilight and during daylight in the Galapagos and on Isla Santa Clara, predation risk for petrels in these colonies is probably reduced in daylight. Short-eared Owls hunt effectively at night, while studies of the eyes of several procellariids suggest that despite their nocturnal activity, petrels do not see well in low light (Brooke, 1989; Brooke, 1990; Martin & Brooke, 1991). Thus a predator that can be seen and evaded probably represents less of a threat than one that cannot be seen. It would be interesting to measure diurnal and nocturnal predator attacks on mounted petrel specimens with and without playbacks of vocalizations, and to test the response of diurnal petrels to mounted specimens of owls.

The diurnal activity of DFPE at its colony might also result from foraging behavior. Harris (1969a) thought that the diurnal activity of *O. tethys* in the Galapagos was likely related to nocturnal foraging in this species. Imber (1975) and Brooke (2004a) have also suggested that colony attendance and vocal activity patterns in petrels are partially related to prey availability

and foraging strategies. STPE, breeding during the austral summer (as opposed to the winter breeding season of DFPE) is strictly nocturnal at its breeding site. However, the activity of non-breeders at the colony site is restricted to a short period after sunset (*Chapter 3*), so it is possible that both of the *Cookilaria* species in the archipelago are nocturnal foragers. Samples of the diet of these species and data loggers would provide more data to test this hypothesis.

Diurnal or nocturnal colony attendance

Whatever the cause, it is noteworthy that the one diurnal *Cookilaria* species (DFPE) does not have broadband repeated notes in its aerial call, a feature that could make a signal easily locatable in the dark (Brumm & Slabbekoorn, 2005). Presumably DFPE lack these features because visual cues in daylight obviate the need for easily locatable calls. Bretagnolle (1989) found similar differences between storm petrel populations with differing colony attendance patterns. In the absence of avian predation (and in the permanent summer daylight) in Adélie Land, Wilson's Storm Petrel *Oceanites oceanicus* display outside of their breeding burrows and vocalizations are accompanied by visual signals. On Kerguelen, where predatory gulls (*Larus dominicanus*) and skuas (*Catharacta lönnerbergi*) are present, individuals vocalize only at night and within breeding burrows. Though both populations had calls consisting of a repeated series of broad-band notes, populations displaying in daylight produced brief vocalizations accompanied by visual display, while nocturnal populations produced long series of repeated notes (sometimes for up to 20 minutes) within the burrow, presumably to allow potential mates to locate the signaler in the dark.

The Black-winged Petrel (*Pterodroma nigripennis*) is expanding its range, and different populations seem to have differing colony attendance patterns (Brooke 2004). It would be

interesting to test whether diurnal populations of this species have vocalizations with reduced numbers of Ti notes.

Coexisting species

Although PYPE and COPE are not known to co-occur on islands today, it is possible that they did in the past (Bartle, 1968). The two breeding colonies visited for this study (COPE = Little Barrier Island or Hauturu, PYPE = Lady Alice Island) were closer to each other (~ 30 miles) than they are to other breeding colonies of their own species (PYPE = ~ 80 miles to Red Mercury Island, COPE = 840 miles to Codfish Island). Where congeners with similar reproductive signals occur together, receivers face the risk of responding to the signals of inappropriate mates. If hybridization reduces reproductive success, species are selected for breeding signals that reduce overlap between the species and decrease the probability of hybridization. The vocalizations used in courtship by the *Cookilaria* species are structurally similar to each other and might be confused by receivers. Therefore it could be predicted that PYPE and COPE might have evolved vocalizations with features that reduce the overlap between the signals of these species. Measurements of the Moan notes of these species did not show any differences, but Ti notes differed significantly in their dominant frequencies. The Ti notes of PYPE have the highest dominant frequencies and longest inter-note intervals of the *Cookilaria*, while COPE have the lowest dominant frequencies and shortest inter-note intervals. COPE2, the population of COPE breeding on Codfish island (800 miles distant), and not overlapping with breeding populations of PYPE do not differ significantly in frequency parameters, as expected for character displacement. Alternatively, differences in the mass of these petrels might explain the observed differences in Ti note frequencies. COPE (209 g) is the

heavier than PYPE (159g), the lightest petrel in the group, and Ti note dominant frequencies show a correlation with body mass across all five taxa where measurements of mass were available. However, both species produce Moan notes of similar low frequency, so not all frequency components of the call are associated with mass. A playback experiment using COPE and PYPE aerial calls with altered frequency and timing parameters might provide interesting information about the importance of these parameters for species recognition.

Finally, coexistence with congeners could also affect communication in other ways. The previous study of the patterns of vocal behavior in STPE (Chapter 3) reported that this species restricted most of its vocal activity to a short period of time after sunset, before the arrival of the larger and more numerous Juan Fernandez Petrel *Pterodroma externa*. One explanation for this pattern of activity is that STPE individuals may face a trade-off between risks of predation during daylight and risks of aerial collision with the larger species later at night. Three islands, (Henderson, Gough, and Crozet) host at least 2 *Pterodroma* petrel species during the same breeding season (Brooke 2004). It would be interesting to compare vocal structure or patterns of vocal behavior where a *Pterodroma* species has populations that breed on the same island and in the same season as other *Pterodroma* species to populations that breed on islands without congeners.

Habitat

For accurate, long-range communication, species breeding in closed habitats should have signals with longer intervals between notes. In addition frequencies are often lower in forested habitats, although the explanation for this pattern is not entirely clear (Wiley and Richards, 1982; Wiley 1991). Comparison of the vocalizations of *Cookilaria* species breeding on forested

islands and open islands provide mixed support for these predictions. Because only one of the two species breeding in open habitat had Ti notes in its vocalizations it is difficult to draw any conclusions about the effects of habitat on the evolution of Ti notes. The species with the longest note-to-note intervals, a feature that can improve transmission of acoustic signals in forested habitat, does breed on a forested island (PYPE). However, four of the other five forest breeding species had note-to-note intervals similar to that measured in the one open-habitat species with Ti notes (STPE).

Dominant frequencies of Moan notes in aerial calls differed between the species in open and forested habitats, and the Ti notes of STPE had the second highest dominant frequencies recorded. However, PYPE, a species recorded at a forested island colony, had the highest dominant frequency Ti notes in the group. Thus, there is no evidence to support the hypothesis that habitat affects the timing between Ti notes in the calls of these species, and mixed agreement with the observed pattern that forest-dwelling species use acoustic signals with lower dominant frequencies (Wiley, 1991). If most of the aerial communication in the *Cookilaria* petrels is between individuals flying in close proximity to each other above the forest canopy, it seems likely that there would be little or no influence of forest structure on the propagation of their calls over the short distances involved. If, however, *Cookilaria* petrels are also communicating with individuals in burrows 15-20 m below the aerial activity, it is more plausible that signals might have adapted to improve accurate transmission over long distances.

Conclusion

The similarity in calls in the *Cookilaria* petrels and the different environmental conditions at their breeding sites make them a useful group for studying the evolution of communication. Overall, the similarities in the vocalizations of these taxa support the current grouping into a *Cookilaria* group. Differences between the aerial calls of the *Cookilaria* species and those of three other species that have been proposed as potential members of *Cookilaria* do not support the inclusion of any of the latter species in this subgenus. The high-frequency moans and similar ground calls of the *Cookilaria* species breeding in the Juan Fernández Islands suggest the possibility that STPE and DFPE are more closely related than currently thought. A cursory comparison between the calls of *P. externa* and *P. neglecta* shows that the calls of these sister species are dissimilar. Other comparisons among several other species of *Pterodroma* suggest that the phylogeny for the genus needs to be revised.

Several interesting differences in the aerial calls and calling behavior of the *Cookilaria* species suggest that local environmental factors can influence the evolution of calls. First, DFPE, the only species breeding in an area with a nocturnal predator and no diurnal predator, is diurnal at its colony sites in the Juan Fernández archipelago unlike other *Cookilaria*. This change to diurnal behavior seems to have changed the properties of their vocalizations. DFPE is the only species that lacks Ti notes in its vocalizations, features that can aid in the location of a signal, presumably because this species can use visual cues at its colony sites. COPE and PYPE, the two *Cookilaria* species with the closest breeding sites have the lowest and highest Ti note dominant frequencies, and the shortest and longest intervals between Ti notes, but COPE petrel populations do not differ in either feature depending on the presence of PYPE nearby. Thus

there is little support for the hypothesis that these species' vocalizations diverge in areas of overlap. Finally, there was mixed evidence that the vocalizations of the *Cookilaria* petrels breeding in forested habitat have adapted for optimal transmission through forests.

These results suggest ways that environmental factors can alter the costs and benefits of signals and signaling behaviors at different colonies. It is therefore conceivable that immigrants adapted to one environment might have different survival and reproductive rates when at a different breeding site. Long-distance dispersal does occur in seabirds, as in the *P. externa* that have been repeatedly heard and observed displaying in the moonlight on the Chatham Islands, across the Pacific from their colony in the Juan Fernández Islands (Imber et al., 1991). It is interesting to note that one of the *P. externa* specimens collected to confirm the presence of this species in the Chathams was found dead near the nest of a skua, a nocturnal predator not present on Isla Alejandro Selkirk, where this individual presumably originated.

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Table 4.1 The *Cookilaria* petrels and the breeding sites where recordings were made

<i>Species</i>	<i>Abbreviation</i>	<i>Mass (g)</i>	<i>Island</i>	<i>Habitat Type</i>	<i>Recordings</i>
Cook's Petrel <i>P. cookii</i>	COPE	209	Hauturu (Little Barrier Island), NZ	Forest	M. McKown
	COPE2	227	Codfish Island, NZ	Forest	M. Rayner
DeFilippi's Petrel <i>P. defilippiana</i>	DFPE	175	Isla Santa Clara, Chile	Open (Shore)	M. McKown
Pycroft's Petrel <i>P. pycrofti</i>	PYPE	159	Lady Alice Island, NZ	Forest	M. McKown
Stejneger's Petrel <i>P. longirostris</i>	STPE	167	Isla Alejandro Selkirk, Chile	Open (Ridge)	M. McKown
Gould's Petrel <i>P. leucoptera leucoptera</i>	GOPE	186	Cabbage Tree Island, Aus	Forest	McPherson Sound Archive
New Caledonian Petrel <i>P. l. caledonica</i>	NCPE	-	New Caledonia	Forest	McPherson Sound Archive
Collared Petrel <i>P. brevipes</i>	CLPE	-	Gau, Fiji	Forest	D. Watling

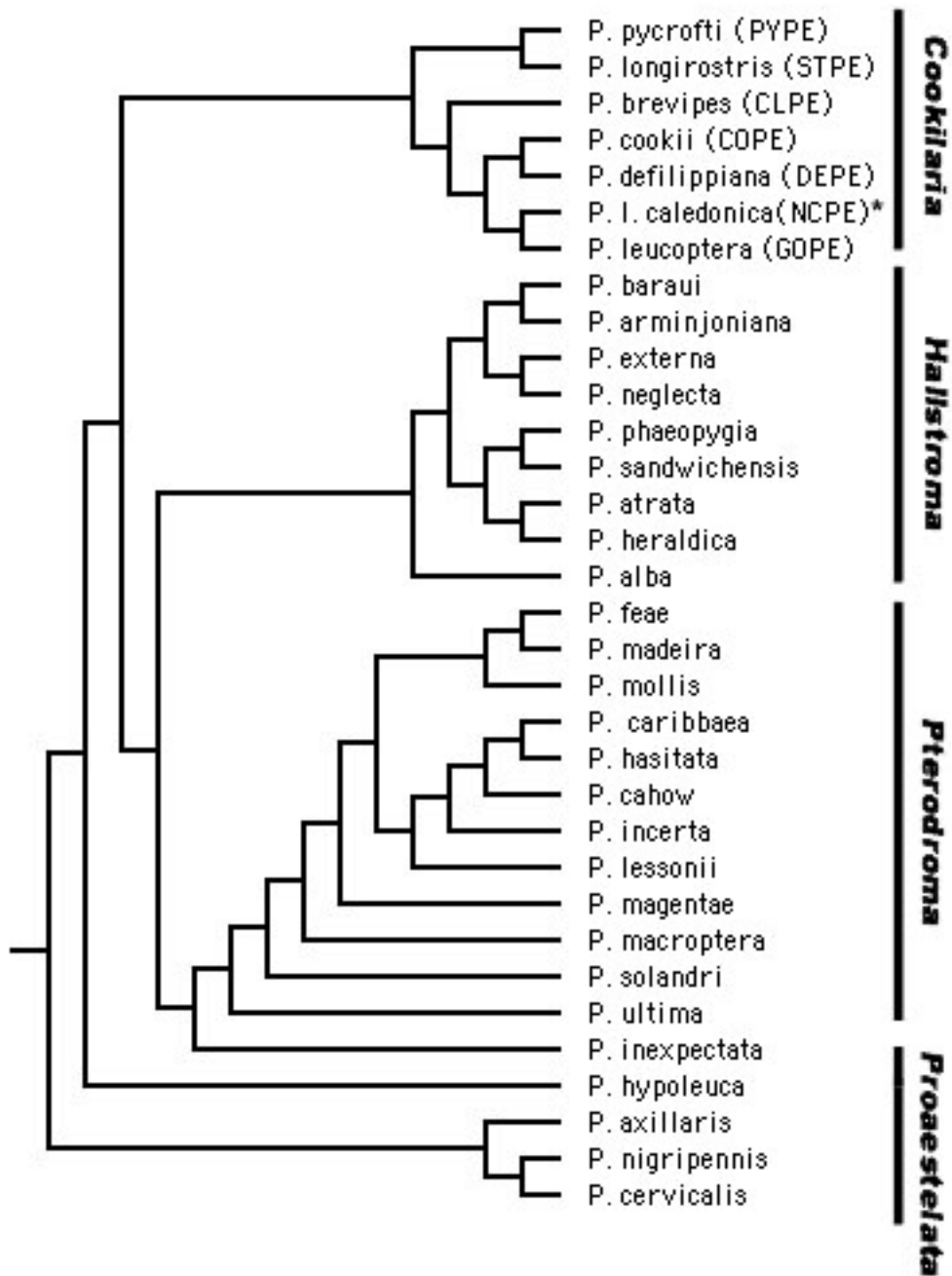
Table 4.2 Summary statistics for the Moan and Ti notes of *Cookilaria* aerial calls (+/- s.e)

<i>Taxa</i>	<i>Breeding site</i>	<i>N</i>	<i>Moan note</i>			<i>Ti notes</i>			
			<i>Dominant frequency (Hz)</i>	<i>Length (ms)</i>	<i>6 dB bandwidth (Hz)</i>	<i>Dominant frequency (Hz)</i>	<i>6 dB bandwidth (Hz)</i>	<i>Mean harmonic interval (Hz)</i>	<i>Note-to-note distance (ms)</i>
COPE	Hauturu, NZ	5	533 (17)	617.2 (48)	155 (50)	3114 (102)	1844 (317)	404 (59)	125 (12)
COPE2	Codfish Is., NZ	5	499 (17)	536.6 (85)	138 (21)	3351(134)	1044 (136)	396 (61)	118 (5)
DFPE	Isla Santa Clara, Chile	5	1033 (47)	716 (60)	224 (59)	-	-	-	-
PYPE	Lady Alice Is., NZ	5	568 (21)	446 (26)	293 (89)	5275 (191)	1504 (135)	442 (10)	227 (18)
STPE	Isla Alejandro Selkirk, Chile	5	1154 (64)	503 (80)	121 (21)	4792 (181)	3220 (356)	716 (29)	134 (11)
GOPE	Cabbage Tree Is., Aus	5	585 (32)	621 (62)	241 (57)	4037 (104)	1812 (151)	314 (4)	132 (4)
NCPE	New Caledonia	5	620 (17)	658(19)	121 (21)	4319 (254)	2149 (274)	417 (28)	143 (4)
CLPE	Gau, Fiji	5	602 (0)	593 (81)	259(38)	3695 (301)	2155 (103)	389 (30)	171 (22)

Table 4.3 Sources of background noise at *Cookilaria* breeding colonies

<i>Species</i>	<i>Island</i>	<i>Background Noise</i>
Cook's Petrel <i>P. cookii</i>	Hauturu (Little Barrier Island), NZ	Cicadas
	Codfish Island, NZ	Mottled Petrel <i>Pterodroma inexpectata</i> 4 other seabirds
DeFilippi's Petrel <i>P. defilippiana</i>	Isla Santa Clara, Chile	Waves on rocky shore
Pycroft's Petrel <i>P. pycrofti</i>	Lady Alice Island, NZ	Cicadas Flesh-footed Shearwater <i>Puffinus carneipes</i>
Stejneger's Petrel <i>P. longirostris</i>	Isla Alejandro Selkirk, Chile	Juan Fernandez Petrel <i>Pterodroma externa</i>
Gould's Petrel <i>P. l.leucoptera</i>	Cabbage Tree Island, Aus	Insects
New Caledonian Petrel <i>P. l. caledonica</i>	New Caledonia	Insects
Collared Petrel <i>P. brevipes</i>	Gau, Fiji	Insects

Figure 4.1 Phylogeny of the genus *Pterodroma* indicating the 4 recognized subgenera, including *Cookilaria*. The tree is based on morphological and anatomical data as well as data on feather lice (Imber 1985; after Brooke 2004).



* The subspecies NCPE is added as a sister species of GOPE

Figure 4.2 Measurement of aerial calls - a) time section of call, b) spectrogram of typical *Cookilaria* call, c) frequency section of Ti note, d) waveform of call.

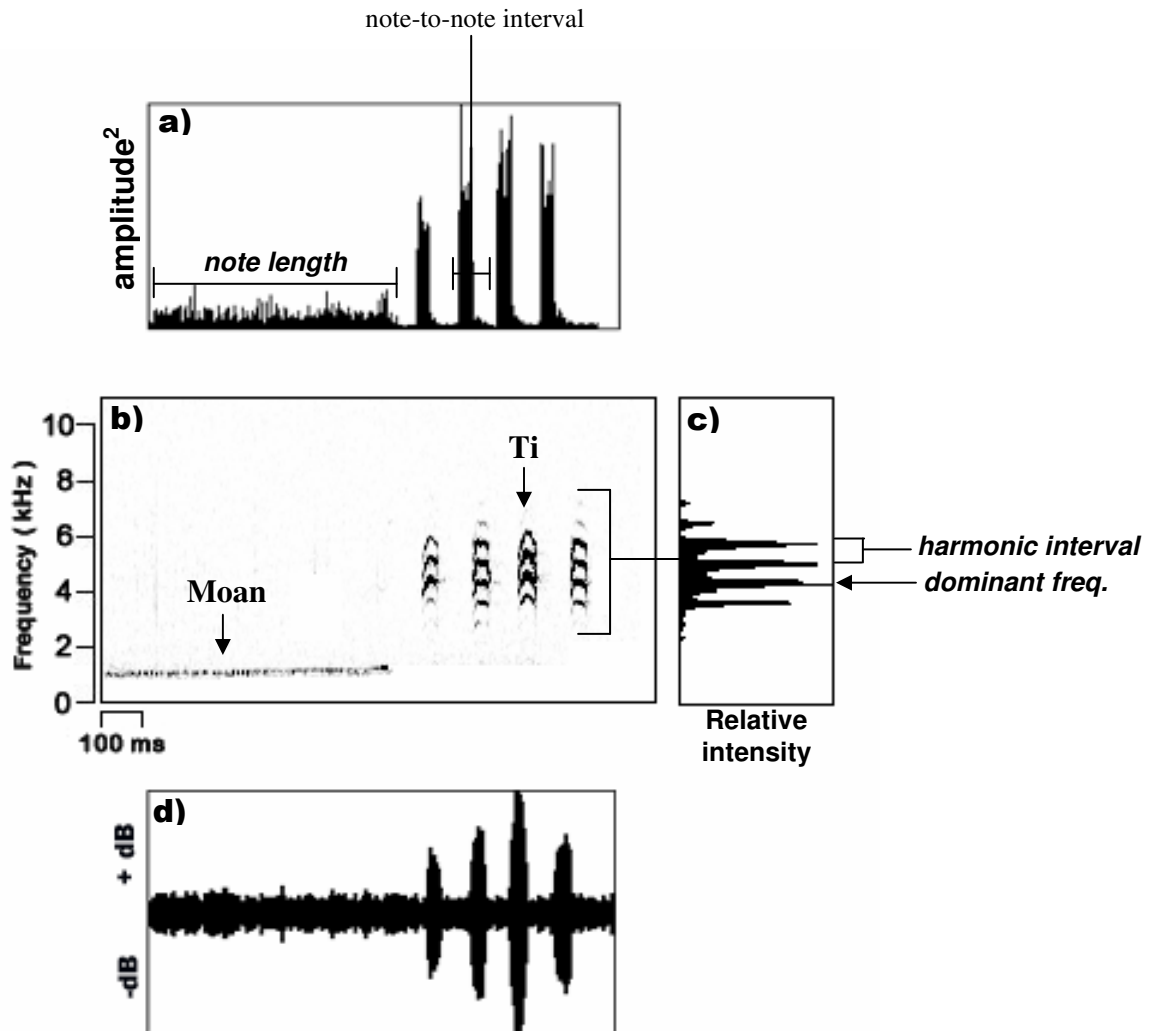


Figure 4.3 Aerial calls of four *Cookilaria* species

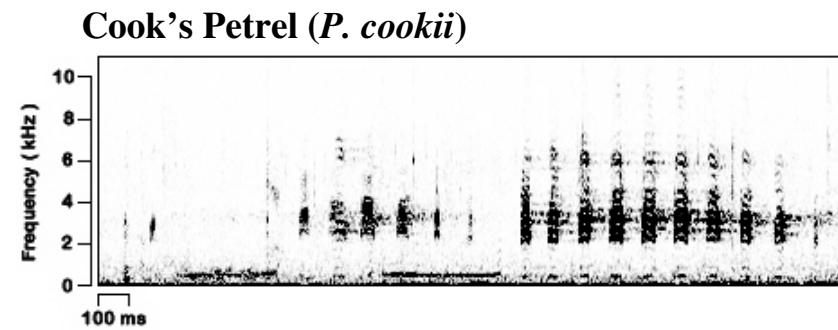
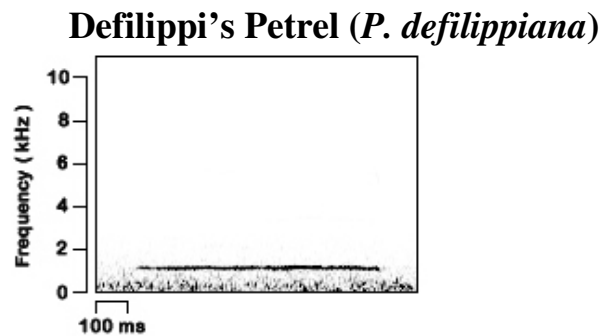
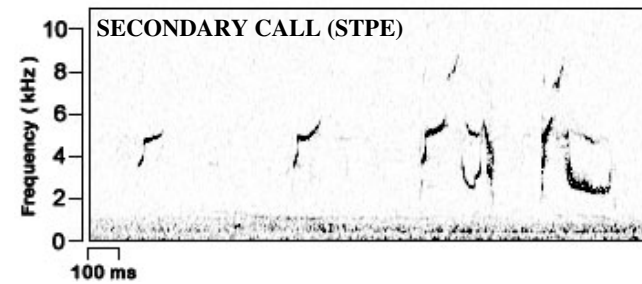
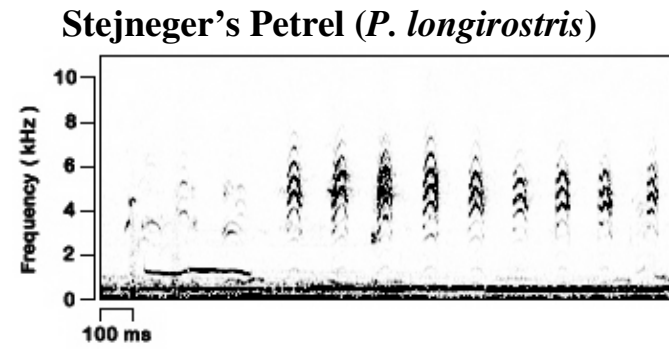
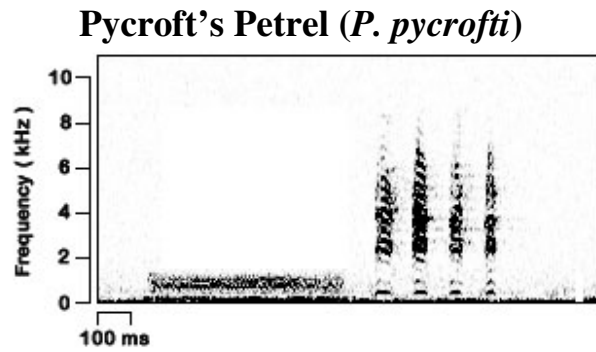


Figure 4.4 Ground calls of four *Cookilaria* species

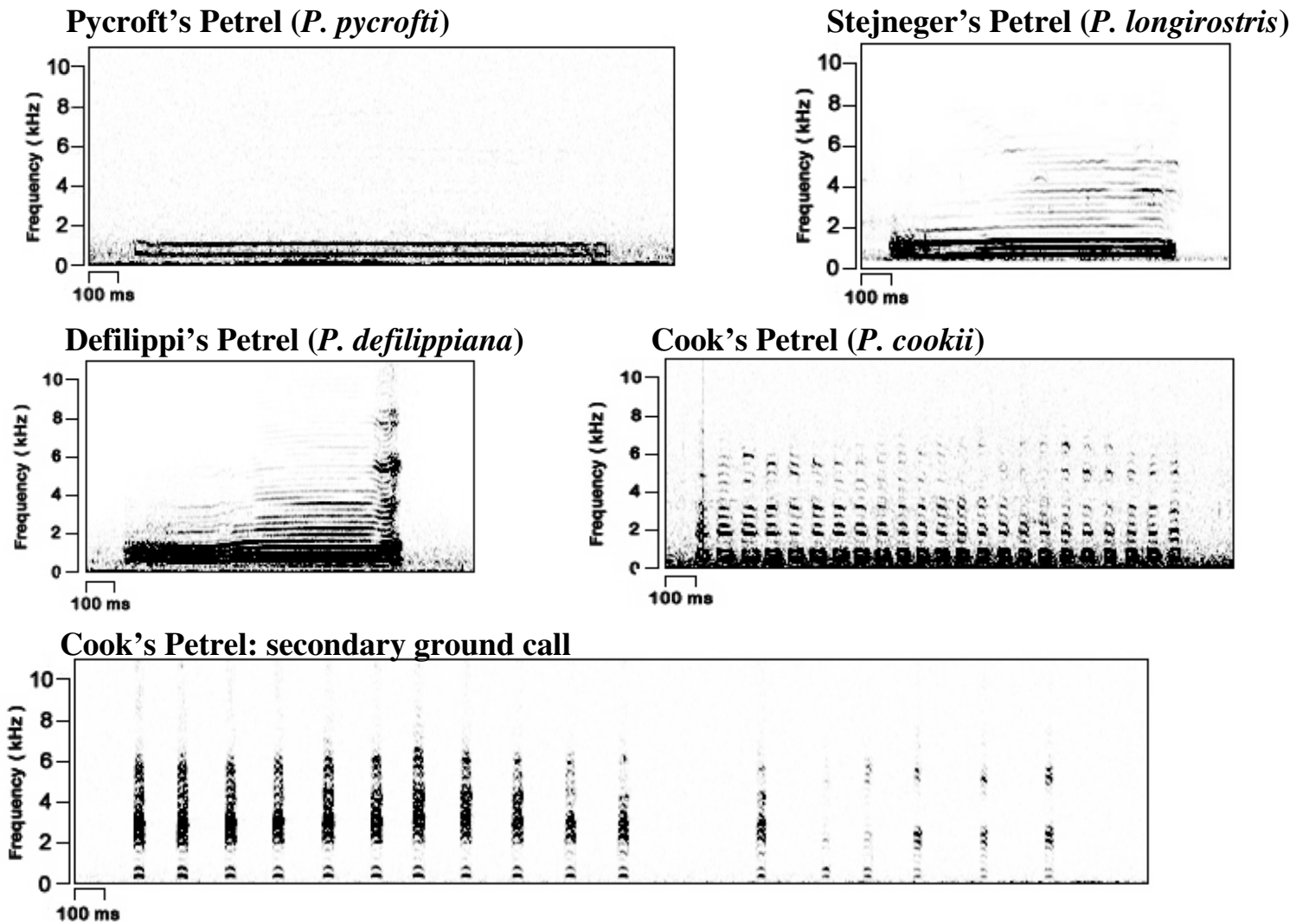


Figure 4.5 Burrow calls of four *Cookilaria* species

Pycroft's Petrel (*P. pycrofti*)



Stejneger's Petrel (*P. longirostris*)



Cook's Petrel (*P. cookii*)



Defilippi's Petrel (*P. defilippiana*)

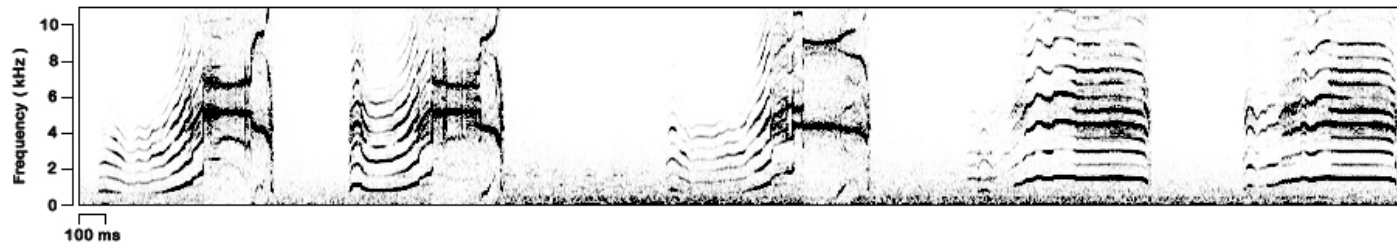


Figure 4.6 Dominant frequency of Moan notes (columns not sharing a letter are significantly different, Tukey's HSD, $\alpha = 0.05$, $q = 3.2$, $p < 0.05$)

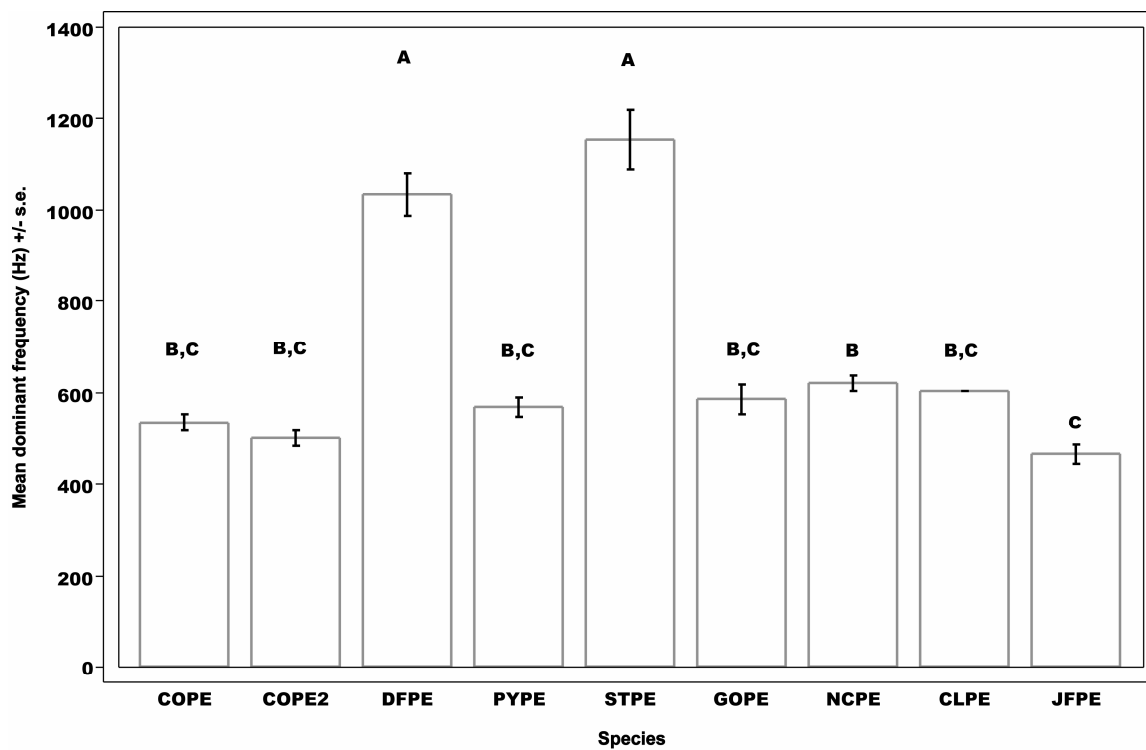
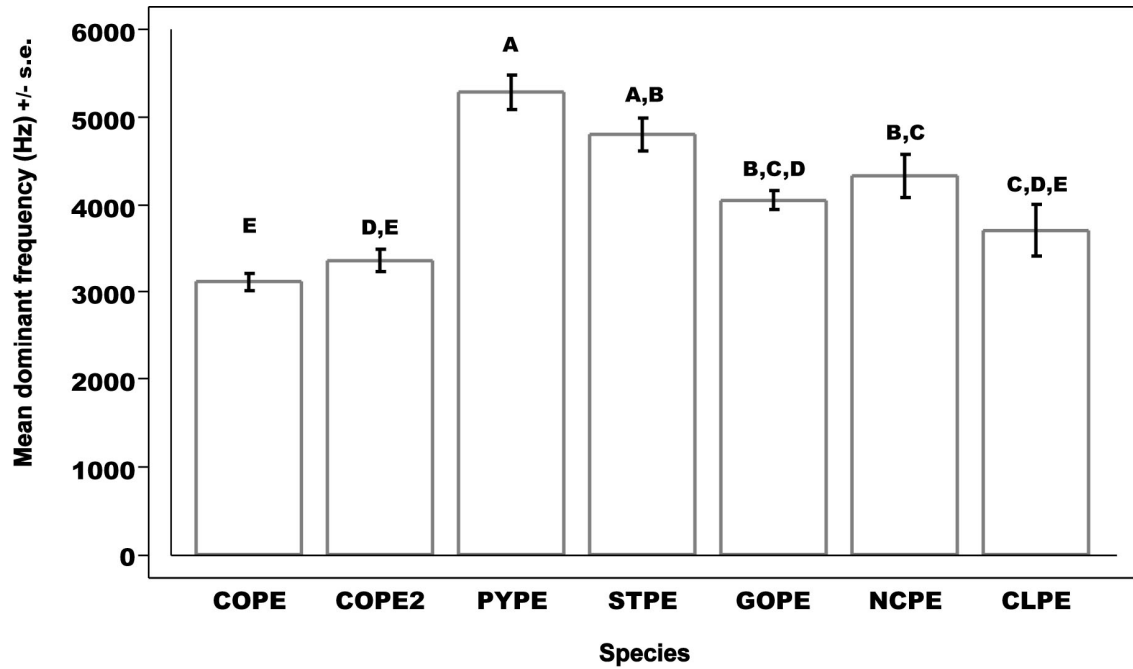


Figure 4.7 Mean dominant frequency (a) and mean interval between notes (b) for Ti notes (columns not sharing a letter are significantly different, Tukey's HSD, $\alpha = 0.05$, $q = 3.17(a)$, $q = 3.18(b)$)

a)



b)

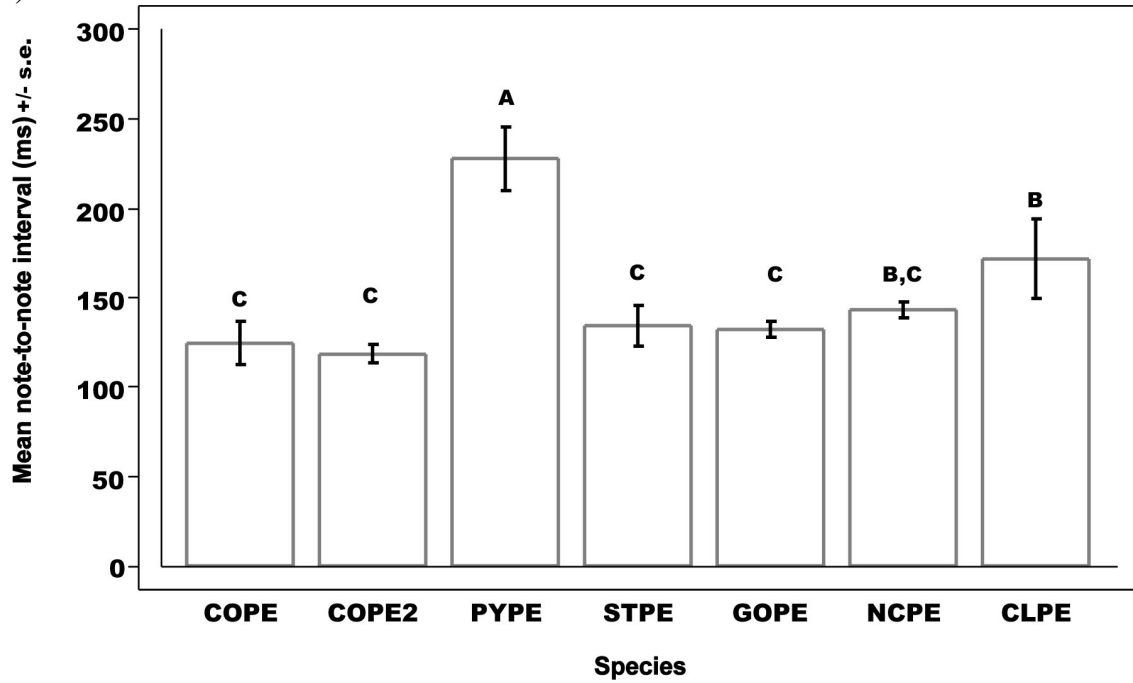
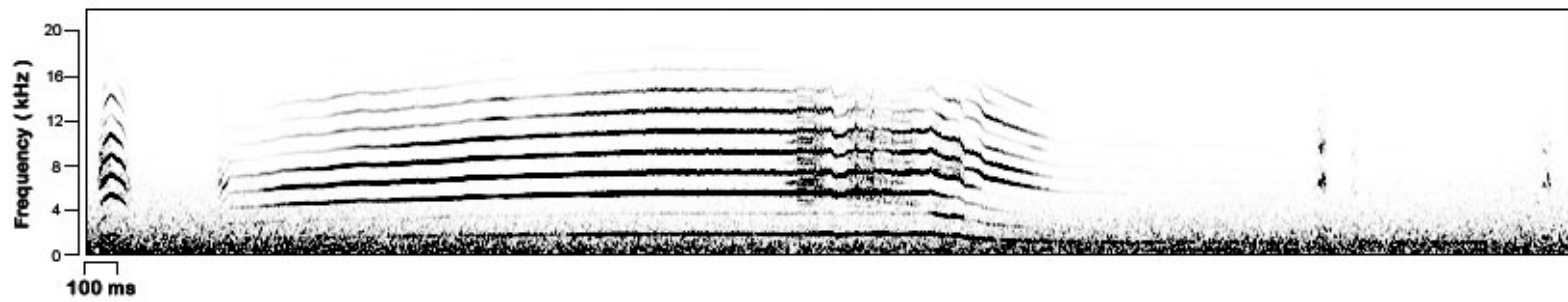
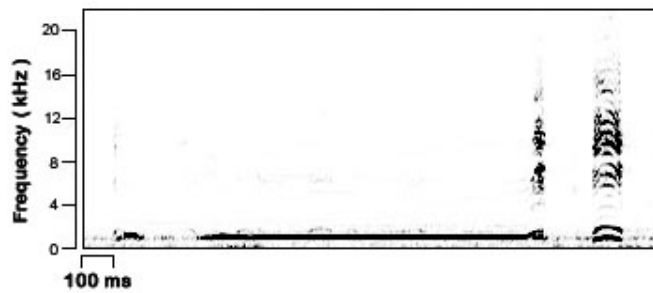


Figure 4.8 Aerial vocalizations from *Pterodroma neglecta* (a), and *P. externa* (b) from the Juan Fernández Islands, Chile

a) *Pterodroma neglecta* (recorded on Moro Juanango, Isla Robinson Crusoe by Joanna Smith)



b) *Pterodroma externa* (recorded on Isla Alejandro Selkirk)



CONCLUSION

Acoustic communication is an integral component of social interactions in procellariid seabirds, and a substantial amount of research has been devoted to the vocalizations and vocal behavior in this Family. Because the majority of the species in the group are nocturnal at colony sites, acoustic communication is the primary channel for communication over long distances. The acoustic signals of these species should therefore contain a variety of information to mediate social interactions between individuals. To date, research has confirmed that the vocalizations of many species in the family do contain important information. Calls used in courtship, mate recognition, and territorial defense have been shown to contain patterns of variation that are specific to species, sex, and individuals. Subsequent experiments in many species have confirmed that these features are used to recognize conspecifics, potential mates, and individuals. This work has also shown that the calls and call repertoires of procellariids provide important information about taxonomic relationships in the family. Vocal characters are important for phylogenetic analyses because many of the characters traditionally used to estimate phylogenies (plumage patterns and morphological features) are strikingly similar in many genera. At finer scales, variation in calls and calling behavior has been documented within species that breed at multiple locations. This variation includes differences in the temporal and spectral qualities of vocalizations, as well as differences in the attendance patterns of breeding and courting individuals. Many questions remain

about how this variation is generated and about the implications of geographic variation in signals that mediate reproductive interactions.

There is, however, a large gap in research on acoustic communication in the Procellariidae. To date only a handful of studies have studied acoustic communication in the *Pterodroma* petrels, a genus that contains 40% of all of the species in the family. For example, sexual variation and individual variation, well described in other procellariids, has not previously been documented in any of the *Pterodroma*. This lack of basic information about communication in the most diverse group of seabirds is largely a result of the remote locations where most species breed.

My research adds the first descriptions of the vocalizations and vocal behavior of three *Pterodroma* species: Juan Fernandez Petrel *P. externa*, Stejneger's Petrel *P. longirostris*, and Defillippi's Petrels *P. defilippiana*. In addition, I present new recordings of the calls of two previously recorded species, Pycroft's Petrel *P. pycrofti* and Cook's Petrel *P. cookii*, and analyze archived recordings of three additional species, Gould's Petrel *P. leucoptera leucoptera*, New Caledonian Petrel *P. l. caledonica*, and Collared Petrel *P. brevipes*. I focused on three aspects of communication in the group: sexual and individual variation in the vocalizations of a *Pterodroma* petrel; patterns of communication in a large breeding colony with two coexisting *Pterodroma* species, and vocalizations of the subgenus *Cookilaria*, a group of seven closely related *Pterodroma* species that provide an opportunity to contrast acoustic signals on islands with differing sound environments. Below, I summarize the implications of the results of this research.

Individual and sexual variation

In this study I describe vocal communication in the Juan Fernandez Petrel *Pterodroma externa* at its primary breeding colony on Isla Alejandro Selkirk. I present molecular confirmation that the calls of a *Pterodroma* petrel contain information about the sex of the individual calling. I have also shown that burrow calls vary more among than within individuals, so they might allow recognition of individuals by their calls. From measurements of the acoustic properties of calls replicated at a number of temporal scales, I estimated that the initial phrases of burrow calls contain 3.06 bits of information for individual recognition, enough to allow discrimination among 8 equally variable individuals on average. This estimate of the effective group size for these calls is compatible with the relatively small number of individuals an incubating JFPE is likely to hear repeatedly during a breeding season. My estimate of the information in burrow calls is slightly larger than the 1.9 bits of information reported for burrow calls of Audubon's Shearwater (*Puffinus lherminieri*) (Mackin, 2004).

Burrow calls have sufficient individual variation to be classified correctly by two multivariate classification techniques (LDA and PNN). I also confirm that call features with the highest amount of information are best for classifying individuals. Finally, a series of simulations based on measurements of real vocalizations was used to determine how well probabilistic neural networks (PNNs) can distinguish between non-equivalent categories of signals. These simulations are a model for receivers that need to distinguish between categories containing widely varying numbers of individuals such as "known

individual” and “all others.” PNNs can categorize these categories at rates that exceed those expected at random. Success rates depend largely on the variability in each category. The inclusion of broadly varying categories in these simulations improved the accuracy of classifying those categories that were less variable.

Patterns of acoustic communication in petrel colonies

The two petrel species breeding at Isla Alejandro Selkirk, STPE and JFPE, increased acoustic activity as moonlight increased. This is the first reported case of nocturnal seabirds that increase activity in moonlight. Many seabirds are nocturnal where there are diurnal predators and are diurnal where there are nocturnal predators. They avoid moonlight where visual predators hunt by moonlight. In addition, STPE and JFPE have largely exclusive aerial activity periods. These patterns are not well explained by the activity of predators or by foraging behavior. Instead, these patterns might result from a trade-off for each species between the risks of predation and aerial collision and the benefits of aerial display. Aerial collisions are common in the main colony in the Islas Juan Fernández. Such collisions are usually inconsequential, but sometimes they result in fatal injuries to one or both individuals. Research on the visual capabilities of Procellariiformes and the experience of many researchers working in the field suggest that navigation in dim light is a challenge for many seabirds. This lack of specialization for night vision in petrels implies that individuals face higher risks of collision and injury on dark nights. One explanation for the increased activity of STPE and JFPE in moonlight is that moonlight reduces the risks of collision without increasing the risks of predation. Furthermore, the early arrival and brief activity of STPE is best explained by a

difference in the risks of predation and collision for STPE and JFPE. The risk of predation in twilight for the small agile STPE is probably less than for the larger JFPE, but the costs of collision during the peak of JFPE activity are presumably greater. Not only are STPE nearly a third the size of JFPE, but they are at least a tenth as numerous. For STPE, there is probably only a brief window after sunset when the risk of both predation and collision are low.

One implication of these findings is that each species and colony of seabird might have an optimal activity pattern that differs from those elsewhere. Whether or not immigrant individuals can learn to make the necessary adjustments in activity remains an important open question.

Calls of the Cookilaria Petrels

The patterns of acoustic behavior at the petrel colony on Isla Alejandro Selkirk suggest that two ecological factors, local predators and co-occurring species, might influence the behavior of petrel species, possibly in different ways. A number of environmental factors (reviewed in the first chapter of this dissertation) can influence the transmission and reception of acoustic signals in natural environments. To investigate whether or not the calls and calling behavior of petrels evolve according to these environmental constraints, I compared the vocalizations of *Cookilaria* petrels, seven closely related petrels that breed on islands with differing habitats. The group provides opportunities for several contrasts between species breeding in different situations that might influence communication. Specifically I compared (1) the vocal behavior of

Cookilaria species breeding on islands with diurnal or nocturnal predators, (2) two *Cookilaria* species breeding in close proximity to one another, and (3) the calls of *Cookilaria* species breeding on forested and open islands.

Numerous similarities in vocalizations within the subgenus *Cookilaria* support the idea that these species are a closely related group within *Pterodroma*. Nevertheless, I present several prominent differences in the aerial calls of these species. First, *P. defilippiana*, the only species with a nocturnal predator but no diurnal predator in its colony, was also the only strictly diurnal species. Second, the two species with nearby breeding colonies (*P. cookii* and *P. pycrofti* breeding on islands less than ~30 miles apart) had vocalizations that were at opposite extremes of the *Cookilaria* group in the dominant frequencies of Ti notes and the time between Ti notes. However, there were no significant differences in these same features between *P. cookii* populations from the colony in proximity to *P. pycrofti*, and a colony not overlapping with any breeding populations of *P. pycrofti*. Thus the differences between *P. cookii* and *P. pycrofti* in call frequency are likely explained by their contrasting mass. There was thus no support for reproductive character displacement in the calls of these species. There was also no evidence for widely spaced elements in acoustic signals used in forested environments. Although the species with the longest note-to-note intervals nested on a forested island (*P. pycrofti*), the five other forest-dwelling species overlapped in this parameter with the one open-habitat species *P. longirostris*. The only strictly diurnal species (*P. defilippiana*) had the only aerial calls without Ti notes. These repeated broad-band notes probably make a signal easier to locate. The calls of *P. defilippiana* lack these features

because individuals can rely on visual cues to locate other individuals over the colony in daylight. Finally, *P. longirostris* and *P. defilippiana*, species breeding in the Juan Fernández Archipelago during opposite seasons, share a novel call feature: Moan notes have almost twice the frequency found in the calls of other *Cookilaria*. These differences in frequency were not associated with mass. One explanation for these high-frequency calls might be that both species breed in colonies with high levels of low-frequency background noise. Another possibility, supported by similarities in the ground calls of these two species, is that they are more closely related to each other than is currently recognized. A molecular phylogeny for *Pterodroma* would make possible a range of comparative studies on the behavior and ecology of these seabirds.

Seabird Conservation

My research also has practical applications for seabird research and conservation. It is currently estimated that 30% of seabirds, and 38% of *Pterodroma* species are threatened or endangered (IUCN 2008). These declines are mostly due to the introduction of mammalian predators to islands where these species breed. Having evolved their extended breeding seasons in the absence of terrestrial predators, many species are extremely vulnerable to terrestrial predators. Increased mortality of adults and predation on eggs and chicks has resulted in drastic population declines in a number of species. Many populations only persist in peripheral habitats (cliffs, offshore rock stacks) that remain inaccessible to introduced mammals. Monitoring populations of these rare, nocturnal, burrow-nesting species is notoriously difficult. Often investigators must excavate access hatches to confirm the presence of marked individuals within burrows.

Access hatches can reduce the structural integrity of burrows and some species increase rates of nest abandonment if handled during the incubation period. In addition, access hatches are not practical in colonies where burrows are situated among rocks or are located on cliffs. Acoustic monitoring, a less invasive yet effective tool for checking occupancy of burrows, has been used to estimate occupancy rates in a number of seabird colonies.

Acoustic identification of individuals might be particularly useful for elusive or inaccessible species. The results of this study confirm that burrowing petrels can easily be identified to sex by vocal characteristics. This vocal difference could facilitate studies of incubation responsibilities and burrow attendance among mates without use of more intrusive methods. It is conceivable that the calls might be useful for identifying individuals, although the methods used to measure and classify calls for this study would probably not be practical for most monitoring programs. However, this study has demonstrated that individual identifications based on individual variation in calls are bound to involve errors. Without permanently marked individuals, it would be difficult to establish the true identity of individuals in a burrow.

Acoustic monitoring might be a useful tool for assessing the status of seabird populations. Finally, a number of successful efforts have already shown the success of broadcasting vocalizations to attract seabirds to predator-free islands. Ensuring that the broadcast recordings contain appropriate vocalizations at appropriate times could improve these efforts.