

MONITORING HABITAT QUALITY AND CONDITION OF
QUEEN CHARLOTTE SAW-WHET OWLS (*AEGOLIUS ACADICUS BROOKSI*)
USING VOCAL INDIVIDUALITY

by

Carmen I. Holschuh

B.Sc., University of Northern British Columbia, 2001

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

February 2004

© Carmen Holschuh, 2004

ABSTRACT

Many of the traditional methods of monitoring individual study subjects become increasingly challenging when dealing with cryptic, nocturnal or secretive species. By exploiting the highly vocal nature of northern saw-whet owls, I sought to test two vocally based monitoring methods on the subspecies endemic to the Queen Charlotte Islands, *Aegolius acadicus brooksi*. First, by using discriminant function analysis, I explored whether individual males could be identified within and between years by their territorial call, to ultimately determine site use and fidelity. Although there is some variation in the calling within males, there appears to be sufficient variation between males to allow for classification, both within years and suggestive for between years, based on temporal and frequency measures of male advertisement calls. Second, by comparing temperature change, a factor thought to affect the condition of an individual, to calling rate within males, I ascertained that calling rate may be related to the condition of these birds. I then compared the calling rate between males and found this correlated with the amount of mature/old forest near the territory core, a relevant measure of habitat quality. Once modelled, this relationship appeared to predict a threshold of required mature/old forest to sustain a relatively high level of condition in the individual. Overall, my results suggest that by monitoring vocal activity of saw-whet owls, individuals can be identified throughout a breeding season and perhaps even between years. As well, using an indirect measure of condition, calling rate, other aspects of the life history of the species can be studied, including habitat factors affecting the condition of the owls.

TABLE OF CONTENTS

ABSTRACT	ii
TABLE OF CONTENTS	iii
LIST OF TABLES	iv
LIST OF FIGURES	v
ACKNOWLEDGEMENT	vi
1 GENERAL INTRODUCTION	1
1.1 Monitoring individuals to learn about their population	1
1.2 Vocal individuality	3
1.3 Site fidelity	8
1.4 Condition-dependent signals	9
1.5 Study species	12
1.6 The Queen Charlotte Islands (Haida Gwaii)	22
1.7 Thesis outline	22
2 USING VOCAL INDIVIDUALITY TO MONITOR QUEEN CHARLOTTE SAW-WHET OWLS (<i>AEGOLIUS ACADICUS BROOKSI</i>)	27
2.1 Abstract	27
2.2 Introduction	28
2.3 Methods	30
2.4 Results	35
2.5 Discussion	45
3 CALL RATE AND HABITAT QUALITY IN THE QUEEN CHARLOTTE SAW-WHET OWL (<i>AEGOLIUS ACADICUS BROOKSI</i>)	48
3.1 Abstract	48
3.2 Introduction	49
3.3 Methods	52
3.4 Results	57
3.5 Discussion	60
4 GENERAL DISCUSSION	65
4.1 Using the advertisement call to monitor northern saw-whet owls	65
4.2 Feasibility and limitations of using vocal individuality to monitor owls	66
4.3 Taking vocal monitoring of saw-whet owls the next step	71
LITERATURE CITED	73

LIST OF TABLES

1.1	Summary of three known <i>Aegolius acadicus brooksi</i> nests found on the Queen Charlotte Islands. The East-Limestone nest was found by researchers on East Limestone Island working as part of the Laskeek Bay Conservation Society. For a detailed account, see Tarver (2001).	17
2.1	Parameters characterizing the notes of advertisement/territorial calling of male Queen Charlotte Islands saw-whet owls.	36
2.2	Coefficients of variation (CV) (%) for each of the predictor variables of notes of advertisement calls of saw-whet owls as well as results of ANOVAs comparing predictor variables between sites. ‘Group’ refers to the CV over the whole data-set, while ‘ind.’ refers to the CVs for each male averaged over the individual males.	38
2.3	Classification of notes in male saw-whet owls with multiple recordings within seasons. The learning set was composed from recordings collected during one or more detections at each site. The test set calls originated from a separate recording session at the same site. Hence, the test set notes were not used in building the actual discriminant function; they were used instead for testing correct classification of novel notes. Sites marked with an asterisk had males wearing radio-telemetry transmitters, allowing confirmation of identity.	39
2.4	Classification of saw-whet owl notes at all 24 active sites in 2002 and 2003. Percent correct classification is indicated for each site separately and for the population as a whole.	42
2.5	Results of multivariate analysis (Wilks test) to determine differences between calling males at each of the contributing parameters measured on the notes.	43
2.6	Classification of notes recorded at sites in both 2002 and 2003. The numbered sites (1-7) refer to control sites, where the test set (2003) recordings were from different males than in the learning set (2002). The lettered sites (A-C) were sites that were active both years of the study. Sites B and C appeared to be defended by the same male, whereas site A likely experienced a territory turnover.	44

LIST OF FIGURES

1.1	Sonograms of three different types of vocalizations given by <i>Aegolius acadicus brooksi</i> on the Queen Charlotte Islands in a territorial context: a) male advertisement call; b) female advertisement call; c) rapid call.	24
1.2	Sonograms of <i>Aegolius acadicus brooksi</i> vocalizations recorded on the Queen Charlotte Islands: a) meow; b) whine; c) high-pitched meow; d) ksew; e) transitional call; f) squeak; g) tssst/female solicitation call.	25
1.3	Map of Graham Island showing sites of Queen Charlotte saw-whet owl (<i>Aegolius acadicus brooksi</i>) detection (black dots) during surveys in the spring of 2002 and 2003.	26
2.1	Sonogram of Queen Charlotte saw-whet owl territorial calling, illustrating measures taken. F(s), F(m), and F(e) refer to measures of frequency at peak amplitude taken from spectral slices at 10%, 50%, and 90% of the note's duration, respectively. Temporal measures were the length of the note (T(note)) and the internote length (T(internote)), referring to the time from the start of one note to the start of the next note.	33
2.2	Comparison of average distances between nearest neighbour to each male saw-whet owl and the average distance to the site any given site was most often misclassified as.	41
3.1	Within male changes in response rate in comparison to changes in daytime high temperatures (while owls were roosting) in Queen Charlotte Islands saw-whet owls.	58
3.2	Calling rate of male saw-whet owls in response to playback stimulus averaged over 5-minutes as measured against habitat, the percent of mature/old forest remaining near the apex of a male's territory. Modeled using Michaelis-Menten relationship ($y=ax/(b+x)$), where 'a' represents the maximum response rate and 'b' represents the amount of mature/old forest at half of this maximum, giving an indication of threshold. The relationship is plotted with (dashed) and without (solid) a significant outlier (indicated with arrow). The bar at the bottom of the x-axis shows the mean and 95% confidence interval of forest content before the call rate deteriorates to 50% of its maximum.	59

ACKNOWLEDGEMENT

I cannot thank my supervisor, Ken Otter, enough for recognizing my potential as a biologist and a researcher long before I did, and tirelessly encouraging me to pursue this potential. As a result of his mentoring, I continuously surprised myself by reaching goals that sometimes seemed unreachable.

Tania Tripp and Harry van Oort were my extraordinary lab mates in the ‘bird cave’. Our conversations continuously inspired new ideas, and they not only helped me make sense of the logistical and theoretical maze I sometimes faced, but they also have become very close friends. My field assistant, Luke Hyatt, endured continuous sleep deprivation, muddy tire changes and sometimes trying field conditions with astonishing and thankfully contagious enthusiasm. While assisting me during the pivotal first month in the field, Jared Hobbs shared his knowledge and infectious love of owls, and he has continued to provide a great amount of advice and support throughout this project. Charlie Holschuh (thanks Dad!), Janet Grey, Jacques Morin, Vanessa Johnson, and Malcolm Hyatt all graciously volunteered their time helping out in the field. Through Frank Doyle’s advice and logistical support, many of the hurdles I faced in Haida Gwaii were greatly reduced. Alvin Cober, Anne Hetherington and Dave Trim also provided a great amount of advice and logistical support. It was mainly through conversations with Paul Levesque that I figured out how to successfully mist-net these owls. I also thank Alvin Cober and Dave Trim for providing the map coverage for the study site, and Scott Emmons for helping me get started in the GIS lab. For his help in statistical matters, I am grateful to Mike Gillingham. My committee members, Kathy Parker and Brent Murray, have provided a balanced view that has greatly guided me through this project.

I am grateful to the following organizations for providing in-kind and monetary contributions to the project: National Science and Engineering Research Council of Canada (NSERC), Canada Foundation of Innovation (CFI), British Columbia Knowledge Development Fund, Vancouver Foundation, British Columbia Ministry of Water, Land and Air Protection, and British Columbia Forest Service. I was funded through an NSERC Industrial Postgraduate Scholarship and a Science Council of British Columbia Great Scholarship, both in generous cooperation with Weyerhaeuser Canada, Coastal Division (Glen Dunsworth).

Finally, to my parents, whose own work ethics have so deeply inspired and shaped me, I thank for their unconditional love and encouragement.

1 GENERAL INTRODUCTION

1.1 Monitoring individuals to learn about their population

Forest generalist species can be found across a wide array of habitat types. Although individuals may be uniformly distributed across the landscape, their success may vary consistently with resource availability or other factors defining habitat quality (reviewed by Harrison 1993). Thus, in order to best manage for a species across a heterogeneous landscape, it is important to define which habitats are of high quality.

Traditional studies of habitat preference often involve surveys of presence versus absence across the landscape. The underlying assumption with these studies is that dense occupation of a particular habitat type reveals a high-quality habitat. Yet, because changes in a landscape may upset the natural source and sink dynamics of a metapopulation (Remeš 2000), this assumption often does not hold true (Van Horne 1983). Further, there may be annual variability in the density of birds or mammals across a landscape due to fluctuations in the food source or other environmental factors. Alternatively, the social structure of the focal species may prevent subordinate individuals from occupying high quality habitats, thereby creating densely occupied population sinks in sub-optimal habitats (Van Horne 1983). In cases where the landscape is changing due to anthropogenic habitat disturbance, this effect could be catalyzed as animals may make poor ‘decisions’ about areas to occupy, using cues that were reliable in the past (Remeš 2000).

Because simply measuring the occupation and densities of individuals across different habitats is not reliable, several other measures have been employed to determine habitat quality. Measuring breeding success appears to reliably indicate habitat quality (Sergio et al. 2003), and even seems to be sensitive to factors such as the level of

fragmentation (Zanette 2001). The habitat quality at the nest site is also an important factor affecting the level of recruitment of avian dispersers (Blums 2002), indicating not only hatch-year survival, but also more long-term success. Alternatively, because birds may breed more consistently in areas where breeding performance is greater (Korpimäki 1988), monitoring sites with increased site fidelity may indicate good quality habitat. Conversely, habitat fragmentation may lead to increased territory turnover (Redpath 1995). Thus, by monitoring the subsequent occupancy by a shifting individual, areas with high quality habitat may be defined (Matthysen 1990).

To be able to measure the success of individuals across habitats, one must first identify individual study subjects in the field. In birds, common ways to mark individuals for re-identification include leg-bands and radio-telemetry (reviewed in McGregor and Peake 1998). These techniques become logistically problematic, however, when dealing with cryptic species where recapture or even non-invasive visual re-identification is unfeasible. Radio-telemetry also has limitations, as transmitter battery life is often too short for multi-year monitoring of individuals without recapture. Also, many traditional marking techniques are fairly invasive, making them particularly undesirable when working on populations of rare or endangered species. Finally, transmitters are expensive, and therefore often only a subset of the population can be marked. Because many cryptic species are conspicuously vocal, and individually distinctive vocalization could allow entire populations to be monitored relatively inexpensively, the use of vocal individuality has been proposed as a working alternative to monitoring and studying the life-history of vocal birds (Saunders and Wooller 1988, McGregor et al. 2000).

1.2 Vocal individuality

1.2.1 *Evolution and maintenance of vocal individuality*

Evidence suggests that differences in the calls or songs of individuals within a species are distinguishable and measurable (e.g. Galeotti et al. 1993, Otter 1996). This is not surprising, considering that previous research has shown that birds use vocal differences for distinguishing between and recognizing members of their immediate population (reviewed by Falls 1982). Birds have been shown to recognize their mates (Davies 1986, Lind et al. 1996), distinguish between neighbours and strangers (Falls 1982; Galeotti and Pavan 1993) and parents and young are able to recognize each other (Falls 1982) via vocal signals. Thus, evolution has favoured variability in vocal structure as it facilitates the effectiveness of an individual to communicate. Along with physiological differences between individuals causing vocal signatures (reviewed in Catchpole and Slater 1995), the need of individual birds to be able to distinguish between conspecifics likely plays an important role in the maintenance of vocal individuality.

1.2.2 *Measuring vocal individuality*

Methods to measure the variability in calls to allow researchers to identify individuals fall into two broad categories: (1) qualitative techniques involving visual classification of the calls by researchers using printed sonograms, and (2) quantitative techniques using detailed measurements of frequency and temporal parameters of the vocalizations (Terry et al. 2001). Because of its lower reliability, qualitative techniques are generally usually only used in a preliminary analysis, preceding more rigorous quantitative techniques.

Several different quantitative approaches for analyzing vocal individuality exist. If the goal is simply to determine whether there are appreciable differences in the vocalizations

to differentiate individuals, a series of nested ANOVAs can be used to compare the measured parameters within versus between individuals (e.g. Otter 1996). If however, the goal is to identify males by their subsequent vocalizations, more elaborate statistical tools must be employed. Often spectrographic cross correlation and discriminant function analysis (DFA) are used for such classification. Spectrographic cross-correlation compares the similarity of two sonograms by calculating overlapping levels of energy of the sounds (reviewed by Terry et al. 2001). Classification of the sound occurs by pre-determining a threshold of similarity that maximizes the chance of correct classification, while minimizing the chances of incorrect classification. This can be difficult to achieve, however, as background noise and minor fluctuations in the call can lead to low cross-correlation scores, despite the call being from the same male. Hence, a certain level of subjectivity is introduced with this technique (McGregor et al. 2000).

Discriminant function analysis (DFA) is a multivariate statistical technique that allows for classification. Several variables are measured from the waveform and/or sonogram of the calls from the focal males. The classification of calls occurs by creating a linear combination of the measured variables to minimize the variation within males while maximizing the amount of variation between the males (Quinn and Keough 2002). When new calls are introduced into the analysis, they are classified into the groups (males) that were used to make the model. Hence, an underlying assumption of this analysis is that all the calls being classified are in fact from one of the males used in building the discriminant function. Calls being classified are ‘forced’ into the category of the individual male used in the initial model to which the call is most similar, regardless if these two males are the same individual. However, violation of this assumption has been used in determining territory

turnover; a high level of misclassification of calls originating from a particular location between two successive breeding seasons may indicate occupancy by a new male at that territory (Galeotti and Sacchi 2001).

Because DFA involves the stepwise building of a function by either sequentially adding or removing variables, the relative impact of each variable on the overall classification ability can be measured, which is useful for subsequent analyses of the same species (Terry *et al.*, 2001). Using DFA in some capacity to analyze vocal individuality seems to have become the standard practice, and has now been used in a variety of different species (e.g. Rebbeck *et al.* 2001, Peake *et al.* 1998, Eakle *et al.* 1989).

Some studies also have used ANOVA in combination with a multiple range test (Duncan's procedure) to measure differences between individuals for each call parameter separately, and then utilized DFA to classify males (Galeotti *et al.* 1993, Galeotti and Pavan, 1991). The utility of this extra step is a preliminary exploration of the variables later used to build the DFA, allowing the authors to confirm that each variable separately differed between males. Even though the stepwise procedure of DFA does not include variables that do not explain significant differences between the males, this preliminary step of analysis allows the investigators to better explore which variables best describe the vocal differences between males.

A newer technique for analyzing vocal individuality employs neural networks to discriminate between and identify individuals. Neural networks are a complex series of interconnected mathematical models that can be used for classification, without data needing to be separated linearly (Terry and McGregor 2002 and references therein). These algorithms are often used in modern speech recognition software. The apparent advantage of using

neural networks is that probabilities of group membership (i.e. male identity) are calculated, allowing the researcher to determine whether a new individual has been introduced into the model. This is an improvement over the underlying assumption of DFA that individuals to classify must come from the pool used to build the discriminant function. However, neural networks are computationally much more complex and require a much greater amount of data if there is variation in calling within an individual (Terry and McGregor 2002).

Neural networks may be a very appealing method for individual identification by vocal characteristics, due to their similar use in human voice recognition. However, the feasibility of consistently applying this technique as a monitoring tool still lies in the future, as the costs of the computational processes involved still outweigh any benefits of a slightly increased ability to correctly classify males. Due to the high amount of subjectivity involved with qualitative and cross-correlation techniques, these methods are becoming less common in vocal individuality studies. Because DFA is an intuitive form of analysis based on the F-statistic that most biologists are very familiar with, it has become the most common tool for vocal classification. More recent research on studying territory turnover is also making use of low classification to identify sites being occupied by a new male (Galeotti and Sacchi 2001). However, the definition of a threshold between a low classification at a site still occupied by the same male versus low classification due to a territory turnover is still quite subjective (but see Chapter 2).

1.2.3 Applications of vocal individuality

In order to successfully apply vocal individuality as a census and monitoring tool in any given species, it must be established that the vocal characters describing a call remain fairly constant, both within and between years. Once this has been established (e.g. Gilbert et

al. 1994, McGregor and Byle 1992), this tool can be applied for both monitoring within year movements (Peake and McGregor 2001) and estimating levels of site fidelity and territory turnover between years (Delport et al. 2002, Gilbert et al. 2002, Galeotti and Sacchi 2001). Using vocal individuality, Peake and McGregor (2001) were able to not only increase census accuracy of corncrakes (*Crex crex*), but also monitor levels of movements and relate this to habitat quality. Interestingly, their findings differed from those of previous radio-telemetry studies, which the authors attributed to possible biases introduced by radio-telemetry studies: (a) by using playback to capture individuals, a subset of more territorial males may be captured, and (b) radio tags may affect the attractiveness of the males, causing them to have to continue calling for longer in order to secure a mate. The biases stemming from such invasive capturing and handling techniques are reduced when utilizing vocal individuality to monitor the birds (Peake and McGregor 2001).

When vocal characteristics remain fairly constant between years, it is possible to estimate levels of site fidelity and territory turnover. For example, after establishing vocal individuality, Delport et al. (2002) were able to estimate annual turnover rates and the duration of territory residency for male and female African wood owls (*Strix woodfordii*). Similarly, despite having consistent activity in certain territories, high levels of territory turnover were measured using vocal individuality techniques in scops owls (*Otus scops*) (Galeotti and Sacchi 2001).

Perhaps the longest-term study employing measures of vocal individuality was to monitor annual survival of great bitterns (*Botaurus stellaris*) over a 10-year period (Gilbert et al. 2002). The authors of this study pointed out some important biases in using this as a long-term monitoring tool. First, if only one of the sexes is vocal, there is an obvious lack of

knowledge about the survival and behaviour of the other sex (Gilbert et al. 2002). Hence, in studies utilizing vocal individuality to monitor males for instance, care must be taken to not extrapolate the findings to females without proper justification. Second, studies may bias the information towards the more vocal males, which may also be in better condition (Gilbert et al. 2002). As such, if outcomes of monitoring or census efforts could be affected by such a detection bias towards males in higher condition, survey protocols should allow for spontaneous calling as well as response to playback, so as to increase chances of detecting males that may not otherwise respond to a territorial dispute. Alternatively, a preliminary study on the likelihood of response by males in different condition may allow for standardized correction of census estimates. In all, recent studies utilising vocal individuality as a tool suggest that it may be an effective way to monitor populations of cryptic and/or nocturnal species over the long term. Being able to monitor individuals over the long term may enable researchers to collect important ecological information that may be critical to management of the species, including apparent habitat preferences (Peake and McGregor 2001).

1.3 Site fidelity

Levels of site fidelity may be powerful indicators of other factors driving a population. Some factors affecting breeding site fidelity are breeding success in the previous year, age (Newton 1993), sex of the bird and food availability (Löfgren et al. 1986). Thus, birds that have had an unsuccessful breeding attempt at a given site in the past tend to switch to a different territory (Newton 1993). Conversely, those that experienced high reproductive success at a particular location tend to have increased fidelity to that breeding site (Bried and Jouventin 1999). Site tenacity appears to be greater when food availability is high (Löfgren et

al. 1986), and high food availability tends to be associated with greater breeding success (Korpimäki 1992). As habitat quality can be associated with resource availability and reproductive success, both of which seem to be related to site fidelity (Bried and Jouvetin 1999, Gavin and Bollinger 1988, Löfgren et al. 1986). Thus, it may be possible to deduce habitat quality from monitoring levels of site fidelity across different habitat types by comparing sites that have an overall greater level of fidelity to those with lower re-occupancy rates. In such a study however, it is important to recognize that a territory turnover may also be caused by over-winter mortality or other factors having little to do with the habitat of the breeding site. As such, efforts to monitor site fidelity and territory turnover should be conducted over a long term before conclusions about habitat quality are drawn. Vocal individuality appears to be a useful tool for such long-term monitoring of the identity of site occupants. However, once individuality has been established, singing behaviour can also be utilized to determine condition of males within a population and even to infer habitat quality.

1.4 Condition-dependent signals

1.4.1 *Condition and honest signals*

Breeding and courtship behaviours often involve elaborate visual and/or vocal displays. Females of many species seem to assess these displays when choosing potential mates (reviewed in Bradbury and Vehrencamp 1998), and in the case of some species, extra pair partners (Forstmeier et al. 2002). The basic reason for this lies in the cost of producing these signals, which is often related to energetic demands (Hogstad 1987), re-allocation of time away from self-maintenance, and increased potential exposure to predators (Bradbury and Vehrencamp 1998). A large signal requires an incrementally higher investment from the signaller because of these costs, and so its resources must be sufficient to allow it to allocate

energy into producing the signal as well as meeting its self-sustaining energy requirements. In other words, to sustain a large advertisement signal (which essentially acts as a handicap to the signaller), a male must be in good phenotypic condition (Kotiaho 2000, Zahavi 1977). In birds, examples of honest, condition-dependent signals are usually related (a) to plumage characteristics, such as plumage brightness (e.g. Eeva et al. 1998) or other sexual ornaments (e.g. Ohlsson et al. 2002), or (b) to long-range vocalizations and songs (e.g. Catchpole and Slater 1995). To the females assessing these signals, being able to determine which males are in better condition may ensure increased reproductive success, be it through increased access to resources in monogamous species or simply through access to ‘good genes’ in more polygynous species (Andersson 1994).

1.4.2 Vocal output

Due to the metabolic costs associated with singing (Oberweger and Goller 2001), high song output and rate in birds have been associated with measures of success such as a higher social rank (Otter et al. 1997) and ability to secure mates (Galeotti 1998, Alatalo et al. 1990), ultimately leading to increased reproductive success (Catchpole 1986). Even in non-passerine species, factors of the long-distance advertising/territorial call are associated with condition. For example, in Tawny owls, call frequency increases and call length decreases in birds with high levels of blood parasite infection (Redpath et al. 2000, Appleby and Redpath 1997). When the effects of food abundance were accounted for, however, parasite loads did not explain differences in response to intruders, indicating that overall food availability may play an important role in the territorial behaviour of these owls (Redpath et al. 2000, Appleby et al. 1999).

Various abiotic factors can cause the condition of birds to fluctuate, the most widely studied of which are food availability and temperature. When temperatures drop below thermoneutral optima during roosting, energetic requirements increase in order to thermoregulate, leaving the birds with diminished energetic stores once awaking (Thomas and Cuthill 2002 and references therein). When the metabolic demands of birds are increased in such a manner, more energy must be used for self-maintainance, leaving less energy for advertising and defending a territory. This energetic strain seems to have two synergistically related behavioural outcomes, a decrease in song production (Garson and Hunter 1979, Higgins 1979) and an increase in foraging behaviour to restore optimal energetic stores (Thomas and Cuthill 2002, Strain and Mumme 1988, Reid 1987). In other words, a cold bird has less energy to sing or call, and restoring that energy by foraging competes temporally with singing or calling. Moreover, decreased food availability itself can have a great effect on song production (Johnson and Rashotte 2002). If the food supply to a bird fluctuates, song rates tend to decrease, indicating a lower energetic investment in singing when it is uncertain that available resources can meet basic metabolic needs (Thomas 1999). It is for this reason that monitoring song rates is a good strategy for females (Alatalo et al. 1990), as it may give cues not only to the phenotypic quality of potential mates, but also may give indications of their territory quality (Galeotti 1998).

This correlation between habitat quality and song rate is likely two faceted: first, high quality males who are likely to acquire rich territories may have more inherent energy to advertise with song; second, even if settling males do not differ in inherent quality, a rich territory will provide greater resources to a male, allowing it to sing. In actuality, both are likely to occur, as high quality males acquire rich resources, which in turn elevate their song

rates. This synergistic effect should result in even greater variation in song rates among habitats that vary in quality.

As habitat quality appears to affect the reproductive success and condition of birds, it seems logical to explore whether habitat quality correlates with song (or territorial call) output in birds. In other words, monitoring an apparent condition-dependent signal, and comparing signal expression across habitats varying in quality may allow researchers to deduce important information about environmental health (Hill 1995, McGregor et al. 2000). Because song or call rate is a plastic trait that can be affected by even subtle abiotic factors, the potential use of vocal rate as a biomonitor to manage for species is significant. In northern goshawks (*Accipiter gentilis*), higher territorial vocalization rates were associated with higher nest-stand quality as well as increased reproductive success (Penteriani et al. 2002). As well, Hoi-Leitner et al. (1995) found evidence that females may be using song rate instead of territory quality to assess potential mates. By detecting subtle changes in condition caused by changes in habitat, impacts may be noticeable at a smaller scale and therefore at an earlier stage. This may allow for more proactive management decisions, as changes in expression of condition dependent signals may be detected before declines in a population occur.

1.5 Study species

1.5.1 *Species status*

The Queen Charlotte Islands' subspecies of northern saw-whet owl (*Aegolius acadicus brooksi*) is endemic to the archipelago located in north-western British Columbia. Provincially, this subspecies is blue-listed, indicating it to be vulnerable or of special concern owing to factors of its life history that make it sensitive to anthropogenic or natural events.

At the national level, these owls are among the highest priority candidates of birds to be assessed for risk of extinction or extirpation by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

1.5.2 Description and range

The *A. a. brooksi* subspecies was first described in by J.H. Fleming (1916). He noted that overall, these owls were darker and more buffy in colour, especially on the breast and facial disk than their *A. a. acadicus* counterpart. Based on their plumage coloration, no hybrids between the two subspecies have ever been identified (Sealy 1998). Overall, the two subspecies are similar in size. Saw-whet owls have reverse sexual dimorphism, with females being significantly larger than males (Cannings 1993).

Although *A. a. acadicus* occasionally has been observed on the Queen Charlotte Islands, it is during post-breeding movements or migration, and not during the breeding season. Further, isotope analysis of both *A. a. brooksi* and *acadicus* reveals that *A. a. acadicus* individuals do not remain on the Queen Charlotte Islands for long (Hobson and Sealy 1991). Similarly, *A. a. brooksi* are not thought to move off the Queen Charlotte Islands, but range on both the larger (Graham and Moresby) Islands, as well as many of the smaller islands in the archipelago (Hobson and Sealy 1991).

1.5.3 Diet

The two dietary analyses carried out on *A. a. brooksi* revealed that this subspecies may be a greater generalist in food choice than *A. a. acadicus* (Hobson and Sealy 1991, Sealy 1999). Because these owls are the only species of owl known to breed in the Queen Charlotte Islands, this finding seems logical, as individuals should be less constrained in their niche,

and have a wider array of resources available to them based on decreased heterospecific competition.

Using a combination of stomach content and isotope analysis, *A. a. brooksi* were found to have much greater contribution of marine protein in their diet than *A. a. acadicus*, which diet consisted of 97 % small mammals (Hobson and Sealy 1991). The marine foods consumed by *A. a. brooksi* are numerous, nocturnal and found at the high-tide line or splash zone. They included beach amphipods (*Crustacea: Talitridae*) and seaweed flies (*Diptera: Coleopidae*) (Hobson and Sealy 1991). However, in a separate analysis, other available foods were also taken, even including ancient murrelets (*Synthliboramphus antiquus*) on East Limestone Island (Sealy 1999). Hence, overall it appears that *A. a. brooksi* are more opportunistic, have a higher level of marine-based foods and take a wider range of prey than the nominate subspecies (Sealy 1999). When considering this finding, it is important to realize that most of the specimens for the analysis were road-killed, and therefore, were located near a beach. Dietary analyses of birds using more interior habitats is still lacking, although the evidence of the generalist nature of these birds suggests their diet composition to be plastic based on availability. Theoretically, birds residing on the islands' interior may have a decreased marine protein contribution, and a greater rodent contribution, more in line with the nominate subspecies.

1.5.4 *Habitat*

In a systematic survey of the habitat use of *A. a. brooksi*, Gill and Cannings (1997) found that owls were detected at points close to riparian areas and in habitats containing greater amounts of old and young forest. They found that elevation, distance to saltwater, and

other habitat types did not influence the probability of detecting owls, nor did habitat descriptions such as dominant tree species.

For this study, I conducted habitat surveys at 25 different occupied sites over the two years. Of these sites, 17 were characterized as being old forest, which can be described as being structurally complex, having evidence of old trees that have survived previous disturbance and with a regenerating layer of shade-tolerant trees. Snags in all stages of decomposition are relatively numerous. Four of the sites were in mature forest, which has some level of canopy complexity due to an upper canopy layer of trees regenerating from disturbance and a lower layer of shade-tolerant trees becoming established. Three of the sites contained a large amount of young forest, which can be described as having less canopy complexity, although layers in the canopy are starting to develop. Finally, one detection site was composed of mostly pole/sapling stage forest, which has little or no vertical structure or self-thinning (Meidinger 1999).

Averaged across all the measured sites (n=25), the mean height of the tallest trees was 37.4 m (± 8.74 m S.D.), while the main tree canopy was 28.2 m (± 7.24 m S.D.) tall, and the sub-canopy trees were 17.5 m (± 5.53 S.D.) tall. The greatest density came from the main tree canopy layer and was generally between 25 and 50%. All other tree and shrub layers independently composed approximately 5-25 % ground cover. In most of the owl sites, vertical canopy structure was apparent, indicating the forest to be mature or old. The most common tree species were western hemlock (*Tsuga heterophylla*), sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and to a lesser and more site specific degree, mountain hemlock (*Tsuga mertensiana*), yellow cedar (*Chamaecyparis nootkatensis*) and shore pine (*Pinus contorta*) were also noted.

Although some rudimentary ideas of habitat use during the breeding season were apparent from the systematic surveys by Gill and Cannings (1997) in combination with the descriptive information I presented here, information on habitat use during the non-breeding season is still lacking. Since these owls are non-migratory (Cannings 1993), the birds may occupy territories year-round. Alternatively, it may be advantageous for birds occupying more interior areas to move to the coastline, due to the rich and highly available food source. This may account for the increased sightings of owls during the fall and winter months (personal communication with local residents), although, those sightings also may be of juvenile dispersers. In order to develop a more holistic picture of the habitat needs of *A. a. brooksi*, both breeding season and non-breeding season habitat use need to be better defined.

1.5.5 Nesting

To date, only three nests of *A. a. brooksi* have been found (Table 1.1). Like the nominate subspecies, these owls are secondary cavity nesters, generally using northern flicker (*Colaptes auratus*) cavities, or hairy woodpecker (*Picoides villosus*) cavities that have been increased in size by squirrels or natural decomposition. To be usable by saw-whet owls, it is thought that cavities must be at least 75 mm in diameter (Cannings 1993).

The timing of breeding and nesting is probably highly asynchronous in *A. a. brooksi*. As levels of territorial calling tend to decrease markedly once nesting begins (K. McKeever and R. Cannings, pers. comm.), the variety of timing in onset and ending of calling activity (2+ month range) confirms that nesting could begin anywhere from late March to late May in these owls.

Table 1.1: Summary of three known *Aegolius acadicus brooksi* nests found on the Queen Charlotte Islands. The East-Limestone nest was found by researchers on East Limestone Island working as part of the Laskeek Bay Conservation Society. For a detailed account, see Tarver (2001).

	East-Limestone (Tarver 2001)	Riley Creek	Port Clements
Year	2001	2002	2003
Distance to nearest creek	~15 m	~ 50 m	~100 m
Distance to ocean	~10 m	~1700 m	~80 m
Distance to forest edge	0 m	~ 80 m	~10 m
Snag species	Sitka Spruce	W. Hemlock	
Snag decomposition class**	5	5	6
Snag height	15 m	28 m	15 m
Snag diameter at breast height	130 cm	125 cm	70 cm
Cavity height	9 m	25 m	12 m
Cavity type	Excavated: Northern Flicker	Excavated: Hairy Woodpecker	Excavated: Northern Flicker
Cavity size	78 x 74 mm	~ 80 mm	~75 mm
Surrounding habitat:			
Structural classification	N/A	Old Forest	Old Forest
Canopy height	N/A	30 m	35 m
Canopy cover/density	N/A	25-50 %	5-25%
Leading tree species	N/A	W. Hemlock	W. Hemlock

**Snag decomposition class follows British Columbia classification of wildlife trees.

Class 5 indicates a dead tree of full height, which has lost most of its branches and bark, and has suffered some internal decay. A class 6 decomposition class also has no branches or bark, but because of more advanced decay has often broken to 2/3 of its height.

1.5.6 *Vocalizations*

Saw-whet owls have a large repertoire of vocalizations, used in several different social contexts. I describe here ten types of *A. a. brooksi* adult vocalizations I encountered and was able to record in the field and the social context in which they were given.

1.5.6.1 *Male advertisement call*

This call uses a series of stereotyped notes 0.113 s (± 0.01 S.D., N=26) in length given at a frequency of 1194 Hz (± 47.2 S.D., N=26). The notes are given at an approximate rate of 2-3 notes per second, but this varies between nights and between males (Chapter 3). Structurally, the call differs between males in terms of note length and various frequency parameters (Chapter 2). Depending on the landscape, this call can travel anywhere from 300 – 1000 m (Cannings 1993). The purpose of this call appears to be similar to that of song in passerines, for males to advertise to potential mates and to defend his territory. When detecting a saw-whet owl, this is the most likely call to be heard after playback during the breeding season (Figure 1.1a).

1.5.6.2 *Female advertisement call*

This call is similar to that of the male advertisement call, only at a higher frequency (~1500 Hz), and with a more ‘barky’ quality. The note frequency is typically not as consistent as in the male advertisement call. Similar to the male’s call, the context of these vocalizations seems to be territorial, as this call is usually heard in response to playback (Figure 1.1b). These calls were observed during the breeding season, and were identified as being from a female based on the auditory quality being so variable from the male advertisement call. The sex of the birds, however, was not confirmed beyond the apparent differences in vocal qualities.

1.5.6.3 *Rapid call*

In quality, this vocal type is similar to that of the male advertisement call, only at a much higher rate (4-5 notes /second). There appear to be a few different contexts for using this call, although they all appear associated with a heightened level of excitement in the male. Most commonly, a quiet version of this rapid calling is given at the beginning of a bout of advertisement calling, as was described by Otter (1996), who called this the ‘introductory component’ of the call. However, not all calling bouts start using this more rapid call, especially if the males are spontaneously vocal. This rapid call was observed to be used by males engaging in pre-copulatory duets with their mates, and was not followed by the main advertisement call. The female responded to his rapid calling using a high-pitched solicitation call (tssst call described below). Immediately after copulation, the male again resumed rapid calling. When a male is highly excited due to a territorial fight, or in the context of copulation, it will often alter the frequency and amplitude of the call, often becoming quieter with heightened excitement. A further context of this rapid call seems to be as a contact call at the nest. The male will approach the nest with food and give a short bout of rapid calling, upon which the female’s head emerges from the cavity to receive the food. Often the female will be giving the ‘tssst’ call from within her cavity. This has also been described as a “visiting call” (Cannings 1993 and references therein) (Figure 1.1c).

1.5.6.4 *Meow*

This contact call is approximately 0.9 seconds in length and has an upward sweeping quality to the sound. Typically the call will start at approximately 1050 Hz and increase to as high as 1300 Hz. The sound’s quality could be described as somewhat hoarse. This call is the “nasal whine or wail” described by Cannings (1993). The context seems to generally be one

of agitation. Often males will respond to playback calling using this call repeatedly for 2-3 minutes at a rate of approximately one call every three seconds and will often then lead into a bout of advertisement calling (Figure 1.2a).

1.5.6.5 Whine

This is yet another contact call, which also seems to be used in a highly agitated context. Although superficially this call may resemble the meow call described above, its auditory qualities differ in that the majority of the call is around 1500 Hz, and it is only approximately 0.4 seconds in length. This call is also often repeated for several minutes. Sometimes males will respond to playback using this call. Alternatively, at the end of a bout of advertisement calling, highly agitated males sometimes transition into these whines, and continue calling for one to two more minutes. While switching from advertisement calling to the whine, often a transitional call is used (described below) (Figure 1.2b).

1.5.6.6 High-pitched meow

This call also bears resemblance to the meow call, but is given at a much higher frequency, starting at 1910 Hz and increasing to 2470 Hz. These calls were observed in response to playback at a site where the male was presumably mated, and two different individuals were making the calls, likely the male and female. Hence, it is unlikely that this is simply the female version of the meow call. The call's high frequency, low amplitude and high frequency modulation make it an unlikely candidate for far transmission through a forested landscape. These general auditory qualities suggest the call may be used to maintain contact between two members of a pair (Figure 1.2c).

1.5.6.7 *Transitional call*

This call is sometimes used by highly agitated males at the end of an advertisement calling bout, to transition into a series of whines. The notes have a fluid quality to them, yet do not have harmonic frequencies, and increase in pitch from approximately 1200 Hz at the start to 1500 Hz towards the middle and end of the note. At the start of a calling bout, call length is around 0.17 seconds and often increases while transitioning into the whine. These calls are generally repeated at a rate of 1-2 notes per second (Figure 1.2e).

1.5.6.8 *Ksew calls*

This short set of contact calls is also given when the owls are agitated and at close range to an intruder or playback. The calls start at a higher frequency (1300 Hz) and decrease pitch to 1000 Hz over the 0.1-second duration of the note. Usually only two or three of these fast calls are given before pausing (Figure 1.2d).

1.5.6.9 *Tssst call*

These solicitation calls are given by females while in the nest (Cannings 1993, pers. obs.), before males deliver food items, and also in a pre-copulatory duet with a male using the rapid call (pers. obs.). These calls are very high-pitched at around 9500 Hz, have a high level of frequency modulation, and are very quiet. Further, they are repeated at a rate of approximately one call every one to two seconds, and are roughly 0.3 seconds in duration (Figure 1.2g).

1.5.6.10 *Squeaks*

This call is likely used as a threat, as it is uttered at very close range while the owl is flying past or attacking an intruder (or person doing playback). It has a two-note component and is approximately 0.3 seconds in length, with the first note being higher pitched than the

second. Both have obvious harmonic qualities. It may be repeated three or four times, but always with several seconds between. This call may be the “short, insect-like buzz” referred to in Cannings (1993, and references therein) (Figure 1.2f).

1.6 The Queen Charlotte Islands (Haida Gwaii)

The Queen Charlotte Islands, also known as Haida Gwaii, are an archipelago of approximately 100 islands located in northwestern British Columbia. With the islands being more than 80 km from mainland British Columbia and Alaska, plus areas of Haida Gwaii having been a glacial refugia, a number of endemic species and subspecies have evolved on these islands, ultimately leading to a title of the “Canadian Galapagos” (Foster 1984). The Queen Charlotte Islands’ subspecies of northern saw-whet owl is one of these taxa.

This study focussed mostly on the southern half of Graham Island, the largest island in the archipelago (Figure 1.3). The main industry on this island is forestry, having led to high levels of harvesting in the accessible central and western watersheds. Most of the northeastern end of Graham Island is protected in a Provincial Park, while remaining areas are being continuously logged. The rapid anthropogenic changes combined with low levels of knowledge about the life history and status of many endemic species create a critical need for study in this area.

1.7 Thesis outline

1.7.1 *Vocal individuality*

Using discriminant function analysis, I examined whether the advertisement call of saw-whet owls has sufficient variation between males to allow discrimination and classification within years, and perhaps even between years. In chapter 2, I investigated the utility of such a vocal-based classification, and explored whether a novel application of

discriminant function analysis allows for greater certainty in determining territory re-occupancy. I discussed the feasibility of monitoring saw-whet owls using this technique over a longer term to ultimately study other factors of life history and ecology, such as abiotic and biotic factors that may affect the condition of the owls.

1.7.2 *Calling rate and habitat*

Rates of advertising calling differ both within and between males. In chapter 3, I explore factors that may cause such differences. I first tested whether changes in calling rates of males related to changes in ambient temperature, indicating that the rate of advertisement calling may be related to an individual's condition. Further, I examined whether changes in calling rate between males were related to a measure of habitat quality, the amount of mature and old forest remaining near the territory core. With this relationship, calling rate may be a useful indicator of the condition of owls in altered habitats.

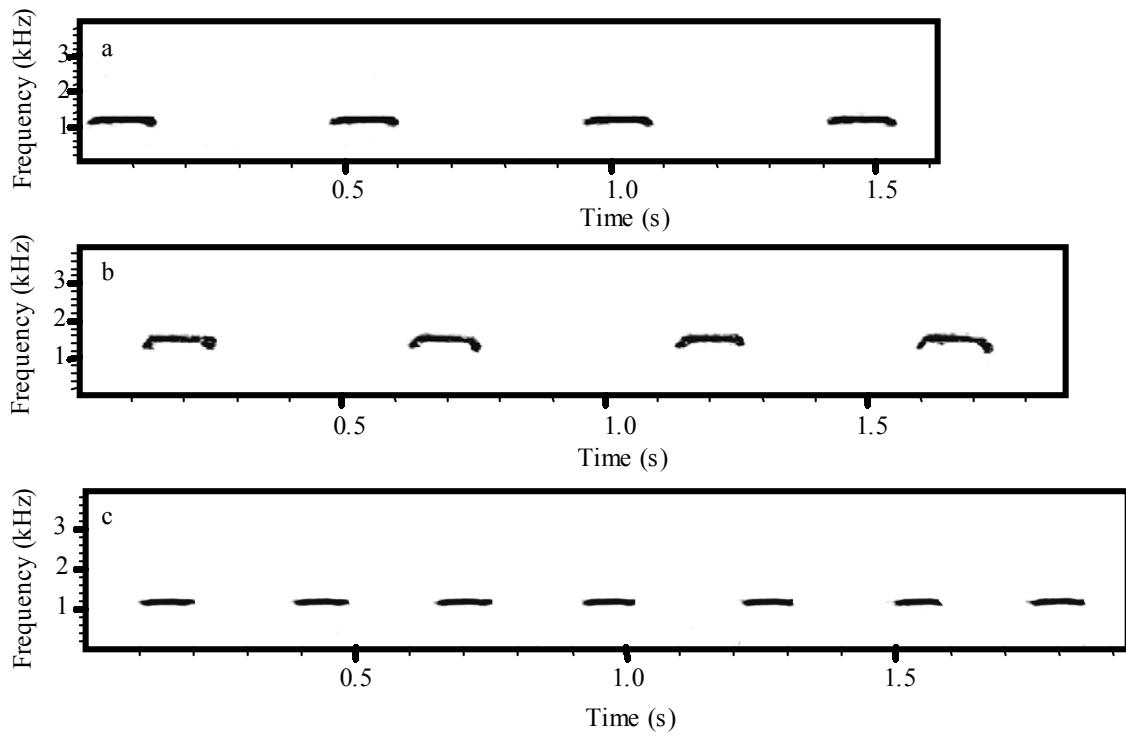


Figure 1.1: Sonograms of three different types of vocalizations given by *Aegolius acadicus brooksi* on the Queen Charlotte Islands in a territorial context: a) male advertisement call; b) female advertisement call; c) rapid call.

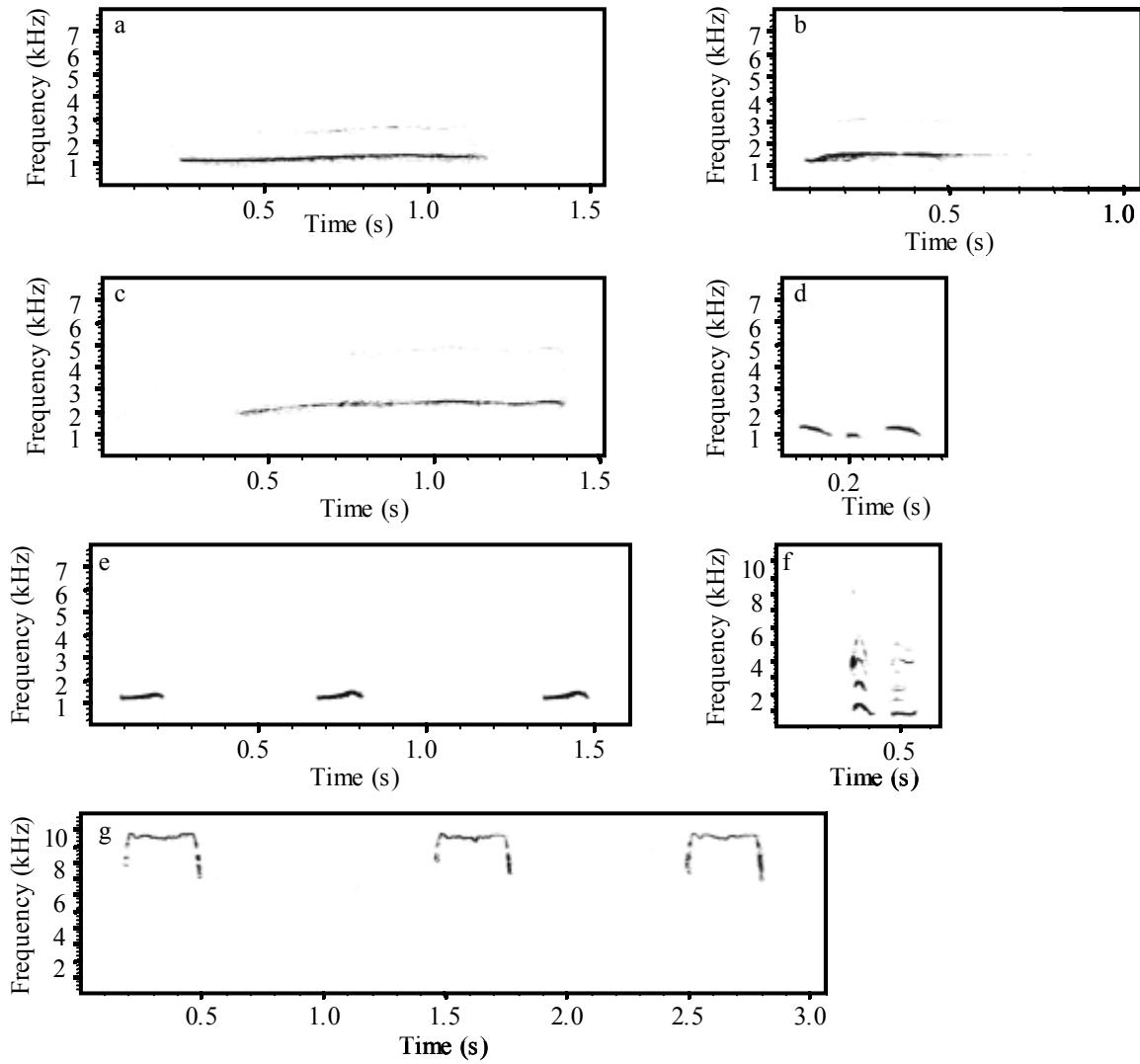


Figure 1.2: Sonograms of *Aegolius acadicus brooksi* vocalizations recorded on the Queen Charlotte Islands: a) meow; b) whine; c) high-pitched meow; d) ksew; e) transitional call; f) squeak; g) tssst/female solicitation call.

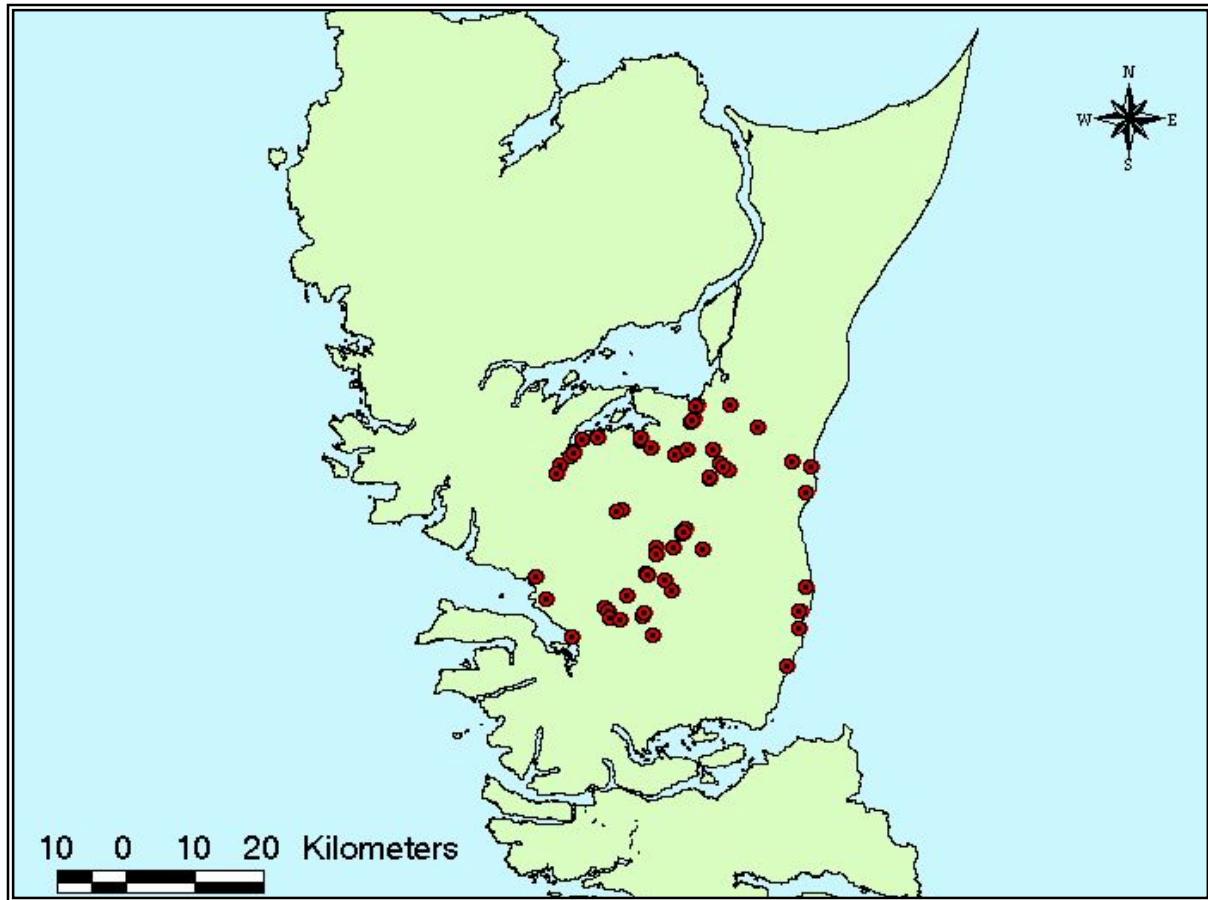


Figure 1.3: Map of Graham Island showing sites of Queen Charlotte saw-whet owl (*Aegolius acadicus brooksi*) detection (black dots) during surveys in the spring of 2002 and 2003.

2 USING VOCAL INDIVIDUALITY TO MONITOR QUEEN CHARLOTTE SAW-WHET OWLS (*AEGOLIUS ACADICUS BROOKSI*)

2.1 Abstract

The purpose of this study was to assess whether individual male northern saw-whet owls in the Queen Charlotte Islands (*Aegolius acadicus brooksi*) have sufficient variation in the notes of their territorial/advertisement call to allow classification of individuals within nights, between nights within season and ultimately between years. Recordings of calling bouts were collected from a total of 24 sites over the two-year study period and analyzed using discriminant function analysis. Using recordings of all 24 males, the discriminant function analysis was able to classify notes to the correct site 64% of the time. For the 13 sites for which I had multiple recordings, 73% of notes measured from a novel night were classified to the correct site. The data also suggested that vocal individuality can be used to monitor site fidelity and rates of territory turnover across years, as correct classification of males re-occupying specific sites across years (>60%) was greater than rates of random classification (mean=3.3%, max.=19%). Overall, results from this study suggest that measuring vocal individuality appears to be a useful tool for monitoring and studying life history parameters of northern saw-whet owls both within and between years.

2.2 Introduction

Avian studies examining various life history parameters frequently employ techniques that allow the investigators to differentiate among individuals in a population, via the application of coloured leg bands and/or radio-telemetry transmitters (Bibby et al. 2000). Often, when working on secretive and cryptic species, the utility of leg bands decreases and the impacts to study subjects associated with a radio-telemetry study, such as stress associated with handling and carrying the excess weight of a transmitter, may make the study counterproductive. Thus, any cues that study animals may inherently give as to their identity should be explored as a non-invasive way to monitor these individuals. One such cue, vocal individuality in birds, has recently gained popularity as a technique to study visually secretive and cryptic species. The following species all have been shown to possess sufficient levels of variation in calls between birds to allow for differentiation: Eurasian pygmy owls (*Glaucidium passerinum*) (Galeotti and Pavan 1993), European nightjars (*Caprimulgus europaeus*) (Reebeck et al. 2001), great bitterns (*Botaurus stellaris*) (McGregor and Byle 1992), tawny owls (*Strix aluco*) (Galeotti and Pavan 1991), bald eagles (*Haliaeetus leucocephalus*) (Eakle et al. 1989), corncrakes (*Crex crex*) (Peake et al. 1998) and northern saw-whet owls (*Aegolius acadicus*) (Otter 1996). For monitoring and studying the ecology of cryptic species, the ability to determine individual identity based on vocalizations promises to be of great use.

By being able to discriminate between individuals counted on multiple nights, census accuracy can be greatly increased (e.g. Gilbert et al. 1994, Peake and McGregor 2001). An extension of this ability to re-identify individuals within a study season is to compare site occupancy between years using vocalizations, and ultimately to learn more about life history

parameters such as site fidelity and between-year territory turnover (e.g. Galeotti and Sacchi 2001, Delport et al. 2002). For both types of studies, analysis requires not only being able to distinguish between individuals based on their vocalizations, but also to correctly classify, and hence recognize, known individuals (McGregor et al. 2000). In this study, I determined the feasibility of monitoring individual saw-whet owls using their vocalizations, within season and between years, ultimately to determine levels of site fidelity and territory turnover.

There are two distinct subspecies of northern saw-whet owl in North America; *Aegolius acadicus acadicus* occupies most of North America, while *A. a. brooksi* is isolated on an archipelago in north-western British Columbia, the Queen Charlotte Islands. *A. a. acadicus* is known to be partially migratory and displays low levels of site fidelity and hence high territory turnover between years (Cannings 1993). Conversely, *A. a. brooksi* is non-migratory, yet little is known about other differences in life history of this subspecies, such as prevalence of site fidelity and rates of turnover. Further, the nocturnal nature of these owls coupled with difficult field conditions makes it problematic to monitor individual owls by traditional means such as banding or colour marking. However, males are highly vocal during the pre-nesting period (Cannings 1993), thereby making saw-whet owls ideal for monitoring via vocal individuality techniques. Although a preliminary analysis has been done on a small sample of *A.a. acadicus* (Otter 1996), a field-based monitoring effort using vocal individuality has not been undertaken on either subspecies, nor has there been an assessment of the practicality of monitoring individuals between years.

2.3 Methods

2.3.1 Study site

Saw-whet owl recordings were collected in the Queen Charlotte Islands of northwestern British Columbia, Canada (53N 131W). This area is a coastal temperate rainforest with a cool mesothermal climate (cool summers and mild winters) with annual precipitation exceeding 130 cm (Environment Canada). The most common tree species are western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata* Donn), sitka spruce (*Picea sitchensis*), yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), shore pine (*Pinus contorta* var. *contorta*), and red alder (*Alnus rubra*). Most of the research, with exception of one site, focussed on the southern half of Graham Island, the largest island in the archipelago.

2.3.2 Surveys

I collected recordings of vocal male *A. a. brooksi* during the pre-nesting period (March – May) of 2002 and 2003 within the first five hours after sunset. Both spontaneous and playback-induced calling bouts were recorded. All calling activity was recorded using either Sennheiser MKH 70 or ME 67 microphones (Sennheiser, Pointe Claire, Quebec) in combination with Marantz PMD 430 tape recorders (Marantz, Scarborough, Ontario). Recordings were restricted to nights with little or no precipitation and low winds. I attempted to approach vocal birds as closely as possible to obtain high-quality recordings, although the structure of the landscape often prevented my approach. Most recordings were made within 100 m of individual birds, with a range up to 300 m in some cases. When considering that unobstructed saw-whet owl advertisement vocalizations can travel as far as 1000 m (Cannings 1993) and that the frequency range and simplicity of this call allows such far

transmission (Wiley and Richards 1982), using recordings collected at a range of up to 300 m should still allow standardized measures to be taken on the individual call notes. When possible, I tried to minimize environmentally induced background noise in the recordings (e.g. stream noise, ocean surf). Once a site was deemed active, it was visited a minimum of once per week for the rest of the season in order to monitor the activity and to obtain repeat-recordings of the males.

I was confident that I was recording the same male between nights because (a) densities of owls were generally very low, and thus in most cases it was unlikely there was a second territory if the focal male had shifted call posts, (b) when there were multiple territories at higher density, simultaneous calling allowed me to identify the males, and (c) the birds were consistent in their calling location, generally calling from within 150 meters of previous detection locations. This justification parallels past studies with similar objectives, (Galeotti and Sacchi 2001, Galeotti et al. 1993, Galeotti and Pavan 1991). Further, to confirm this assumption, I fitted a subset of three owls with small (0.5 g) tail-mount radio-transmitters (Holohil Electronics, Carp, Ontario), thereby assuring me that I was in fact recording the same male over multiple nights. These known males showed all the above listed behaviours consistently, suggesting my criteria should be reliable for assuming the unmarked males I recorded between nights were the same.

2.3.3 Sonographic analysis

For each male, I measured a minimum of 25 representative notes of territorial calling, if I only had a single recording session, and up to 56 notes if I had multiple recording sessions. When first screening the recordings, I saved sections of calling that were of high quality (minimal background noise and closest possible proximity to the bird). From those

saved files, I randomly chose notes to analyze. Because recordings came in response to a series of one-minute playbacks of the advertisement/territorial call, I analyzed only the typical advertisement call and avoided measuring notes given during the more rapid and quiet call (see Chapter 1 for description) that some males seem to use when highly agitated (also called “introductory notes” by Otter 1996).

All notes were analyzed using Avisoft SAS Lab Pro 3.8 (Specht 2000) (Figure 2.1). The temporal measures taken were note length (T-note) and inter-note length (T-internote), which were measured on the waveform screen at a resolution of 2.9 ms. To focus in on the birdcall signal itself, I filtered out all noise below 900 Hz and above 1500 Hz. I defined note length as being from the start of the note where the amplitude first begins to increase to the end of the note where the amplitude is at one third of its maximum. This technique was used to account for any differences in the degradation of the notes and to reduce measuring reverberation noise as being part of the note length. This allowed me to measure notes from calls collected at variable distances (100-300 m) from birds without fear of including signal degradation into the temporal variation between males. The inter-note length spans from the start of the focal note to the start of the following note. The frequency parameters I measured were the frequency at the beginning (F(s)) (spectral slice at point 10% into note, as defined by temporal measures), middle (F(m)) (point at 50% of note length) and end (F(e)) (point at 90% of note length) of the note. I measured frequency parameters at a frequency resolution of 20 Hz, a temporal resolution of 2.9 ms, and a bandwidth of 56 Hz.

2.3.4 Data analysis and individual recognition

To assess the variability within each of the five parameters used to classify calls, I ran some preliminary statistics (Galeotti and Sacchi 2001). First, I ran ANOVA tests for each of

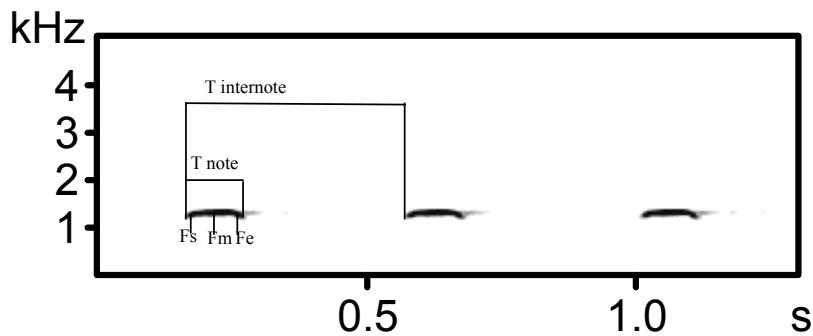


Figure 2.1: Sonogram of Queen Charlotte saw-whet owl territorial calling, illustrating measures taken. $F(s)$, $F(m)$, and $F(e)$ refer to measures of frequency at peak amplitude taken from spectral slices at 10%, 50%, and 90% of the note's duration, respectively. Temporal measures were the length of the note ($T(\text{note})$) and the internote length ($T(\text{internote})$), referring to the time from the start of one note to the start of the next note.

the variables, using site identity as the grouping factor. Ultimately, this allowed me to measure whether there were appreciable differences in the notes of individual birds at each of the variables. To successfully classify males, it is necessary for the variation in the individual variables to be less within individual males/sites than the variation between males. I confirmed this by calculating coefficients of variation of each parameter for all the sites combined, and then averaged across each of the sites.

To test the ability to correctly classify individuals based on their vocalizations, I used the General Discriminant Analysis function (forward stepwise, P to enter/remove = 0.05) in STATISTICA (ver. 6 StatSoft, Inc. 2003). I first analyzed males from each year separately to see how well I could identify the males within a given season. For a large number of males, I combined the recordings of the two years together. If I had multiple recordings of the same site over two years, I randomly chose one of the years for inclusion in the analysis. To test correct classification of novel notes (those not included in building the discriminant function) of the calling males, I randomly assigned 2/3 of the notes to a learning set (from which the discriminant function was built), and the remaining 1/3 of notes to a test-set. The cross-validation function of STATISTICA (ver. 6 StatSoft, Inc. 2003) classified these test notes to specific sites using the discriminant function it had built from the learning set. By using this approach of classifying novel notes, the estimation of correct classification rates should be more representative than when using more traditional analysis techniques where the same notes that were used to build the discriminant function are later classified.

2.3.5 *Site fidelity/ territory turnover*

To determine whether territories were being occupied for both field seasons, I regularly revisited all active sites from 2002 throughout the 2003 field season. The sites were

deemed active if I found calling activity on any of these visits, and I monitored active sites regularly (once per week). When possible, I obtained recordings of the males for analysis. For sites with two years of recordings, I ran a discriminant function analysis to (a) determine the levels of correct classification if males are incorrectly categorized (i.e. by chance) and (b) examine whether the correct classification of the three focal sites was greater than this, indicating the same males were re-occupying the same territories. I achieved this by using the cross-validation function in the general discriminant analysis module of STATISTICA (ver. 6 StatSoft Inc. 2003) and developing a learning set including data from my three focal sites (occupied both years) in addition to seven more sites and a test set composed of my focal sites with recordings from seven completely novel sites. By assigning known novel males to the sites of different males used to create the learning set, I mimicked a situation where different males occupy the same site between the two years, thereby giving me the ability to quantify random classification rates to use as a control. Also, by increasing the total number of sites to 10 (7 control and 3 focal sites), the likelihood of the actual focal sites (occupied both years) being classified correctly by random chance decreases. Thus, if the level of correct classification of the focal males was greater than the level of classification in sites with known different individuals (random chance), I assume the site was occupied by the same male. Conversely, if re-classification between years was low and similar to the control set, it suggested that a territorial turnover had occurred.

2.4 Results

2.4.1 *Advertisement/territorial call of saw-whet owls*

Table 2.1 shows a summary of the average calling parameters describing the notes. Owls differed from each other significantly at each of the variables defining their

Table 2.1: Parameters characterizing the notes of advertisement/territorial calling of male Queen Charlotte Islands saw-whet owls.

	Valid N	Mean	Std.Dev.	Minimum	Maximum
T-note	25	112 ms	13 ms	72 ms	142 ms
T-internote	25	431 ms	64 ms	273 ms	697 ms
F(s)	25	1173 Hz	41 Hz	1070 Hz	1310 Hz
F(m)	25	1194 Hz	48 Hz	1090 Hz	1350 Hz
F(e)	25	1197 Hz	51 Hz	1090 Hz	1370 Hz

advertisement call (Table 2.2). Because mean CVs of individuals were less than the overall group variation, there is less variability within individual birds than between birds, and hence there is a possibility for classification via discriminant function analysis.

2.4.2 *Within year vocal individuality*

Across the two field seasons, I was able to obtain multiple nights of within-year recordings for 13 males. On average, I analyzed 46 (± 9 S.D., range 31-56) notes for each of these males. I used an average of 30 (± 9 S.D., range 15-39) of these notes as the learning set to create the discriminant function and 15 (± 4 S.D., range 9-22) in the test set to test the discriminant model in cross-validation analysis. I then was able to correctly classify notes within the learning set an average of 79% of the time, while classification of notes from a different night (test set) had an average of 74 % correct classification (Table 2.3). Correct classification of recordings across different nights from males fitted with radio-transmitters ranged from 38-100%, indicating that there is variation between nights in the note structure of some males. One particular site (a non-telemetered male; site #12 in Table 2.3) had a disproportionately lower level of correct classification than the others, indicating that a different male may have taken over the territory between the two recordings (separated by 5 weeks). When this male was excluded from the analysis, rates of correct classification remained similar (78% for learning set, 77% for cross-validation of test set), indicating that including this male made little difference in the overall classification accuracy. Closely examining classification success of specific cases, however, may give insight into a specific event at a given territory.

In total, I recorded calls from at least one night for males at 24 different sites, 8 during 2002 and 16 during 2003. For this analysis, I only used the first year of recordings at

Table 2.2: Coefficients of variation (CV) (%) for each of the predictor variables of notes of advertisement calls of saw-whet owls as well as results of ANOVAs comparing predictor variables between sites. ‘Group’ refers to the CV over the whole data-set, while ‘ind.’ refers to the CVs for each male averaged over the individual males.

	CV (group)	CV (ind.)	F-ratio	d.f.	p
T-note	12.03	6.64	85	24	<0.001
T-internote	14.80	9.47	46	24	<0.001
F(s)	3.50	1.37	191	24	<0.001
F(m)	3.98	1.41	210	24	<0.001
F(e)	4.37	1.49	224	24	<0.001

Table 2.3: Classification of notes in male saw-whet owls with multiple recordings within seasons. The learning set was composed from recordings collected during one or more detections at each site. The test set calls originated from a separate recording session at the same site. Hence, the test set notes were not used in building the actual discriminant function; they were used instead for testing correct classification of novel notes. Sites marked with an asterisk had males wearing radio-telemetry transmitters, allowing confirmation of identity.

		Learning set													
	Site	Percent	1	2	3	4*	5	6	7	8	9	10*	11*	12	13
Test set	1	87.50		14										2	
	2	87.50	1	14							1				
	3	60.00		1	6		1							2	
	4*	60.00	1			9			1	4					
	5	87.50		2		14									
	6	78.57				11		1	2						
	7	80.95					17	2		1	1				
	8	95.00				1		19							
	9	85.00				3			17						
	10*	100.00									12				
	11*	38.71	3					13	1		2	12			
	12	6.90		5	17		5						2		
	13	72.73	3		1					1	1		16		
	Total	67.36													

each site to make the composite database. With all 24 males, I had a discriminant ability of 68% for the learning set and 64% for the test set (Table 2.4). All variables significantly contributed to the discriminant function (Table 2.5), although the variables that loaded most heavily on building the function were the note length and the frequency at the end of the note. I explored the misclassification of particular males by comparing the distances to the nearest neighbour and to the site to which a focal male was most often misclassified. I found that males were usually misclassified not with adjacent sites, but with sites that were significantly further away than average inter-male spacing ($t=-7.531$, d.f.=19, $p<0.0001$) (Figure 2.2). When analyzing each year separately, correct classification was 85% for the learning set, and 75.8% for the test set in 2002 (N=8), and 77% for the learning set and 69% for the test set in 2003 (N=17).

2.4.3 *Site fidelity and territory turnover in saw-whet owls*

Of the 13 sites from 2002 that I monitored regularly for both field seasons, 7 sites were active again in 2003, indicating a 53% re-occupancy rate of sites. I was able to collect recordings of sufficient quality at three of these sites to analyze whether in fact the same males were occupying those territories. By examining the correct classification rate of control sites, I determined a random correct classification rate averaging 3%, with a maximum of 19%. Two of the three focal sites occupied both years had much greater levels of correct classification (>60%) than this, suggesting that the same male was occupying the sites during both breeding seasons. One site, however, had 0% correct classification of notes, indicating a turnover had likely occurred (Table 2.6). Overall, these results suggest that there may be some level of site fidelity in these owls.

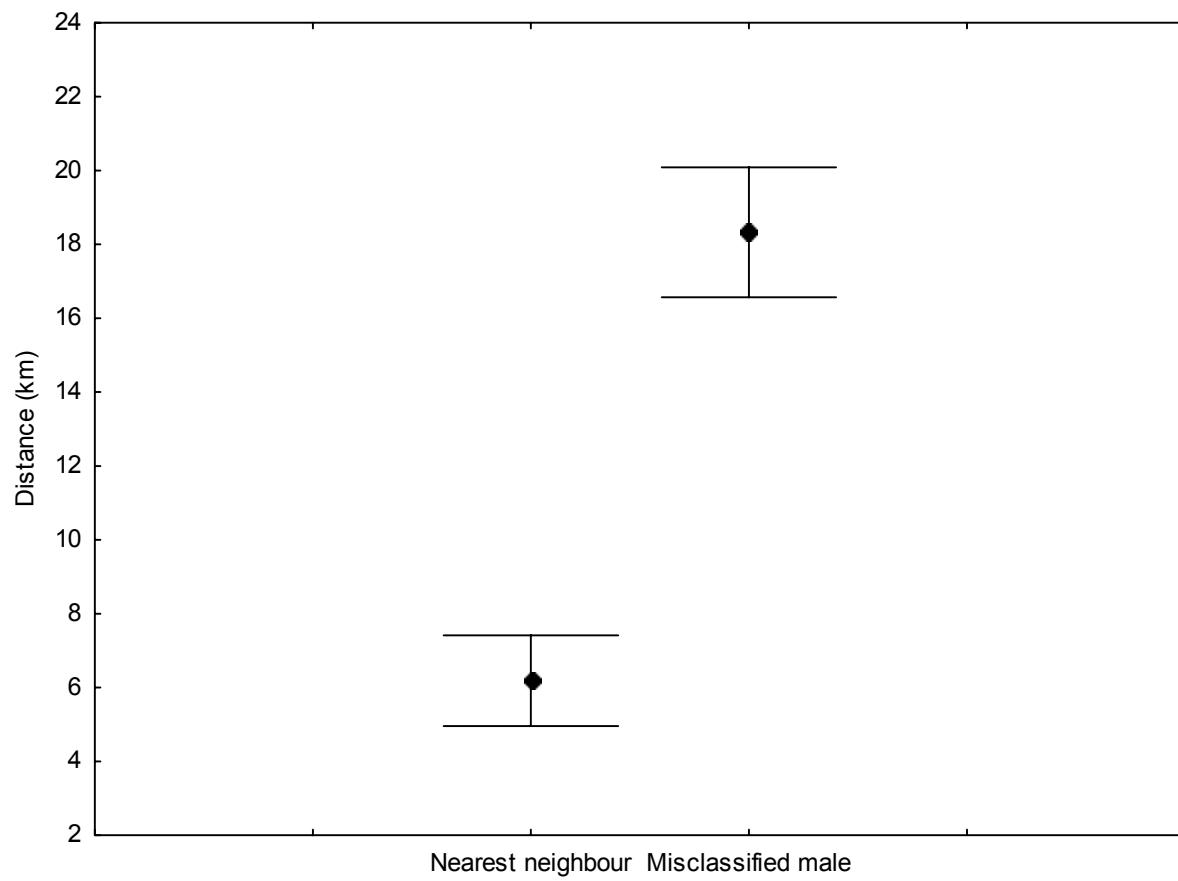


Figure 2.2: Comparison of average distances between nearest neighbour to each male saw-whet owl and the average distance to the site any given site was most often misclassified as.

Table 2.4: Classification of saw-whet owl notes at all 24 active sites in 2002 and 2003.

Percent correct classification is indicated for each site separately and for the population as a whole.

	Percent	Learning set																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	81.25	13				1			1																1
2	30.00	1	3	1					3											1				1	
3	15.38			2								4	2		1		2			1			1		1
4	100.00				16																				
5	63.64					7	2																		2
6	54.55					6			4																
7	90.00						9										1								
8	54.55					1	2	6				1												1	
9	100.00							10																	
10	33.33	1							3			1	2											2	
11	57.89	1	2					2	11	2													1		
12	50.00		1		1					4	15							2							
13	75.00		2	1				2				15													
14	93.75									15														1	
15	80.00			1							8													1	
16	23.08		2	1						2	1		3	2		1		1		1			1		
17	63.64												3	7											1
18	44.44						2			2	1				4										
19	41.18	2		1					7								7								
20	100.00																	10							
21	100.00																		5						
22	43.75	1			1	1		1	2			1			2								7		
23	100.00																							6	
24	66.67	1								1									1	1				8	
Total	64.01																								

Table 2.5: Results of multivariate analysis (Wilks test) to determine differences between calling males at each of the contributing parameters measured on the notes.

	F-ratio	d.f.	p
T-note	47.7656	23	<0.00001
T-internote	25.6395	23	<0.00001
F(s)	21.9992	23	<0.00001
F(m)	24.9339	23	<0.00001
F(e)	37.6732	23	<0.00001

Table 2.6: Classification of notes recorded at sites in both 2002 and 2003. The numbered sites (1-7) refer to control sites, where the test set (2003) recordings were from different males than in the learning set (2002). The lettered sites (A-C) were sites that were active both years of the study. Sites B and C appeared to be defended by the same male, whereas site A likely experienced a territory turnover.

Learning set (2002 recordings)												
Site	Percent	1	2	3	4	5	6	7	A	B	C	
1	0.00	0		4	16	3			14	1		
2	0.00	1	0	5	8			1	12	4	1	
3	0.00		13	0		7	4					
4	4.26	4		27	2	1			13			
5	0.00		27		0	3						
6	0.00				0			10	5			
7	18.75	4		12			9	2	2	19		
Control	3.29											
A	0.00	1	3			3	5		0	5		
B	64.91	5	2	5		5	2		1	37		
C	61.29			9			3			19		

2.5 Discussion

My results suggest that saw-whet owls have sufficient variation in their advertisement calls to allow successful discrimination between individuals, and that it may be possible to use this technique to monitor these owls across years. Although my ability to correctly classify birds by their calls may be lower than in some other species, such as tawny owls (Galeotti and Pavan 1991) or European nightjars (Rebbeck et al. 2001), my results are more inline with past studies of birds with similar structural simplicity to their calls, including pygmy owls (Galeotti et al. 1993) and bald eagles (Eakle et al. 1989). Further, because my study site was characterized by a highly rugged landscape and therefore prevented close approach to vocal owls, the recording quality was sometimes compromised. Although I took steps to limit measuring reverberation in calls, such degradation could still introduce some variability that can result in lowered discriminant ability to identify birds. However, it is *because* of the logistic difficulties presented by my study system, that this technique is of such high utility for monitoring these birds over the long term and to ultimately learn about their life history.

When the model misclassified males, it usually attributed the note to a male distant from the singer. This suggests that neighbours do not overlap or match each other in call structure, the converse of which is common in passerines (e.g. Beecher *et al.*, 2000; McGregor et al. 1992, Krebs et al. 1981). Thus, a combination of vocal cues and knowledge of male location should provide an even higher certainty of correctly identifying resident males. Another reason for misclassifying males seemed to be linked to a large number of males in the analysis. When the number of owls included in the analysis was decreased by analyzing each year separately, the discriminant ability increased. Because the owl call is so

simple, it is more likely that the calling pattern of two males will be similar in a larger sample. In all, when dealing with a large number of sites it may therefore be advantageous to subdivide the study population into smaller subpopulations and analyse the vocalizations of these subsets separately.

As the difference in vocalizations seems to be greater between neighbouring sites, some may argue that males taking over a territory may converge on the calling patterns of previous residents, and the note structure may somehow be linked to location. This seems highly unlikely, however, as the particular call type I measured in all of the males is already stereotyped for transmission through forest habitat and has a sufficiently narrow range of variation between individuals that it would likely be of no benefit for increasing sound transmission. Hence, any inherent relationship of call parameters to a specific site would have to arise from learning from a tutor. Again, this is unlikely as non-passerines, including owls, do not learn their advertisement call from tutors (Catchpole and Slater 1995). My data also provide evidence that vocal characteristics are not linked to a particular site, as one of the test sites occupied both years had a classification rate (0%) akin to random. It therefore appears that variation in the advertisement call between males is due to inherent individual differences, thereby providing a useful tool for monitoring.

Recently, some studies have started exploring the technique of vocal individuality to monitor population trends and to learn about site fidelity and territory turnover. For example, Delport et al. (2002) had great success monitoring individual African wood owls (*Strix woodfordii*) and determining turnover rates over a 12-year period. Turnover rates between two years in scops owls (*Otus scops*) have also been determined using similar analyses to mine (Galeotti and Sacchi 2001). Gilbert *et al.* (2002) was able to not only determine annual

survival rates and site fidelity, but also between-year site movements in great bitterns (*Botaurus stellaris*). Being able to monitor and track individuals using their calls may present an opportunity to further study the life history of a species. For example, using knowledge of individual identity, the territory core of an individual can be determined. By then measuring calling rate, thought to be condition dependent, and comparing it to various biotic and abiotic factors, monitoring projects may be able to measure habitat parameters important to the maintenance of the species (see Chapter 3).

Although my sample is small, the preliminary analysis of site fidelity leads me to believe that this technique may have utility in monitoring the Queen Charlotte Islands' subspecies of saw-whet owl. It appears that there may be some level of site fidelity at active sites between years, a behaviour which although occurring at low rates, is largely uncommon in the *A. a. acadicus* subspecies (Cannings 1993). My preliminary results with this analysis suggest that further study may be warranted to determine the levels of site fidelity in the *A. a. brooksi* subspecies, given that, in general, high site fidelity is associated with increased reproductive success (Newton 1993) as well as a steady food supply (Löfgren et al. 1986). Being that this subspecies is not migratory, it is less likely to be as nomadic as the *A. a. acadicus* counterpart, and hence I would expect the breeding behaviour to potentially differ in regards to site fidelity. Because a lack of site fidelity is often associated with reproductive failure in the previous year (Bried and Jouvetin 1999), and high breeding success is often associated with high quality habitats, future monitoring of levels of site fidelity may give insight into the habitat types that offer increased reproductive success.

3 CALL RATE AND HABITAT QUALITY IN THE QUEEN CHARLOTTE SAW-WHET OWL (*AEGOLIUS ACADICUS BROOKSI*)

3.1 Abstract

Stressful environmental conditions, whether owing to biotic (i.e. habitat) or abiotic (e.g. temperature) factors are known to affect the body condition of individuals. These effects should be noticeable through monitoring indirect measures of condition dependence, such as calling rate. I assessed whether measuring call rate can be used as a surrogate to measuring condition in individual male Queen Charlotte saw-whet owls (*Aegolius acadicus brooksi*) and then compared call rates among males in varying habitats to indirectly determine if habitat alteration impacted male condition. I found that a change in call rate between nights within individual owls was linked to corresponding changes in temperature during the roost day preceding recordings, suggesting that call rate variation may indirectly reflect subtle changes in male condition. I also found a significant relationship between individual male call rate and the amount of remaining mature/old forest near the core of the territory. I fit a non-linear model describing this relationship, allowing me to estimate a threshold of required mature/old forest near the territory core below which call rate, and presumably condition, shows significant deterioration. I argue that this technique is of particular use in vocal species such as the saw-whet owl, for which conventional techniques to test effects of habitat alteration, such as measuring reproductive output, are logistically difficult.

3.2 Introduction

Studies assessing the effects of habitat change on individual species of birds often involve surveys of presence versus absence, and then assume that densely populated areas indicate high-quality habitats. Frequently, however, high density may not equate with high productivity (Van Horne 1983). Generalist species found in relatively high densities in a variety of habitats may experience decreased fitness in sub-optimal ecotypes (e.g. Franklin et al. 2000, but also see Matthysen and Adriaensen 1998), which could result in population sinks even in densely populated areas (Reměš 2000).

If density is not a sensitive indicator of reproductive success in different habitats, alternative indices may be necessary. Detailed studies of species demographics, such as comparisons of age and/or breeding experience, turnover rates and pairing success of territory holders (e.g. Zanette 2001) are the most sensitive indicators. However, these studies also have particular disadvantages: the labour intensive nature of such data collection can limit the size and area of populations being assessed, and they rely heavily on being able to readily find individuals and their nests. When studying cryptic species for which nests are not easily found and territories are not easily delineated, such traditional methods may become logistically infeasible. In these instances, it may be possible to infer both habitat quality and the resulting condition of individuals that settle in these areas by monitoring condition-dependent signals of the birds (Hill 1995; McGregor et al. 2000), because expression of such signals is closely associated with resource availability.

A major component of habitat quality that contributes to the reproductive success of birds is food availability (e.g. Arcese and Smith 1988, Hakkarainen et al. 2003). Although prey availability can sometimes be measured directly, it can also be inferred through the

expression of condition-dependent signals. Such signals are often used for honest advertisement during sexual selection (Zahavi 1977) and as a result are both conspicuous and correlate with resource access and reproductive success (reviewed by Bradbury and Vehrencamp 1998). One example of such a signal is song and call output in birds (Andersson 1994), which has often been shown to correlate with factors such as territory quality (Galeotti 1998), reproductive success (Catchpole 1986), social rank (Otter et al. 1997), ability to defend a territory (Galeotti 1998), ability to secure mates (Alatalo et al. 1990) and ability to attract extra-pair partners (Forstmeier et al. 2002). In addition, song and other territorial calling output appears to be food limited in almost all species tested (e.g. Thomas 1999, Reid 1987), suggesting it is a sensitive indicator of food availability in the habitat.

Bird song and calling is also sensitive to very short-term changes in the environment that may have even small energetic impacts on the animal, such as temperature or climatic fluctuations. For example, song and call rates tend to decrease with ambient temperature (Higgins 1979, Garson and Hunter 1979). Because of the high energetic costs of singing, coupled with decreased energetic stores from thermoregulation, birds emerging from roosting in cool temperatures generally have depressed vocal output (Thomas and Cuthill 2002). To increase their energetic stores, the birds must spend time foraging, thereby further decreasing their ability to advertise vocally. Thus, song and call rate reflects male energetic status, especially in energetically demanding situations (Thomas 1999, Reid 1987, but see Johnson and Rashotte 2002).

Due to the strong influence of both the male's metabolic state and ability to secure resources on the ability to maintain a high vocal output, assessing such traits may provide a proactive approach to monitoring environmental health (Hill 1995, McGregor et al. 2000).

As such traits are used as honest advertisement in sexual selection, they also provide a relatively conspicuous means of monitoring the condition of otherwise cryptic species (e.g. Peake et al. 1998, Galeotti and Pavan 1991).

I examined whether the conspicuous calling behaviour of owls could be used as an indirect indicator of the condition of males in varying habitats. The subspecies of northern saw-whet owl (*Aegolius acadicus brooksi*) endemic to the Queen Charlotte Islands in north-western British Columbia, Canada make an excellent subject for analysis. Saw-whet owls are very vocal, having a simple territorial call of repeated whistles at about 1.1 – 1.2 kHz and a typical rate between 120-180 notes/minute (Cannings 1993). These owls are often associated with mature and old forests across the landscape (Gill and Cannings 1997). However, areas of the Queen Charlotte Islands have undergone extensive habitat alteration through logging, causing a mosaic of habitat structures across the landscape (mature/old forest interspersed with various ages of regenerating forest) and resulting in the subspecies being listed as “threatened” by the British Columbia government. The owls’ nocturnal behaviour coupled with the logistical hurdles presented by the landscape, make traditional measures of success in different habitats (e.g. reproductive output) difficult and expensive to pursue. Thus, measuring the condition of individuals as related to the amount of mature/old forest remaining in areas defended by the owls may be an efficient indicator of the habitat needs of this sub-species.

The objectives for this study were two-fold. First, I sought to confirm that call-rate is an indirect measure of condition in this species by examining changes in calling rate of individuals with changing temperature. If calling rate was costly to maintain, I expected a decreased call rate following cold roost days, as such periods would have increased demands

on metabolic reserves and thus leave less energy available for calling the following evening. Second, considering these owls are associated with mature and old forests, a marked decrease in this habitat type may also lead to a decrease in condition of the territory occupants. If this is true, then I expected a decrease in call rate when moving away from optimal levels of mature/old forest content in the area being defended by males. Assuming this relationship between call rate and habitat was apparent, I sought to model the data in hopes of estimating a threshold of required mature/old forest for forest management of this species.

3.3 Methods

3.3.1 Study site

Data for this study were collected in the Queen Charlotte Islands of north-western British Columbia, Canada (53N 131W). This area is a coastal temperate rainforest with a cool mesothermal climate (cool summers and mild winters) with annual precipitation exceeding 130 cm (Environment Canada). The most common tree species are western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), sitka spruce (*Picea sitchensis*), yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), shore pine (*Pinus contorta* var. *contorta*), and red alder (*Alnus rubra*). The area has some of the most productive forests in Canada (Meidinger and Pojar 1991); thus, forestry activities (logging) are widespread.

Most of the research (with exception of one site on East-Limestone Island) focussed on the southern half of Graham Island (the largest island in the archipelago). This area presents a mosaic of forest cover types ranging from recently logged clearings, to young regenerating stands, to structurally complex mature and old forests. Young regenerating forest can be described as having a canopy of mostly uniform height and minimal self-

thinning. Conversely, more mature and old forests have evidence of self-thinning and therefore have multiple canopy layers and structure. Across the landscape of the study site, patches of mature and old forest are generally surrounded by large areas of young regenerating forests. These younger stands are a result of logging activities within the last 50 years or a large stand-replacing fire on the east end of the island around 120 years ago, which did not start regenerating until roughly 80 years ago.

3.3.2 Detecting and monitoring activity

I conducted playback surveys for northern saw-whet owls during the spring (March to May) of 2002 and 2003. In order to increase the probability of detecting owls, I chose survey stations along accessible roads at sites exhibiting moderate to high suitability habitat for saw-whet owls, thus avoiding surveying in large contiguous areas of low suitability habitat (i.e. cutblocks and regenerating plantations) (based on Gill and Cannings 1997).

I initiated surveys one hour after sunset, and typically continued surveying for approximately 6 hours thereafter. The survey protocol involved five minutes of listening for spontaneous calling upon arriving at a site, followed by a series of three one-minute playbacks of male northern saw-whet owl calling, separated by one-minute pauses. At the end of the playback bouts, I listened for 5 more minutes for owl response. In total, a minimum of 15 minutes was spent at each survey station. At each station, the following information was collected: time of night, location of the station (GPS co-ordinates), whether an owl was detected, temperature and an estimate of forest stand type. Once a site was deemed active, it was re-visited at least once per week for the remainder of the season in an attempt to determine the core of territorial activity, collect further recordings, and monitor behaviour.

Owl calling activity was recorded using either a Sennheiser MKH 70 or ME 67 microphone (Sennheiser, Pointe Claire, Quebec) and a Marantz PMD 430 tape recorder (Marantz, Scarborough, Ontario). If an owl was spontaneously vocal upon arrival at a station, I recorded five minutes of this unsolicited calling. This was to allow me to determine the area the owl was spontaneously advertising/defending. Thereafter, I did a one-minute bout of playback and recorded five minutes of the male's response. If an owl was detected using playback, I recorded five minutes of this induced calling and suspended any further playback for that trial. Data collected at active sites included the time, meteorological conditions, location of the owl in relation to the station (using triangulation of the source of the sound), and relevant behavioural notes (e.g. approach, female presence, other vocalizations used).

3.3.3 Measuring response

Tapes of owl calling activity were transcribed using Avisoft SAS Lab Pro 3.8 (Specht 2000). To standardize the territorial context in which males were calling, I measured call rate only from playback-induced responses, and not from spontaneous calling. From playback-induced responses, I measured the average calling rate (notes per minute) for the first 5 minutes of calling, beginning when the male first starts using the rapid and/or territorial call. To specify, a lower response rate could result from a male ceasing to call for the full 5-minute response interval, utilizing less of the rapid call, and inserting more pauses between calling bouts.

3.3.4 Measuring habitat

The core of a male's territory was estimated from information gathered by repeated visits to the territory. When possible, the nest and/or roost site was located for the male, which would give the strongest indication of territory core. When this was not possible,

spontaneous calling sites and/or initial playback response sites were taken as an indication of areas that the male was actively defending, and thus were indicative of the territory core. A circle with a 500-meter radius was drawn around this core to delineate the actively defended area. A past telemetry study of *A.a. acadicus* showed the owls to range in an area of approximately 150 ha in size (Cannings 1987, Forbes and Warner 1974). Owls, however, seemed less likely to mount a territorial response if I was more than 500 meters from the estimated core (CIH pers. obs). In all, this 78 ha circle seemed most representative of the area the owls were actively defending and thus was appropriate for measuring habitat factors affecting the territory (Tarvin and Garvin 2002).

I measured the amount of old and mature forest within the territory core using digital ortho-photography, updated forest cover maps showing the location of current cutblock boundaries and ground-based surveys of the area. The measurements were taken by drawing area polygons using ArcView GIS 3.2 (ESRI Inc. 1999). A percentage of old/mature forest was calculated for each male's core.

3.3.5 Temperature measures

I obtained readings of minimum temperature for the night and maximum temperature for the day from the Sandspit Airport, south of the study site. The relative measures taken at Sandspit Airport corresponded to readings I took at individual survey stations.

3.3.6 Data analysis

Over the duration of the study, I was able to collect repeat recordings in a standardized manner to test for the effect of temperature on call rate for 13 territorial males. I tested for within male changes in call rate and how these relate to ambient temperature using a paired design of two days, a cooler and a warmer day preceding the night the male had

been recorded. Specifically, I compared the change in temperature and corresponding change in call rate between two days for each of the males using a Spearman Rank Correlation.

The call rate relationship to remaining mature/old forest was examined by comparing the response rate of the first representative night of monitoring for each male with the percentage of forest content within 500 m of the core of his territory. When comparing between males, I tested whether the daytime-high temperature and Julian date (showing possible seasonal effects) explained any of the variation in call rate. For an initial test of relation between call rate and percentage of mature/old forest, I used a general linear model with Julian date and daytime-high temperature as covariates. When screening my data with a linear model, I found a relationship between call rate and percent mature/old forest. Further examination of the residuals suggested that this relationship was non-linear and had an apparent maximum call rate. To model this curvilinear trend and to be able to approximate parameters about this relationship, I fitted a Michaelis-Menten model, which is appropriate for a system where the dependent variable increases only to a limiting value (Edelstein-Keshet 1988). This model is of particular utility, as it allowed me to calculate the value of my x-variable (habitat), at the point where the y-variable (call rate) was at 50% of its maximum. In other words, using this relationship, I am able to measure a threshold of mature/old forest below which call rate began to deteriorate to half of its maximum. I used the least-squares loss function to fit the model and the Levenberg-Marquardt estimation method. Inferential statistics were performed at an alpha-level of 0.05. Statistical analyses were done using STATISTICA ver.6 (StatSoft, Inc. 2003).

3.4 Results

3.4.1 Temperature and call rate change within males

The change in call rate of individual males between nights was greatest when the temperature difference between the two nights was highest ($R=0.555$, $n=13$, $p=0.049$) (Figure 3.1). A similar trend, though not significant ($R=0.412$, $n=13$, $p=0.16$) was observed when I compared overnight low temperatures of the nights the birds were recorded. Thus, nightly call rates among males increased following days with higher temperature, while colder daytime temperatures resulted in decreased call rates.

3.4.2 Relationship between habitat and call rate between males

The amount of mature and old forest content within 500 m of the territory core varied from 15 to 80%. Call rates between males varied from 38 to 157 notes/minute when averaged over the five-minute response interval. When comparing call rate *between* males, temperature did not significantly affect the call rate ($F=0.341$, $p=0.565$, $n=26$), nor did Julian date ($F=0.662$, $p=0.425$, $n=26$). For this reason, I did not include these factors in analyzing changes in call rate between males.

I found a significant relationship between call rate and habitat using the Michaelis-Menten relationship to fit the data ($F=153.9$, d.f. =2, $n=26$, $p<0.0001$). However in exploring the detailed parameters of this relationship, I found one male appeared to be a significant outlier, with a very low call rate despite settling in an area with 67 % mature/old forest in the defended core. This outlier may have sufficient leverage and discrepancy to significantly skew accurate estimation of the proportion of mature habitat where call rate drops to 50% of the maximum (threshold). Thus, I fitted the non-linear Michaelis-Menten model with and without this single outlier (Figure 3.2). With the outlier removed, 41.1% of the variance in

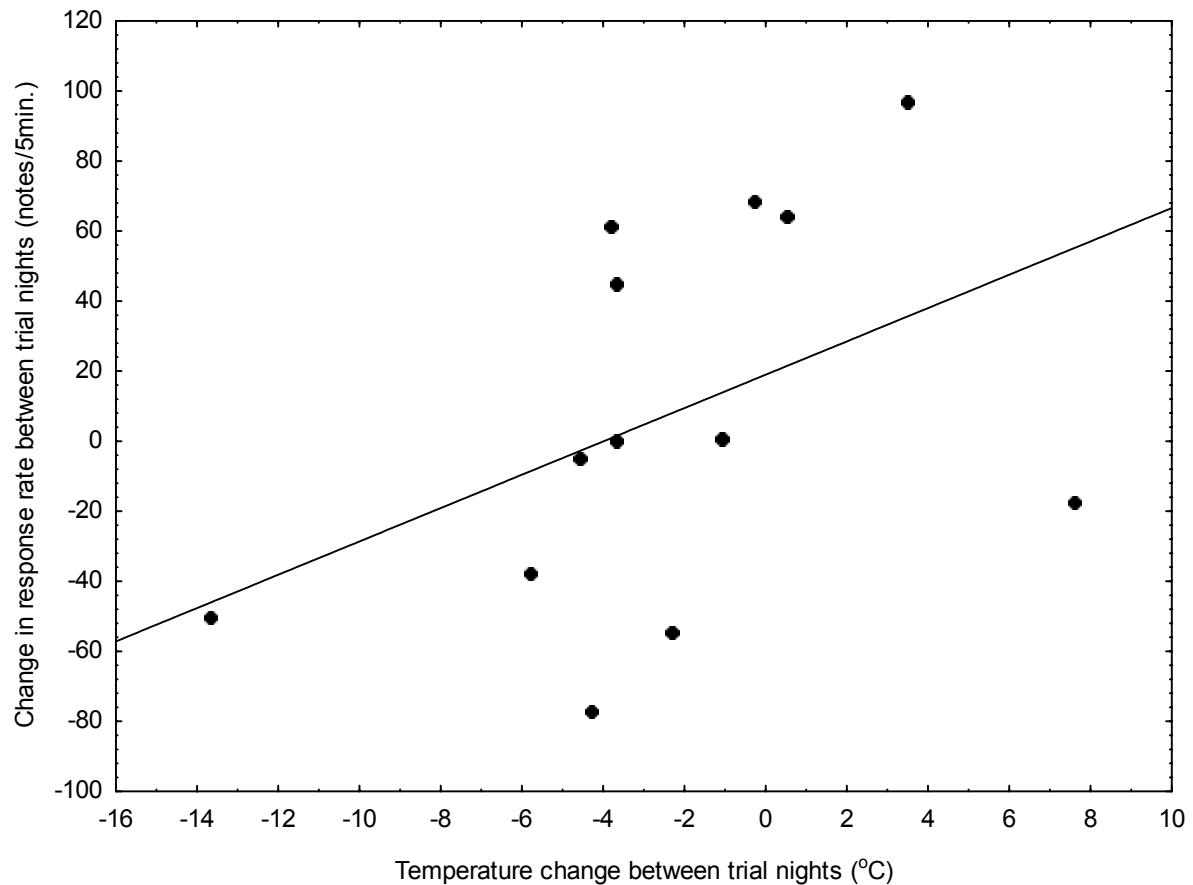


Figure 3.1: Within male changes in response rate in comparison to changes in daytime high temperatures (while owls were roosting) in Queen Charlotte Islands saw-whet owls.

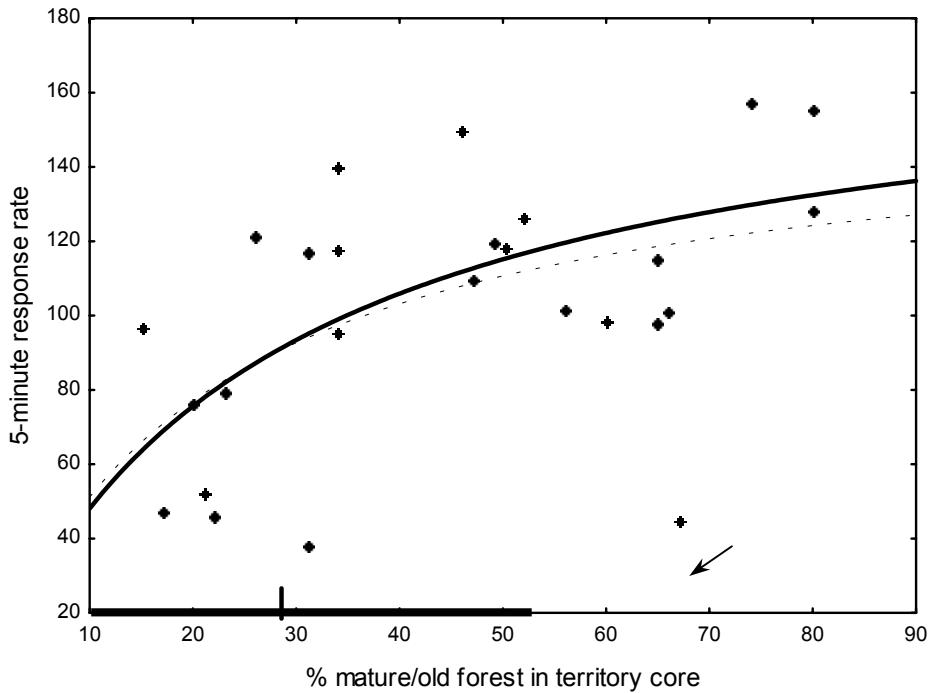


Figure 3.2: Calling rate of male saw-whet owls in response to playback stimulus averaged over 5-minutes as measured against habitat, the percent of mature/old forest remaining near the apex of a male's territory. Modeled using Michaelis-Menten relationship ($y=ax/(b+x)$), where 'a' represents the maximum response rate and 'b' represents the amount of mature/old forest at half of this maximum, giving an indication of threshold. The relationship is plotted with (dashed) and without (solid) a significant outlier (indicated with arrow). The bar at the bottom of the x-axis shows the mean and 95% confidence interval of forest content before the call rate deteriorates to 50% of its maximum.

call rate between males was explained by the amount of mature and old forest within 500 m of the territory core ($n=25$, $r=0.641$). The Michealis-Menten model estimated two parameters: (1) a maximum call rate as explained by habitat and (2) a difference in the influence that increasing mature/old forest content has on the increase in call rate. Maximum call rate asymptotes at 176.7 ± 32.24 calls/5-min response. (95% confidence interval 109.99-243.40) among males in relation to increasing mature/old forest content ($t=5.48$, d.f.=23, $p<0.0001$). The threshold level of habitat where call rate drops to 50% of this maximum is 26.7 ± 12.8 % (95% confidence interval 0.26-53.2) mature/old forest cover ($t=2.09$, df=23, $p=0.048$).

When the single outlier male was included in the analysis, proportion of variance in call rates accounted for by habitat decreased to 27.3% ($n=26$, $r=0.523$). Although the ability to detect a maximum response rate in the model remained significant ($t=5.24$, df=24, $p<0.0001$), the ability to determine a possible threshold, was no longer significant ($t=1.71$, df=24, $p=0.1$).

3.5 Discussion

My data indicate that a change in call rate between nights within individual owls may be linked to corresponding changes in temperature. As temperature during the daytime roosting of owls will influence metabolic costs of thermoregulation, owls beginning to call at dusk following a cold day should be in lower condition than following a warm day, similar to low overnight temperatures affecting daytime singing in diurnal birds (Thomas and Cuthill 2002). I found a positive relationship between changes in daytime temperature and changes in call rate within individual owls. As the comparison was made between successive recordings of the same individuals, I controlled for the influence of the male's habitat, thus

the change in call rate likely reflected a decreased metabolic reserve following a cold roost day. My results, thus, suggest that call output indirectly reflects subtle, short-term, changes in the condition of males. Because insufficient resource availability is a continuous and long-term stress on territory occupants, resulting differences in the condition of males should, therefore, be detectable via vocal output.

Territorial calling is known to be resource limited, as has been shown by past experimental studies linking increased food availability to higher vocal output (e.g. Reid 1987, Strain and Mumme 1988). Conversely, birds that are more stressed by a lack of resources, or endure instability in accessing those resources, tend to have depressed call rates (Thomas 1999). Thus, when comparing males across a population with different levels of potential resources, one would expect individual condition to vary depending on their resource availability and such variability to be reflected in the expression of condition dependent signals. As habitat composition will likely affect the availability and stability of resources for a given male, I would expect the observed differences in call rate to be a reflection of the condition of the males as well as indicating how well the core habitat is meeting the resource needs of the occupant. I observed that call rate among males increased asymptotically between males with increasing amounts of mature/old forests within a male's territorial core. There appeared to be a maximum call rate that could be explained by habitat, and thus call rate plateaued among males that had high amounts of mature forest within their territory. My model suggests that call rate drops to 50% of maximum when the habitat around the male's core territory drops to 26.7% mature/old structure, but the fairly large standard error ($\pm 12.8\%$) of this estimate suggests that losses of mature forest structure below

53% (upper limit of 95% confidence interval) retention may still result in such dramatic declines in male call rate, and hence condition.

It has been suggested that information on territory quality can be inferred through the study of condition-dependent signals such as call rate (Penteriani et al. 2002, Hill 1995).

Recent literature strongly suggests a link between call and call rate, condition and ultimately reproductive output in various species of birds, both passerines (Hoi-Leitner et al. 1995) and raptors (Penteriani et al. 2002). There are two mechanisms that could produce such an association between call or song rates and habitat variability: limited resources in the territories could decrease the resident male's condition with a resulting decrease in his ability to maintain costly vocal output; or, poorer quality males (that are unable to maintain high call output) are forced to settle in less preferred habitats. These two explanations may not be mutually exclusive; the relative quality of males may influence their settlement among patches, and the resources within the territory they obtain may either enhance or diminish their potential to express condition dependent signals used in inter or intrasexual selection.

Immediate resource access, however, is only one facet affecting the expression of condition dependent traits. One would not necessarily expect the condition of males with high-quality territories to continue increasing even if they had a further surplus of resources. At this point, variation in call rate may reflect other aspects of the male's quality, such as social status (Otter *et al.*, 1998). If resources become limiting, however, I would expect to see a decrease in the condition of males occupying a territory, either through settlement bias in male quality, resource availability, or a combination of the two. The nature of the relationship in my results supports this theory, as call rates are increasing with habitat at low levels of mature/old forest content, but this increase becomes incrementally less when there

is a greater amount of mature/old forest in the territory core. If the habitat dependably provides sufficient resources for self-maintenance, other factors affecting the condition of individual males, such as age or experience, will affect the expression of condition dependent signals. When important habitat conditions become suboptimal however, extra costs may be imposed on the male in order to defend his territory. Thus, it should be of no surprise that below a certain level of mature/old forest content, call rate begins to decrease markedly. Overall, these results suggest that the condition of individuals may decrease when their core territory contains low levels of mature and old forest and that there may be a possible threshold of forest habitat composition where condition of territory occupants changes due to habitat induced stress.

Whether it is by a mechanism of habitat quality affecting the condition of territory holders, or by the condition of males dictating the quality of habitat patches they are able to secure, or a combination of both, a relationship between habitat quality and condition of the occupying individual is inherent. Habitat quality is well known to affect the reproductive output of its occupants (Przybylo et al. 2001, Sergio et al. 2003). Evidence of this ranges from higher winter survival rates by individuals occupying high-quality territories in Eurasian nuthatches (Matthysen 1990), to tengmalm's owls in good habitats being more resilient to fluctuations in food supply (Korpimaki 1988). The size of high quality habitat fragments across the landscape likely plays an important role also, as larger contiguous tracts of superior habitats are likely secured by more experienced birds, collectively leading to a greater reproductive output (Zanette 2001). At a finer scale, the condition of individual males is known to predict reproductive output (e.g. Drent and Dann 1980). For example, increased food and decreased predation pressure (two factors that may weigh heavily on individual

condition) lead to a marked increase in reproductive output (Zanette et al. 2003). Overall, the effects caused by sub-optimal habitat composition may go beyond affecting the condition of territory occupants, and on a grander scheme may impact the reproductive output of individuals occupying territories lacking in resources. Being able to indirectly measure the condition of individuals therefore may provide the proactive means necessary for successful detection of habitat-induced problems.

In attempting to manage the species, it is useful to be able to determine a point where the habitat composition becomes insufficient to sustain a high level of individual condition. Applying the Michealis-Menten relationship to this problem poses exciting opportunities, as I not only determined the average call rate when males have high levels of suitable habitat available to them, I also determined the mean amount of habitat required before dropping to half of this maximum call rate. In other words, using this model, I may be able to estimate an amount of required habitat before the condition of individuals begins to deteriorate. With that said, any management decisions based around such a model should always err on the side of caution, and I suggest setting retention thresholds well above the upper limit of the 95% confidence interval around the mean habitat composition where call rate, and condition may have declined to 50 % of the optimum.

4 GENERAL DISCUSSION

4.1 Using the advertisement call to monitor northern saw-whet owls

In chapter 2, I established that the male advertisement call of northern saw-whet owls could be used to identify individuals across nights. By knowing individual identity, it is possible to monitor owls throughout the territorial phase of the breeding season and thereby gain knowledge regarding the habitat use and territory location of individuals (Peake and McGregor 2001). This information regarding the habitat use can further be applied to other facets of condition and success of individuals to ultimately understand the species' habitat requirements. As habitat quality may be defined as the likelihood of sustaining a target species over the long term, relating the energetic condition of individuals to different habitats may provide an avenue to assessing such habitat quality (Godfrey 2003). However, measuring the energetic condition of individuals directly is often challenging and invasive to study animals, and hence other indices that avoid these pitfalls are valuable.

The rate of territorial/advertisement calling appears to be linked to condition in numerous species (e.g. Redpath et al. 2000) as was described in more detail in Chapter 3. To confirm that the rate of advertisement vocalizations indirectly represents the energetic condition of individuals, it is important to compare factors affecting the energetic condition within individuals and see whether these factors also affect trait expression. The findings in Chapter 3 confirmed this; a change in temperature during roosting between days corresponded to a change in advertisement call rate. Once I had established a link between calling rate and condition, I compared calling rates across males settling in sites that differed in habitat quality. A significant relationship was apparent; below a certain level of available mature/old forest, the calling rate decreased markedly among males. As calling rate appears

indicative of condition, this may point to territories containing less mature/old forest as having owls in decreased condition. Overall, by monitoring vocalizations of owls, it is possible to not only define the areas used by individuals throughout the breeding season, but also the types of forest content that provide better habitat for the owls.

4.2 Feasibility and limitations of using vocal individuality to monitor owls

In Chapter 2, the comprehensive analysis of vocal individuality containing 24 males proved to have slightly lower discriminant ability (correct classification) than other similar studies. There are, however, factors of my study design that differ from other studies, which may explain my lower discriminant scores. Many of these result from the larger sample size and more rigorous analyses I conducted compared to previous research in the field. Studies that use a small sample of males may bias the individual variation encountered in a population. As the learning set has few individuals to distinguish, fewer classification errors are likely. Larger sample sets should define a more continuous sample of variation in each call parameter across the study population, especially among species with highly stereotyped calls. This can lead to greater overlap among males and thus greater misclassification of calls.

My sample of 24 owls is much higher than most studies addressing individuality. A similar study on African Wood owls using 9 males had 81% correct classification (Delport et al. 2002). Pygmy owls have simple calls not unlike saw-whet owls, and the rate of correct classification of 10 males was 84% (Galeotti et al. 1993), which is in line with a smaller sample analysis within year in Chapter 2 (8 males, 85% in learning set). Although a study including 17 male Tawny owls had a 99% correct classification rate (Galeotti and Pavan 1991), the complexity of the call of this species is much greater than that of the saw-whet owl

calling, and thus provides a greater range of variables to measure that may thereby better define individual differences.

By using the cross-validation function in the analysis, I am also testing the true ability of the discriminant function to correctly classify novel notes that were not used in developing the original discriminant function. It is often unclear whether past studies test this ability; most results given are often discriminating calls within the ‘learning set’ used to build the function. This leads to elevated discrimination, as the calls used to create the models are the easiest to classify. In each of the Chapter 2 analyses, I demonstrated an increase in discriminant ability in the learning sets as compared to using cross-validation techniques, or a ‘test set’. However, using the cross-validation technique is more realistic and useful in a long-term monitoring context, as new recordings are introduced into the analysis to be classified. Thus, if the correct classification is quite high at a particular site, it indicates the same male is likely occupying the site. Conversely, if the correct classification is very low, it may indicate a territory turnover has occurred.

A third factor possibly leading to decreased discriminant ability in this particular study is related to the sheer size of the study area. Where the monitored sites in this study span over approximately 152 800 ha, other studies commonly monitor owls in an area of 1000-2000 ha (Delport et al. 2002, Galeotti and Pavan 1991). Because a smaller number of males included in the analysis increased the discriminant ability and the study area was spread over such a large geographical area, it may be useful in future monitoring efforts to break large study areas into smaller geographical populations, so long as the objectives of the overall analysis allow it. For example, if the objective of a study is to confirm individual

identity throughout a given breeding season, it may be prudent to subdivide the population to prevent misclassification of males that are geographically too far removed to be a focal male.

As useful as it may be to monitor individual owls using their vocalizations, depending on the larger objectives of the study, there are limitations involved with this technique. Depending on the research objectives, these limitations, however, can be managed with a sound study design that accounts for the logistical challenges that may be encountered. More specifically, because the measurements that give insight into the vocal identity of an individual are often subtle, recordings of calls must experience little degradation. Hence, recordings must be collected close to the birds, which in some systems may be challenging. Once active sites have been identified, they must be monitored on a regular basis. In my experience with radio-tagged individuals, it appears that males, although present, may not always respond to playback stimuli; instead they may be more focussed on conflicting activities such as foraging. By monitoring males at different times of night, the probability of having a male respond seems to increase. Thus, through consistent monitoring of males, the likelihood of collecting high quality recordings increases.

As has been pointed out by Gilbert et al. (2002), some males may be more vocally active than others, and surveys may bias against less vocally active males that may be in lower condition (Chapter 3). If repeated detection of a male within a study season is an important factor, timing surveys of less active males on evenings with ideal conditions (e.g. warm and moonless nights that respectively decrease thermal stress and visual exposure to possible predators on already stressed males) may increase the chances of getting a response from a focal male.

If conducting a study utilizing vocal individuality to monitor a species, it is important to be aware of the inherent biases involved with surveying only a specific subset of the population during a specific time, usually males during the breeding season (Gilbert et al. 2002). Thus, conclusions drawn about habitat use cannot necessarily be extrapolated to females, or to times outside the breeding season. However, due to the highly vocal nature and apparently large repertoire of calls of saw-whet owls (Chapter 1), there may be utility in further exploring vocalization types other than the advertisement call. Calls such as the meow seem to be given in response to playback in the fall (pers. obs. of *A. a. acadicus*), and may thereby provide a monitoring tool outside the breeding season.

Ultimately, if the goal of monitoring individuals is related to habitat use, the information extrapolated from a calling male must be considered with care. Although the area being defended by males may be quite constricted, the territory and/or home range of an individual likely spans beyond this core. Nonetheless, a consistent location of high territorial activity and calling may be a good indicator of an area of importance, such as a nest site. Consequently, although the more precise locations obtained by telemetered males may shed light on important territory attributes being used in foraging, the use of calling behaviour may give a more accurate representation of habitat the owl perceives as worth actively defending (as was done in Chapter 3).

An inherent limitation of using vocal individuality to identify individuals instead of radio-telemetry is that it does not allow for immediate identification of the bird in the field. Identification requires office/lab-based analysis, which is often performed at the end of the field season. This may pre-empt knowledge of phenomena such as a within-season site turnover that may be more immediately detectable by other means, unless analysis of new

calls is conducted more frequently during the field season. Depending on the study goals, however, the costs of this limitation may be far less than the costs associated with a radio-telemetry study, such as increased stress to study subjects. A further advantage of using vocal individuality over using radio-telemetry to monitor individuals is a potentially greater sample size. The highly vocal nature of species such as saw-whet owls facilitates monitoring a large number of individuals, thereby potentially increasing the power of a vocal individuality study in comparison to capturing and monitoring a small subset of individuals for telemetry.

The overall goals of a study will dictate whether the benefits and limitations of vocal individuality render this technique a practical alternative to more traditional means of monitoring. For example, if a study's objective is to determine fine-scale habitat use throughout the year, a telemetry study may be more suitable. If, however, the goals are to determine rates of territory turnover in different habitat types, vocal individuality may be a better technique than radio-telemetry; although the battery-life of the small transmitters suited for owls does not last over several years, evidence suggests that the vocal characteristics of individual owls do (Gilbert *et al.* 2002). Alternatively if the purpose is to apply vocal individuality to confirm the identity of owls occupying a certain area within a season, this technique is also appropriate.

As has recently been shown in several species (e.g. Galeotti and Sacchi 2001, Gilbert et al. 2002), using vocal individuality may be an excellent way of monitoring long-term population trends, survival and life-history patterns that would otherwise be difficult to track. Although my preliminary findings of site fidelity in saw-whet owls in the Queen Charlotte Islands show some promise that this technique may work in this system, the logistics of working in this archipelago's landscape (e.g. rugged terrain that complicates access to owls

and frequent foul weather conditions) may make confirming such a possibility difficult. It may hence be useful to further develop methods of monitoring territory turnover on the *acadicus* subspecies of northern saw-whet owls, where populations are denser, and the study conditions are logically easier (i.e. more open woodlands for tracking owls at night). When these techniques have been validated in an environment where vocal signatures can be more easily cross-checked against banded individuals, they may be easier to apply in logically more challenging situations.

4.3 Taking vocal monitoring of saw-whet owls the next step

In Chapter 3, I was able to establish that calling can be used to assess habitat quality by providing an indirect measure of condition of focal males. From this basis, further studies around this idea can be taken in more theoretical and/or in more conservation ecology oriented realms. A theoretical extension of examining call rate relationships to habitat quality addresses the underlying principles of condition dependence. In chapter 3, an indirect comparison between changes in call rate within males corresponding to changes in temperature was made, suggesting that call rate is representative of the energetic status, or condition of a male. A more experimental approach to testing such an assumption would be to alter the amount of food available to males in different habitats. Theoretically, the males occupying poorer territories would benefit more from such an increase in food availability and thus males occupying marginal habitats should experience a disproportionately greater increase in call rate than males in higher quality habitats. Alternatively, with a larger sample size, one could more closely examine the scale of within male changes in call rate as caused by energetic stressors such as temperature fluctuations. As males occupying poorer territories may inherently experience more energetic stress (Godfrey 2003), the effects of temperature

fluctuations may be greater in males occupying poor territories than in males occupying more optimal habitats.

Whatever the underlying theory may be, it appears that calling rate is linked to the amount of mature and old forest available to males near their territory core (Chapter 3). The benefit of measuring such a condition dependent trait is that it may give an early warning signal to potential problems if insufficient habitat is available. Energetic problems can thus be detected earlier than problems such as lowered reproductive success that may follow (Godfrey 2003, Drent and Daan 1980), thereby giving the technique of measuring call rate an advantage in early detection of problems. Such early detection may allow prevention of subsequent declines in the population through proper management.

For proper management of a species to occur, however, it is vital that required habitat types are well defined. As such, future studies of Queen Charlotte saw-whet owls should also consider analyses using more fine-scaled information about the habitat attributes that create a high-quality territory. For example, more detailed information about the forest ecosystem type may also be related to condition. The advent of GIS technology can therefore provide a powerful tool for such analyses, by comparing fine scale habitat detail to the condition of territory occupants. A further extension in the context of forest management may be to compare the condition of owls occupying experimental forest harvest blocks, ultimately determining which techniques of harvesting have the least effect on the condition of the owls. In conclusion, by measuring the condition of owls across specific habitat treatments, a potentially potent biomonitor may be available to forest and land managers.

LITERATURE CITED

- ArcView GIS . 1999. Environmental Systems Research Institute, Inc.
- Alatalo, R.V., Glynn, C. & Lundberg, A. 1990. Singing rate and female attraction in the pied flycatcher: an experiment. *Animal Behaviour* **39**, 601-603.
- Andersson, M. 1994. *Sexual Selection*. Princeton: Princeton University Press.
- Appleby, B.M., Anwar, M.A. & Petty, S.J. 1999. Short-term and long-term effects of food supply on parasite burdens in tawny owls, *Strix aluco*. *Functional Ecology* **13**, 315-321.
- Appleby, B.M. & Redpath, S.M. 1997. Variation in the male territorial hoot of the tawny owl *Strix aluco* in three English populations. *Ibis* **139**, 152-158.
- Arcese, P. & Smith, J.N.M. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology* **57**, 119-136.
- Beecher, M.D., Campbell, S.E., Burt, J.M., Hill, C.E. & Nordby, J.C. 2000. Song-type matching between neighbouring song sparrows. *Animal Behaviour* **59**, 21-27.
- Bibby, C.J., Burgess, N.D. Hill, D.A & Mustoe, S.H. 2000. *Bird Census Techniques*, 2nd Ed. Academic Press. San Diego.:
- Blums, P., Clark, R.G. & Medins, A. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European Ducks. *Journal of Animal Ecology* **71**, 280-295.
- Bradbury, J.W. & Vehrencamp, S.L. 1998. *Principles of Animal Communication*. Sinauer Associates, Sunderland.
- Bried, J. & Jouvetin, P. 1999. Influence of breeding success on fidelity in long-lived birds: an experimental study. *Journal of Avian Biology* **30**, 392-398.
- Cannings, R.J. 1987. The breeding biology of northern saw-whet owls in southern British Columbia. In: Nero, R. W., Clark, R. J., Knapton, R. J., and Hamre, R. H. *Biology and the Conservation of Northern Forest Owls*. U.S. Forest Service General Technical Report RM-142. 193-198.
- Cannings, R.J. 1993. Northern saw-whet Owl. In: Poole, A. and Gill, F. *The Birds of North America*. The American Ornithologists' Union. Washington, D.C., 1-20.
- Catchpole, C.K. & Slater, P.J.B. 1995. *Bird Song*. Cambridge University Press. Cambridge, UK.
- Catchpole, C.K. 1986. Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology* **19**, 439-445.

- Davis, W.J. 1986. Acoustic recognition in the belted kingfisher: cardiac response to playback vocalizations. *Condor* **88**, 505-515.
- Delport, W., Kemp, A.C. & Ferguson, J.W.H. 2002. Vocal identification of individual African wood owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency. *Ibis* **144**, 30-39.
- Drent, R.H. & Daan, S. 1980. The Prudent Parent: Energetic adjustments in avian breeding. *Ardea* **68**, 225-252.
- Eakle, W.L., Mannan, R.W. & Grubb, T.G. 1989. Identification of individual breeding bald eagles by voice analysis. *Journal of Wildlife Management* **52**, 450-455.
- Edelstein-Keshet, L. 1987. *Mathematical Models in Biology*. McGraw-Hill. New York, USA.
- Eeva, T., Lehikoinen, E. & Rönkä, M. 1998. Air pollution fades the plumage of the great tit. *Functional Ecology* **12**, 607-612.
- Falls, J.B. 1982. Individual recognition by sounds in birds. In: Kroodsma, D.E. & Miller, E.H. *Acoustic Communication in Birds*. Academic Press, New York. 237-278.
- Fleming, J.H. 1916. The saw-whet owl of the Queen Charlotte Islands. *The Auk* **33**, 420-423.
- Forbes, J.E. & Warner, D.W. 1974. Behaviour of a radio-tagged saw-whet owl. *The Auk* **91**, 783-795.
- Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society of London, Biological Sciences* **269**, 1479-1485.
- Foster, J.B. 1984. The Canadian Galapagos. In: *Islands at the Edge: Preserving the Queen Charlotte Islands Wilderness*. Douglas and McIntyre. Vancouver.
- Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burham, K.P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* **70**, 539-590.
- Galeotti, P. 1998. Correlates of hoot rate and structure in male tawny owls *Strix aluco*: implications for male rivalry and female mate choice. *Journal of Avian Biology* **29**, 25-32.
- Galeotti, P., Paladin, M. & Pavan, G. 1993. Individually distinct hooting in male pygmy owls *Glaucidium passerinum*: a multivariate approach. *Ornis Scandinavica* **24**, 15-20.
- Galeotti, P. & Pavan, G. 1991. Individual recognition of male tawny owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethology, Ecology and Evolution* **3**, 113-126.

- Galeotti, P. & Pavan, G. 1993. Differential responses of territorial tawny owls *Strix aluco* to the hooting of neighbours and strangers. *Ibis* **135**, 300-304.
- Galeotti, P. & Sacchi, R. 2001. Turnover of territorial scops owls *Otus scops* as estimated by spectrographic analyses of male hoots. *Journal of Avian Biology* **32**, 256-262.
- Garson, P.J. & Hunter, M.L. 1979. Effects of temperature and time of year on the singing behaviour of wrens *Troglodytes troglodytes* and Great Tits *Parus major*. *Ibis* **121**, 481-487.
- Gavin, T.A. & Bollinger, E.K. 1988. Reproductive correlates of breeding-site fidelity of bobolinks (*Dolichonyx oryzivorus*). *Ecology* **69**, 96-103.
- Gilbert, G., McGregor, P.K. & Tyler, G. 1994. Vocal individuality as a census tool: practical considerations illustrated by a study of two rare species. *Journal of Field Ornithology* **65**, 335-348.
- Gilbert, G., Tyler, G.A. & Smith, K.W. 2002. Local annual survival of booming male great bittern *Botaurus stellaris* in Britain, in the period 1990-1999. *Ibis* **144**, 51-61.
- Gill, M. and Cannings, R.J. 1997. Habitat selection of northern saw-whet owls (*Aegolius acadicus brooksi*) on the Queen Charlotte Islands, British Columbia. In: Duncan, J. R., Johnson, D. H., and Nicholls, T. H. *Biology and the conservation of owls in the northern Hemisphere, 2nd international symposium*. USDA Forest Service Technical Report NC-190.
- Godfrey, J.D. 2003. Potential use of energy expenditure of individual birds to assess quality of their habitats. *Science for Conservation* **214**, 11-24.
- Hakkarainen, H., Mykrä, S., Kurki, S., Korpimäki, E., Nikula, A. & Koivunen, V. 2003. Habitat composition as a determinant of reproductive success of Tengmalm's owls under fluctuating food conditions. *Oikos* **100**, 162-171.
- Harrison, S. 1993. Metapopulations and conservation. In: P.J. Edwards, R.M. May & N.R. Webb *Large Scale Ecology and Conservation Biology*. Blackwell Scientific Publishing. Oxford, U.K. 111-128.
- Higgins, R.M. 1979. Temperature-related variation in the duration of morning song of the song thrush *Turdus ericetorum*. *Ibis* **121**, 333-335.
- Hill, G.E. 1995. Ornamental traits as indicators of environmental health. *Bioscience* **45**, 25-31.
- Hobson, K.A. & Sealy, S.G. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable isotope approach. *The Auk* **108**, 437-440.
- Hogstad, O. 1987. It is expensive to be dominant. *The Auk* **104**, 333-336.
- Hoi-Leitner, M., Nechelberger, H. & Hoi, H. 1995. Song rate as a signal for nest site quality in blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology* **37**, 399-405.

- Johnson, F. & Rashotte, M.E. 2002. Food availability but not cold ambient temperature affects undirected singing in adult male zebra finches. *Physiology and Behavior* **76**, 9-20.
- Korpimäki, E. 1988. Effects of territory quality on occupancy, breeding performance and creeding dispersal in Tengmalm's owl. *Journal of Animal Ecology* **57**, 97-108.
- Korpimäki, E. 1992. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. *Journal of Animal Ecology* **61**, 103-111.
- Kotiaho, J.S. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioural Ecology and Sociobiology* **48**, 188-194.
- Krebs, J.R., Ashcroft, R. & Van Orsdol, K. 1981. Song matching in the great tit, *Parus major*. *Animal Behaviour* **29**, 918-923.
- Lind, H., Dabelsteen, T. & McGregor, P.K. 1996. Female great tits can identify mates by song. *Animal Behaviour* **52**, 667-671.
- Löfgren, O., Hörfeld, B. & Carlsson, B.G. 1986. Site tenacity and nomadism in Tengmalm's owl (*Aegolius funeris*) in relation to cyclic food production. *Oecologia* **69**, 321-326.
- Matthysen, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian nuthatch (*Sitta europaea*). *The Auk* **107**, 86-95.
- Matthysen, E. & Adriaensen, F. 1998. Forest size and isolation have no effect on reproductive success of Eurasian Nuthatches (*Sitta europaea*). *The Auk* **115**, 955-963.
- McGregor, P.K., Dabelsteen, T., Shephard, M. & Pedersen, S.B. 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Animal Behaviour* **43**, 987-998.
- McGregor, P.K. & Byle, P. 1992. Individually distinctive bittern booms: potential as a census tool. *Bioacoustics* **4**, 93-109.
- McGregor, P.K. & Peake, T.M. 1998. The role of individual identification in conservation biology. In: Caro, T. *Behavioral Ecology and Conservation Biology*. Oxford University Press, New York.
- McGregor, P.K., Peake, T.M. & Gilbert, G. 2000. Communication behaviour and conservation. In: Gosling, L.M. & Sutherland, W.J. *Behaviour and Conservation*. Cambridge University Press, Cambridge, UK. 261-280
- Meidinger, D. & Pojar, J. 1991. *Ecosystems of British Columbia*. British Columbia Ministry of Forests, Victoria, Canada.
- Newton, I. 1993. Age and site fidelity in female sparrowhawks, *Accipiter nisus*. *Animal Behaviour* **46**, 161-168.

- Oberweger, K. & Goller, F. 2001. The metabolic cost of birdsong production. *The Journal of Experimental Biology* **204**, 3379-3388.
- Ohlsson, T., Smith, H.G., Råberg, L. & Hasselquist, D. 2001. Pheasant sexual ornaments reflect nutritional conditions during early growth. *Proceedings of the Royal Society, Biological Sciences* **269**, 21-27.
- Otter, K. 1996. Individual variation in the advertisement call of male northern saw-whet owls. *Journal of Field Ornithology* **67**, 398-405.
- Otter, K., Chruszcz, B. & Ratcliffe, L. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology* **8**, 167-173.
- Peake, T.M. & McGregor, P.K. 2001. Corncrake *Crex crex* census estimates: a conservation application of vocal individuality. *Animal Biodiversity and Conservation* **24**, 81-90.
- Peake, T.M., McGregor, P.K., Smith, K.W., Tyler, G., Gilbert, G. & Green, R.E. 1998. Individuality in corncrake *Crex crex* vocalizations. *Ibis* **140**, 121-127.
- Penteriani, V., Faivre, B., Mazuc, J. & Cezilly, F. 2002. Pre-laying vocal activity as a signal of male and nest stand quality in goshawks. *Ethology, Ecology and Evolution* **14**, 9-17.
- Przybylo, R., Wiggins, D.A. & Merilä, J. 2001. Breeding success in blue tits: good territories or good parents? *Journal of Avian Biology* **32**, 214-218.
- Quinn, G.P. & Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press. Cambridge, UK.
- Redpath, S.M. 1995. Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. *Journal of Animal Ecology* **64**, 652-661.
- Redpath, S.M., Appleby, B.M. & Petty, S.J. 2000. Do male hoots betray parasite loads in tawny owls? *Journal of Avian Biology* **31**, 457-462.
- Reebek, M., Corrick, R., Eaglestone, B. & Stainton, C. 2001. Recognition of individual European nightjars *Caprimulgus europaeus* from their song. *Ibis* **143**, 468-475.
- Reid, M.L. 1987. Costliness and reliability in the singing vigour of Ipswich sparrows. *Animal Behaviour* **35**, 1735-1743.
- Remeš, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? *Oikos* **91**, 579-582.
- Saunders, D.A. & Wooller, R.D. 1988. Consistent individuality of voice in birds as a management tool. *Emu* **88**, 25-32.
- Sealy, S.G. 1999. Further data on food items of northern saw-whet owls (*Aegolius acadicus brooksi*) on the Queen Charlotte Islands, British Columbia. *Western Birds* **30**, 200-205.

- Sealy, S.G. 1998. The subspecies of northern saw-whet owl on the Queen Charlotte Islands: an island endemic and a nonbreeding visitant. *Western Birds* **29**, 21-28.
- Sergio, F., Pedrini, P. & Marchesi, L. 2003. Spatio-temporal shifts in gradients of habitat quality for an opportunistic avian predator. *Ecography* **26**, 243-255.
- Specht, Raimund. Avisoft SAS Lab Pro. 2000.
- STATISTICA (data analysis software system). StatSoft, Inc. 2003.
- Strain, J.G. & Mumme.R.L. 1988. Effects of food supplementation, song playback and temperature on vocal territorial behaviour of Carolina wrens. *The Auk* **105**, 11-16.
- Tarver, C. 2003. Northern saw-whet owl nest on East Limestone Island. In: *Laskeek Bay Research* (Ed. by A.J. Gaston), pp. 19-21. Laskeek Bay Conservation Society. Queen Charlotte City, BC.
- Tarvin, K.A. & Garvin, M.C. 2002. Habitat and nesting success of blue jays (*Cyanocitta cristata*): importance of scale. *The Auk* **119**, 971-983.
- Terry, A.M.R. & McGregor, P.K. 2002. Census and monitoring based on individually identifiable vocalizations: the role of neural networks. *Animal Conservation* **5**, 103-111.
- Terry, A.M.R., McGregor, P.K. & Peake, T.M. 2001. A comparison of some techniques used to assess vocal individuality. *Bioacoustics* **11**, 169-188.
- Thomas, R.J. 1999. The effect of variability in the food supply on the daily singing routines of European robins: a test of a stochastic dynamic programming model. *Animal Behaviour* **57**, 365-369.
- Thomas, R.J. & Cuthill, I.C. 2002. Body mass regulation and the daily singing routines of European robins. *Animal Behaviour* **63**, 285-295.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**, 893-901.
- Wiley, R.H. & Richards, D.G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection., pp. 131-181. New York, Academic Press.
- Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* **67**, 603-605.
- Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* **32**, 38-46.
- Zanette, L., Smith, J.N.M., van Oort, H. & Clinchy, M. 2003. Synergistic effects of food and predators on annual reproductive success in song sparrows. *Proceedings of the Royal Society, Biological Sciences* **270**, 799-803.