OCCUPANCY AND ABUNDANCE OF GOLDEN-CHEEKED WARBLERS (*DENDROICA CHRYSOPARIA*) ON THE BALCONES CANYONLANDS PRESERVE

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Degree

Master of SCIENCE

by

Jason W. Hunt, B.S.

San Marcos, Texas

August 2010

ACKNOWLEDGEMENTS

I would like to express my thanks to the City of Austin for funding my research, and to the biologists at the Balcones Canyonlands Preserve who facilitated access to the preserve. I would like to thank my advisors, Dr. Butch Weckerly and Dr. Jim Ott, not only for their helpful guidance throughout my graduate studies, but for their diligent efforts in the field that made this research project possible. To my committee member, Dr. Joseph Veech: for his helpful comments and insight that strengthened the quality of this research project. Thanks to Garrett Street and Chris Warren, who took time out of their busy schedules to assist with field work. I would also like to reconginze the invaluable help of Stephen Rameriez, who guided me through the process of creating the map in Figure 3.

I am grateful to my parents, Ron and Becky Hunt, who have always been there to support me and offer words of encouragement. They instilled in me the determination to follow my dreams and to preserve through the challenges and difficulties encountered in pursuit of those dreams. I thank them for believing in me and their continued love and support inspires me to keep reaching for the stars.

This manuscript was submitted on June 7th 2010.

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ABSTRACT

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By

Jason W. Hunt, B.S.

Texas State University-San Marcos

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SUPERVISING PROFESSORS: FLOYD W. WECKERLY AND JAMES R. OTT

Reliable estimates of population parameters derived from logistically feasible wildlife survey methods are essential for making management decisions regarding endangered species. Observer variability in detection can be a substantial source of error in avian survey methods, resulting in biased population estimates. Additionally, the degree of among-observer variability in detection may be influenced by population density. I evaluated the degree of within-and among-observer variability in detection of the federally endangered golden-cheeked warbler (GCWA, *Dendroica chrsoparia*) by means of point-count surveys conducted at two sites exhibiting high and low population densities. Surveys consisted of four surveyors simultaneously, but independently recording the number of GCWA detected during five-minute intervals at each of 36 points at each site. Count data were analyzed using both multi-season occupancy models and binomial mixture models (BMM) to estimate each observer's probability of detection at both the species and individual level. Model selection revealed that observer had a strong influence on detection of GCWA. I found significant variation in detection probabilities among observers and the degree of observer variability was greatest at the low density site. Extrapolating observer-specific estimates of detecting the species to four survey occasions revealed that observer variability was negligible at the high density site, yet observer variability was still substantial at the low density site. Among-observer variability in detecting individuals was more extensive at both sites, therefore I concluded that the inclusion of a covariate for observer would be necessary for modeling abundance. Herein, I also investigated the utility of point-count surveys in conjunction with occupancy and BMM as a feasible and reliable approach for monitoring the golden-cheeked warbler on the Balcones Canyonlands Preserve in Travis County, Texas. Occupancy and abundance were estimated using data from point-count surveys conducted on each of five 100 hectare detection girds in 2008 and seven grids in 2009. Data were analyzed using both single season occupancy models and BMM to estimate occupancy and abundance, respectively. Occupancy estimates per grid ranged from 0.48 to 1.0 in 2008 and 0.52 to 1.0 in 2009. Estimates of abundance were compared with territory densities independently estimated using a more labor-intensive spot-mapping method. The BMM generated abundance estimates that were nearly five times as high as estimates of territory density based on spot-mapping. Thus, I concluded that BMM estimates of abundance for this species were biologically unrealistic. Using an alternative approach, I also estimated abundance using a novel C/p estimator that incorporated the probability of detecting individuals obtained from occupancy models. This alternative approach provided abundance estimates similar to territory density estimates obtained from spot-mapping. Point-count surveys conducted for this study required considerably less time and surveyed a larger area compared to spot-mapping. The results of this study suggest that using a model-based approach to estimate occupancy and abundance from point-count data is a reliable and feasible monitoring alternative to spot-mapping.

CHAPTER I

THE INFLUENCE OF OBSERVER VARIABILITY IN DETECTION OF GOLDEN-CHEEKED WARLBERS (*DENDROICA CHRYSOPARIA*)

Introduction

Variation in the detectability (i.e., probability of detecting a species if present) of avian species is a significant source of bias for survey methods used to estimate population parameters (Alldredge et al. 2007, Johnson 2008). Many avian species are often imperfectly detected by surveyors, hence nondetection of individuals at a survey site does not always confirm the absence of a species (MacKenzie et al. 2002, Thompson et al. 2002). Standardization of survey protocols has been advocated as a means of minimizing some of the variability in detection (Ralph et al. 1995). Additionally, the development of methods for estimating probabilities of detection has been applied to directly addressing the problem of imperfect detection by adjusting population estimates (Royle 2004, MacKenzie et al. 2006, Alldredge et al. 2007). The factors that influence detection probabilities are diverse and include time of year (Best 1981, Skirvin 1981), time of day (Robbins 1981a), habitat characteristics (Diehl 1981, McShea and Rappole 1997), weather conditions (Mayfield 1981, Robbins 1981b, Simons et al. 2007), and species (Alldredge et al. 2007, Kubel and Yahner 2007).

Multiple surveyors are often involved in both large-scale avian monitoring programs (Sauer et al. 1994) and species-specific population studies (Anders and Dearborn 2004). Thus, observer variability in detection of birds has long been recognized as an important source of error in avian survey methods (Faanes and Bystrak 1981, Emlen and DeJong 1992, Sauer et al. 1994, Alldredge et al. 2007, Riddle et al. 2010). However, few studies measure observer variability or incorporate techniques to effectively mitigate or decrease observer variability when developing their methods or study design (Diefenbach et al. 2003). The few recommendations typically given to mitigate observer variability in detection include training surveyors (Kepler and Scott 1981), testing hearing ability (Ramsey and Scott 1981), and hiring experienced observers (Faanes and Bystrak 1981). The inherent assumption of these recommendations is that observer variability in detection will be negligible under these guidelines (Rosenstock et al. 2002). Yet variability in detection of avian species is often evident even among well-trained and experienced observers (Diefenbach et al. 2003, Alldredge et al. 2007).

The point-count method is a commonly used avian survey technique by which one or more surveyors record all birds detected within a fixed or an unlimited distance from a point during a specified period (Hutto et al. 1986). Count data collected using this method is often treated as an index and used to infer the relative abundance of populations over time or across locations (Caughley 1977, Johnson 2008). In recent years, point-count data has also been applied to models that incorporate probabilities of detection to estimate directly population parameters such as occupancy (proportion of area occupied) and abundance (MacKenzie et al. 2002, Rolye 2004). However, since multiple surveyors are often employed to conduct point-count surveys, observer variability in detection is a potential source of error that can bias count data and thus lead to biased population estimates (Sauer et al. 1994, Diefenbach et al. 2003, Alldredge et al. 2007).

A second factor influencing detection of avian species is the interaction of singing behavior with population density (Howell et al. 2004, Sillet et al. 2004). Point-count surveys, which are primarily aurally based, can exhibit density-related biases in the number of birds detected (Bart and Schoultz 1984, Tarvin et al. 1998, Jones et al. 2000, Howell et al. 2004). In higher-density avian populations singing rate can be greater (Jones et al. 2000, Howell et al. 2004, Sillet et al. 2004, Rios Chelen et al. 2005, Sexton et al. 2007, Laiolo 2008, Laiolo and Tella 2008, Robbins et al. 2009), and singing rate of passerines can influence detection probabilities (Mayfield 1981, Wilson and Bart 1985, McShea and Rappole 1997, Alldredge et al. 2007). If singing behavior of individuals is positively correlated with density, then detection probabilities may also be correlated with population densities. However, no studies have directly examined the magnitude of such an effect. If present a correlation between population density and detection of avian species could affect the degree of observer variability in point-count surveys used to monitor threatened and endangered avian species with low population densities.

Correcting these types of biases is difficult when counts are used as indices of relative abundance (Bart and Schoultz 1984, Johnson 2008). However, using a model-based approach to estimate population parameters adjusted for imperfect detection provides a way of explicitly addressing these sources of variation in detection (Alldredge et al. 2007, Riddle et al. 2010). Furthermore, correcting biases stemming from both observer variability and population density can be accomplished by increasing the number of repeated survey occasions, a recommendation advocated especially when surveying species with low detectability (MacKenzie and Royle 2005). Herein, I first quantify within- and among- observer variability in the probabilities of detection for an endangered songbird surveyed at low- and high- density sites and then I use a model-based approach to explore practical techniques to account for and mitigate these biases in the design of point-count surveys.

The golden-cheeked warbler (GCWA, *Dendroica chrysoparia*) is a federally endangered neotropical songbird with a breeding range restricted to central Texas (Pulich 1976). Surveys used to monitor this species heavily rely on aural detections of singing males (U.S. Fish and Wildlife Service 1992). Given the forgoing standardized survey protocols and the documented variation in population density noted across its range (Wahl et al. 1990), the GCWA is a suitable species for investigating both the degree of observer variability in detection and the correlation between detection and population density.

The goals of this study were to evaluate the degree of observer variability in detection in point-count surveys of the GCWA among sites known to exhibit contrasting population densities and to develop practical solutions that can be applied to the design of point-count surveys to mitigate the influence of observer variability.

Methods

Point-count surveys of GCWA were conducted at two locations with different population densities. The study area for this project was the Balcones Canyonlands Preserve (BCP) located in Travis County, Texas. This 5,355-ha preserve contains woodlands of mature Ashe juniper (*Juniperus asheri*) mixed with Texas oak (*Quercus buckleyi*), live oak (*Q. fusiformis*), shin oak (*Q. sinuate*), cedar elm (*Ulmus crassifolia*), Texas ash (*Fraxinus texensis*), and escarpment black cherry (*Prunus serotina*) (Pulich

1976, Ladd and Glass 1999, Dearborn and Sanchez 2001). The terrain of this area consists of rolling hills interspersed with steep-sided canyons. Two sites within the BCP were selected to represent extremes in the range of suspected GCWA densities, with the Ivanhoe site having a high density of GCWA (53 and 44 territories/100 ha in 2008 and 2009, respectively) and the Bohls site having a considerably lower density (7 and 9 territories/100 ha in 2008 and 2009, respectively) (City of Austin 2009). The densities at these two sites fall within the range of known GCWA densities across its geographic range (Wahl et al. 1990). A 100-ha grid consisting of 36 points, each positioned 200 m apart, served as the framework for conducting point-count surveys. Surveys consisted of four surveyors simultaneously surveying the 36 points at a site, with each observer independently recording the number of GCWA aurally detected during a five-minute period at each point. During the five-minute period, surveyors did not communicate. The five-minute sample period per point was deemed adequate to provide sufficiently high probabilities of detection, as this interval has proven sufficient for most species of forest songbirds (Ralph et al. 1995, Dettmers et al. 1999). Each site was surveyed once in both 2008 and 2009 by the same four surveyors. Surveys required an average of about six hours to complete.

The four surveyors represented a broad range of experience and age. Three surveyors had prior experience conducting avian surveys and one had no prior survey experience. The ages of the surveyors ranged from two surveyors in their 20s (1 experienced, 1 nonexperienced) to two surveyors in their 50s (both experienced). The four surveyors are henceforth labeled as observer 1 (young, experienced), observer 2 (young, nonexperienced), observer 3 (older, experienced), and observer 4 (older, experienced).

To estimate detection probabilities for each surveyor, point-count data were analyzed using both occupancy and binomial mixture models to estimate probabilities of detecting the species and individuals, respectively (program PRESENCE 2.3, MacKenzie et al. 2002). Since survey data were collected in each of two years, multi-season occupancy models were used to estimate probabilities of detecting GCWA at the species level for each observer (MacKenzie et al. 2003). Multi-season occupancy models included parameters for occupancy (ψ), colonization (γ), extinction (ε), and probabilities of detection (p). The parameter estimates for occupancy, colonization, and extinction were not of direct interest in this study; however, the models in this analysis included a site covariate for these parameters because it was suspected that these parameters would differ between the high- and low- density sites.

Since occupancy models utilize detection–nondetection data, the estimate of detection for each surveyor produced refers to the probability of detecting the species (i.e., $\geq$1 GCWA) in a single survey (MacKenzie et al. 2002). I developed nine multi-season occupancy models to assess the influence of the following potential covariates on probability of species-level detection: observer, site, year, time of day with a linear effect (time/linear), and time of day with a quadratic effect (time/quadratic). The covariates site, season, and observer were discrete variables, whereas time of day (the minutes after sunrise that a detection was recorded) was considered a continuous covariate.

To evaluate observer variability in detecting GCWA individuals, survey data was analyzed using binomial mixture models (BMM) that included parameters for abundance (λ) and probability of detecting individuals (*p*). Currently, there are no multi-season BMM available, thus abundance data were analyzed separately in each year (Royle 2004). Eight models were considered in each year to assess the influence of covariates on probability of detecting individuals. The covariates included site, observer, time/linear, and time/quadratic. The observer covariate for the BMM was coded using dummy variables that pooled observers 1–3 together and compared them to observer 4. The arrangement of this observer covariate was chosen based on the degree of observer variability in detection found in the multi-season occupancy models. Model selection was conducted for both multi-season occupancy and BMM using the information-theorectical approach with Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). I selected the model or models that fit the data best, relative to the other candidate models, based on small AIC_c values and high Akaike weight (Akaike 1973).

Detection probabilities estimated in this study represented the probability of detecting the species or the individual during a single survey. Repeated surveys at a location are often suggested to obtain higher probabilities of detection and more precise parameter estimates (MacKenzie and Royle 2005). Therefore, to extrapolate single-survey detection probabilities to multiple survey occasions, estimates of detection for each observer were extrapolated to multiple survey occasions by means of an equation from MacKenzie et al. 2006:

$$P^* = 1 - (1 - p)^s \qquad (1)$$

Where, P* is the probability of detecting the species among all survey occasions, p is the detection probability of a single survey, and s is the number of survey occasions. The number of survey occasions considered in both occupancy models and BMM is constrained by the assumption that the population is closed during the total sampling season (MacKenzie et al. 2002, MacKenzie et al. 2003, Royle 2004). I evaluated the effect of four survey occasions using equation (1) since it's likely that with a weekly sample interval the assumption of population closure for this species is met during a sampling season of four weeks (Watson et al. 2008). Thus, observer-specific probabilities of detection representing a sampling season of four weeks were used to assess variability among the four surveyors in this study.

Results

Both multi-season occupancy and BMM indicated that the probability of detecting GCWA varied among observers (Tables 1 and 2). The selected multi-season occupancy model with the lowest AIC_c contained site (my proxy for GCWA density) and observer covariates for detection and was competitively superior to all other candidate models (Table 1). This indicates that both density and observer had a strong influence on the probability of detecting GCWA within a single survey. Estimates of detection for observers ranged from 0.68-0.90 at the high-density site (Ivanhoe) and 0.32-0.66 at the low-density site (Bohls) (Figure 1). There was a consistent pattern in the variability among the four observers across sites as observers 1, 2, and 3 had similar probabilities of detection. However, observer 4 had a considerably lower probability of detection compared with the other observers at both sites. The variation in detection between observers 1–3 and observer 4 was greatest at Bohls, the low-density site.

Despite the comparatively lower probability of detection for observer 4 during a single survey occasion, estimates of detection when extrapolated to four survey occasions showed that variability among observers in detecting GCWA became negligible. For example, using equation (1), estimates of detection for the surveyor with the lowest detection probability, observer 4, at Ivanhoe (0.68) were extended to four survey occasions:

$$P^* = 1 - (1 - 0.68)^4 \tag{1}$$

$$P^* = 0.99.$$

The probability value of 0.99 indicates that each of the four observers in this study would thus have cumulative probabilities of detection for the species near 1.0 when extrapolated to four survey occasions. Therefore, increasing the number of survey occasions to four diminished the effect of the variability among the surveyors in detecting GCWA at the high-density site. However, increasing the number of surveys to four at the low-density site is not adequate to mitigate observer differences in detection of this species. Observers 1, 2, and 3 had sufficiently high probabilities of detection during a single survey occasion at the low-density site, such that each of these observers would have probabilities of detection of the species greater than 0.95 when extrapolated to four

Table 1. Model Selection Summary (Influence of Observer).
Summary of model selection for the multi-season occupancy models. The four parameters estimated included occupancy (ψ), colonization (γ), extinction (ε), and probability of detection (*p*). Possible covariates included site, observer, year, time of day with a linear effect (time/linear), time of day with a quadratic effect (time/quadratic), and no influence of a covariate (.). Model selection statistics were Akaike Information Criterion value corrected for small sample size (AIC_c), AIC_c weight (W), number of parameters (N. par.), and twice the log likelihood (-2LL). Sample size was 144.

Model	AIC_c	W	N. par.	-2LL
ψ(site), γ(site), ε(site), p(site, observer)	**419.62**	**0.907**	**11**	**395.61**
ψ(site), γ(site), ε(site), p(site, observer, year)	425.77	0 042	14	394.53
ψ(site), γ(site), ε(site), p(site)	426.19	0.034	8	409 15
ψ(site), γ(site), ε(site), p(site, time/linear)	428.46	0.011	9	409.19
ψ(site), γ(site), ε(site), p(site, time/quadratic)	429.90	0 005	10	408.23
ψ(site), γ(site), ε(site), p(observer)	434.43	<0.001	10	412.85
ψ(site), γ(site), ε(site), p(time/linear)	441.14	<0.001	8	424.12
ψ(site), γ(site), ε(site), p(time/quadratic)	442.06	<0.001	9	422.77
ψ(.), γ(.), ε(.), p(.)	471.82	<0.001	4	463.53

Table 2. Model Selection Summary (Influence of Observer).

Summary of model selection for the binomial mixture models in 2008 and 2009. The two parameters estimated in these models were abundance (λ) and probability of detection (p). Possible covariates included site, observer, time of day with a linear effect (time/linear), time of day with a quadratic effect (time/quadratic), and no influence of a covariate (.). Model selection statistics were Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c weight (W), number of parameters (N. par.) and twice the log likelihood (-2LL). Sample size was 72 in both years.

	2008				2009			
Model	AIC_c	W	N. par.	-2LL	AIC_c	W	N. par.	-2LL
λ(site), p(site, observer)	**306.54**	**0.885**	**4**	**297.92**	377.56	0.021	4	369.01
λ(site), p(observer)	311.62	0.070	4	303.01	**369.85**	**0.978**	**4**	**361.32**
λ(site), p(site)	313.71	0.024	3	307.45	391.54	<0.001	3	385.23
λ(site), p(site, time/linear)	315.46	0.010	4	306.93	393.78	<0.001	4	385.24
λ(site), p(site, time/quadratic)	315.85	0.008	4	307.24	391.08	<0.001	4	382.58
λ(site), p(time/quadratic)	319.57	0.001	4	311.06	384.60	<0.001	4	376.09
λ(site), p(time/linear)	320.26	<0.001	4	311.74	384.68	<0.001	4	376.14
λ(.), p(.)	340.17	<0.001	2	336.09	420.70	<0.001	2	416.54

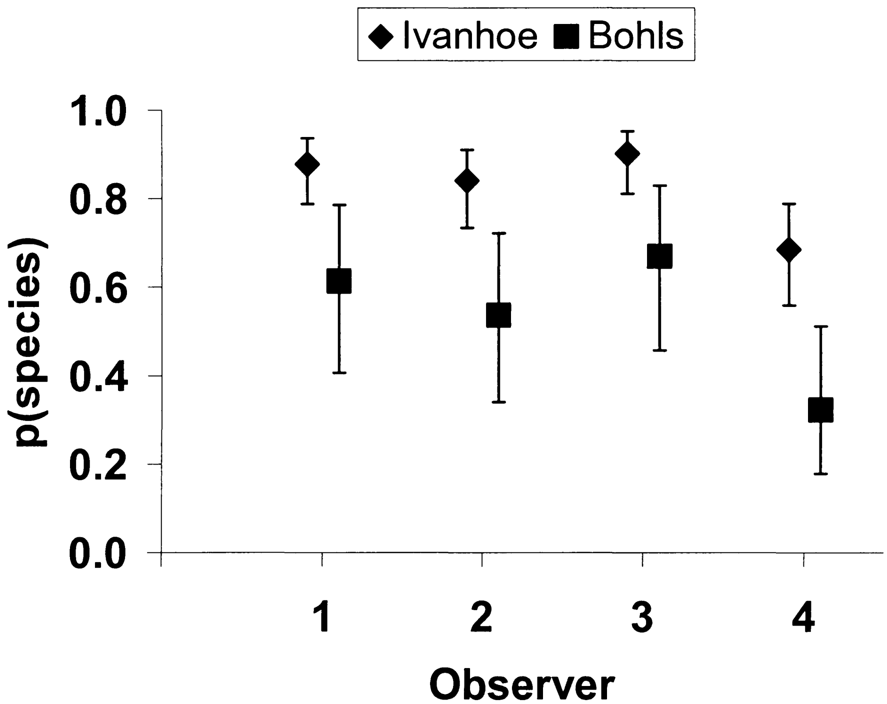

Figure 1. Observer Detection Probabilities (species).
Probability of detecting GCWA at the species level, p(species), for observers 1, 2, 3, and 4 estimated from the selected multi-season occupancy model. Detection probabilities for each observer are shown at both the high (Ivanhoe) and low (Bohls) density sites. Error bars represent 95% CI.

surveys occasions. However, observer 4, who had a considerably lower probability of detection (0.32) at the low-density site during a single survey occasion, would require at least eight repeated surveys in order to have a cumulative probability of detection greater than 0.95. Variability in the probability of detecting GCWA individuals was also evident among the four observers in this study as the BMM containing both site and observer as covariates for probability of detecting individuals was selected in 2008 (Table 2). At Ivanhoe the probability of detecting individuals ranged from 0.47 to 0.73 among observers and at Bohls ranged from 0.18 to 0.40 (Figure 2). Again, observers 1–3 had a much higher probability of detecting individuals than did observer 4 at both the high and low density sites. Extrapolating single survey probabilities of detecting individuals for observers 1–3 to multiple survey occasions revealed that four repeated surveys would yield a 0.99 probability at the high-density site while at least six surveys would be required at the low-density site to raise detection probabilities to ≥0.95. However, due to observer 4's comparatively lower single survey probability of detecting individuals, at least 5 surveys at the high-density site and 15 surveys at the low-density site would be required to raise detection probabilities to ≥0.95. The BMM selected in 2009 contained only an observer covariate, indicating again, significant differences among observers in the probability of detecting individuals (Table 2). Observers 1–3 had an average probability of detection of 0.66, whereas observer 4 had a 0.38 probability of detection (Figure 2). Again, equation (1) reveals that observers 1–3 would have a probability of detection for individuals of 0.98 for four survey occasions, whereas observer 4 would require at least seven surveys to achieve a detection probability greater than 0.95.

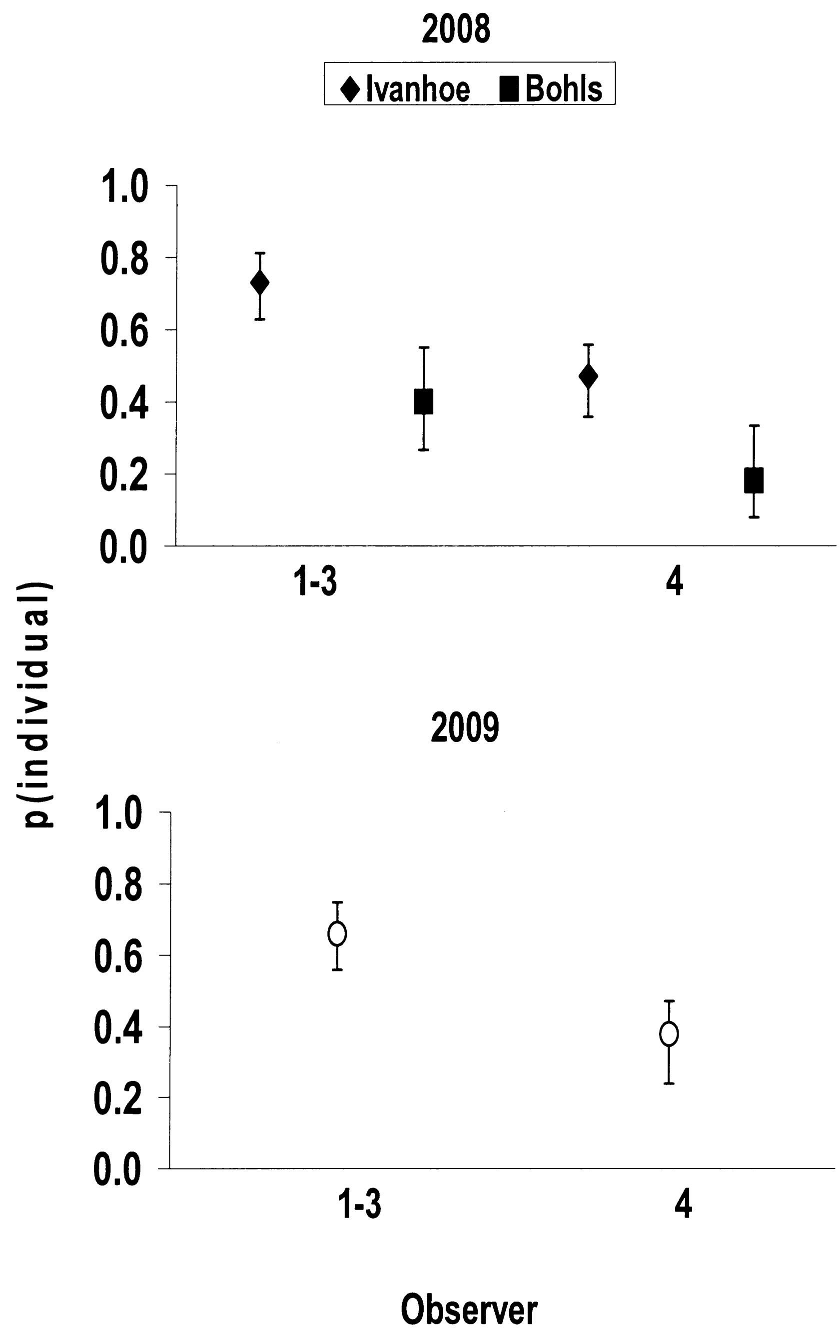

Figure 2. Observer Detection Probabilities (individuals).
Probability of detecting GCWA at the individual level, *p(individual)*, for observers 1–3 (combined) and observer 4, as estimated from the selected binomial mixture models in 2008 and 2009. The selected model in 2008 contained site and observer as covariates of detecting GCWA individuals, thus detection probabilities for observers are shown for both the high (Ivanhoe) and low (Bohls) density sites. The selected model in 2009 contained only an observer covariate for probability of detecting individuals, thus estimates of detection for that year represent only observer differences. Error bars represent 95 % CI.

Estimates of GCWA occupancy and abundance based on the single survey occasions used for this study differed between the two sites. Occupancy estimates (± SE) for 2008 and 2009, respectively, were 0.61 (± 0.08) and 0.83 (± 0.06) for Ivanhoe and 0.17 (± 0.06) and 0.20 (± 0.07) for Bohls. Estimates of abundance (average number of male GCWA per point) for 2008 and 2009, respectively, were 1.05 (± 0.17) and 1.59 (± 0.22) for Ivanhoe and 0.26 (± 0.07) and 0.23 (± 0.08) for Bohls.

Discussion

The analysis I conducted documented significant variability among four surveyors in the probability of detecting GCWA at both the species and individual level. Moreover, I found that variation in the degree of observer variability differed among two sites characterized by low and high densities of GCWA. Together these results point to the need to develop survey designs for monitoring GCWA that explicitly acknowledge and account for within- and among- observer variability in detection as a function of population density. Alldredge et al. (2007) have pointed out the broad ramifications for monitoring avian species if these sources of error are not accounted for in survey design.

The variation in detection probabilities I observed among surveyors in this study is consistent with the among-observer variation reported by Sauer et al. (1994), Diefenbach et al. (2003), and Alldredge et al. (2007). There are several potential solutions that can be implemented in the design of avian point-count surveys to diminish the influence of observer variability (Sauer et al. 1994, Alldredge et al. 2007). For example, if comparisons are being made concerning the relative occupancy or abundance among different sites, then one solution is to employ a study design in which every observer surveys every site at least once during the field season (Sauer et al. 1994).

However, this approach may not be feasible for large-scale monitoring programs involving many sites for which extensive training may be required to familiarize surveyors with the multiple survey locations. As shown herein, simply increasing the number of survey occasions may sufficiently mitigate the effects of observer variability for some study designs (MacKenzie and Royle 2005). The effectiveness of this solution for mitigating observer variability, however, may be influenced by population density. I found low detection probabilities at sites with low GCWA population densities, and my analysis revealed that the number of repeated surveys necessary to obtain reasonably high detection probabilities for each observer may be impractical in such cases, from both a logistical and survey design perspective. For example, when using single-season occupancy models the number of survey occasions should be constrained to meet the assumption of population closure (MacKenzie et al. 2002). This study demonstrated that even when one observer had a significantly lower detection probability for the species compared with the other observers at the site with high GCWA density, increasing the number of survey occasions to four resulted in detection probabilities of near 1.0. Therefore, in this case, the variability among the observers did not bias estimates of occupancy. Multi-season occupancy models, however, allow for changes in occupancy within a breeding season (MacKenzie et al. 2003). Relaxation of the assumption of population closure under multi-season models provides a more flexible framework for including additional surveys within the sampling season (MacKenzie et al. 2003, Watson et al. 2008).

As expected, there was much more variability among the four observers in the probability of detecting individuals, and the significance of the discrepancy cannot be ignored. Even after extrapolating detection probabilities to four survey occasions for each observer, observer 4 still had estimates of detection considerably lower than did the other observers in the study, potentially leading to biased estimates of GCWA abundance. Logistical constraints often limit the number of repeated surveys that can be conducted (Thompson 2002, MacKenzie and Royle 2005,). Additionally, meeting the assumption of population closure necessary for BMM can also limit the number of survey occasions within a sampling period for which this assumption is reasonable (MacKenzie et al. 2002, Royle 2004). Therefore, to account for greater variation among observers in detection of individuals it may be necessary to include covariates representing observers with significantly lower detection probabilities in models used to estimate population parameters. The ability to incorporate such covariates illustrates the advantage of using a model-based approach to estimate population parameters over the commonly used approach of using count data as an index of relative abundance (MacKenzie et al. 2002, Johnson 2008).

Directly investigating the relationship between detection and population density of passerines is a complicated task, confounded by unknown sources of variability in detection (Bart and Shoulzt 1984, Alldredge et al. 2007). However, my study indicated that site was an important covariate influencing detection of GCWA, both on the species and individual level. The two sites considered in this study had independently estimated high and low population densities; however, it is uncertain if other variables not considered in this analysis (e.g., habitat characteristics) may have contributed to this difference in detection.

I found considerable variation in the degree of observer variability among the two sites with high and low densities of GCWA. My results showed higher variation in the probability of detecting GCWA among the four observers at the low-density site, indicating that observer bias could be especially problematic at low-density sites. Additionally, observer estimates of detecting individuals showed more variability at the low-density site. Therefore, observer differences in detection may be further influenced by an additive effect of population density (Bart and Shouzltz 1984). The results of this study suggest that future research is warranted into the relationship between observer variability in detection and population density. For example, in this system surveying additional sites selected to represent a range of GCWA densities and applying a multiple observer approach would provide information on the functional form of the probability of detection by density relationship within and among observers.

The results of this study also reinforce the view that estimation of probabilities of detection using a model-based approach is the most appropriate way to account for variability in detection (MacKenzie et al. 2002, Alldredge et al. 2007). Furthermore, my results suggest that correcting for the bias introduced by observer variability in detection can be addressed by implementing survey designs that incorporate methods to estimate and mitigate variability in detection among observers (Alldredge et al. 2007). Researchers and managers who rely on point-count surveys conducted by multiple observers to monitor avian populations may want to consider assessing variability in detection among observers as part of a pilot study, prior to the sampling season. Conducting point-count surveys in which all observers simultaneously survey each point allows for the direct evaluation of the degree of observer variability in detection, largely independent of other confounding factors influencing detection. Finally, this study provides additional support to the view that the effects of observer variability can be mitigated by increasing the number of surveys during the sampling season (Thompson 2002, MacKenzie and Royle 2005). Ignoring the issue of observer variability in detection may introduce bias into survey data and result in misleading conclusions regarding population parameters.

CHAPTER II

OCCUPANCY AND ABUNDANCE OF GOLDEN-CHEEKED WARBLERS ON THE BALCONES CANYONLANDS PRESERVE

Introduction

Reliable population estimates, that are unbiased and precise, are essential for making informed management decisions regarding endangered species (MacKenzie and Nichols 2004). Survey techniques used in estimating population parameters must also be feasible given limitations on time, personnel, and resources. Therefore, achieving a balance between obtaining reliable population estimates and developing feasible survey techniques is a fundamental challenge in the design of any wildlife survey method (MacKenzie and Royle 2005).

Estimating abundance, or population size, has long been a parameter of interest in ecological studies (Dice 1941, He and Gaston 2000). Obtaining estimates of abundance is often logistically unfeasible, therefore counts obtained from population surveys are often used as indices of relative abundance (Johnson 2008). Indices can be used to make inferences about abundance across temporal and spatial scales, if the count is the same proportion of the population that is surveyed each sampling occasion.

However, the condition of constant proportionality is rarely met in most field studies (Thompson et al. 2002). Consequently, variation in counts can indicate both variation in actual population size and variation in the detectability of the species. This relationship is described by the equation:

$$C = N * p. \tag{2}$$

Where, C is the recorded count of a species during a survey, N is the true number of individuals in the survey area, and p is the probability of detecting an individual of the species (Johnson 2008). Imperfect detection (i.e. species is present at a sampling unit but is not detected during a survey) leads to variation in p, which confounds the ability of indices to make inferences regarding relative abundance across time and space. Failure to account for imperfect detection may lead to misleading inferences about spatial and temporal population dynamics (MacKenzie et al. 2002). Estimating detection probabilities is thus a necessary step for dealing with imperfect detection in survey design. A conceptual framework of how survey methods account for imperfect detection is illustrated by rearranging equation (2):

$$N = C/p. \tag{3}$$

Although this equation is the basic premise of detectability-adjusted estimators, there are different approaches to estimating p. Capture-recapture techniques, for example, use information from the re-sighting or re-capturing of marked individuals to estimate p (Seber 1982, Williams et al. 2002). However, capture-recapture approaches involve frequent efforts to capture or observe marked animals and the logistics of using this technique on a large spatial scale is not feasible for some species (Royle 2004).

The inherent challenges associated with obtaining detectability-adjusted estimates of abundance have prompted interest in the development of methods for estimating occupancy (MacKenzie et al. 2002). Occupancy is defined as the proportion of surveyed area occupied by a species, and thus is estimated using data regarding the presence or "absence" of a species from a series of sampling units. Methods for occupancy estimation have been refined over the last few decades (Geissler and Fuller 1987, Azuma et al. 1990, MacKenzie et al. 2002, Tyre et al. 2003). MacKenzie et al. (2002) developed a comprehensive model from likelihood based methods that estimates both occupancy and detection probabilities for closed populations. A valuable feature of occupancy models is the ability to incorporate covariates such as habitat type, weather conditions, and time of season that may influence occupancy and detection probabilities (MacKenzie 2005). Occupancy models have an expanding range of applications in ecological studies, including research on species distribution (Ceballos and Ehrlich 2002, Goehring et al. 2007, Karanth et al. 2009), habitat and resource use (MacKenzie 2006, Krishna et al. 2008, Zylstra and Steidl 2009), and metapopulation biology (Moilanen 2002, Hodgson et al. 2009).

The recent advances in survey design for estimating occupancy have also spurred the development of similar approaches for estimating abundance (Royle 2004, Kery et al. 2005). Additionally, the difficulties of implementing capture-recapture techniques on large spatial scales, has lead to interest in developing feasible alternatives to estimating population size. (Kery et al. 2005). Royle (2004) developed binomial mixture models (BMM) that directly estimate abundance and detection probabilities of closed populations using temporally and spatially replicated count data. This class of models assumes that site-specific abundance is governed by some type of prior statistical distribution (e.g. Poisson). The Poisson distribution is often considered as a likely candidate for modeling abundance when the abundance at each sampling unit is assumed to be random across the surveyed area (Royle 2004, Kery et al. 2005, Joseph et al. 2009). The negative binomial and zero inflated distribution have also been applied to modeling abundance using BMM (Wenger and Freeman 2008, Joseph et al. 2009). The mean of the prior distribution, representing the average abundance across all sampling units in the surveyed area, can be estimated by integrating the binomial likelihood of the count data over possible values of abundance for each site (Royle 2004).

Previous studies have demonstrated that BMM generate unbiased estimates of abundance under simulated conditions and can provide ecologically realistic abundance estimates under field conditions (Dodd and Dorazio 2004, Royle 2004, Kery et al. 2005, Wenger and Freeman 2008). This method does not require individual identification of animals during successive surveys and its ability to estimate abundance is not limited by sparse survey data (Royle 2004). Thus the advantages offered by BMM over other abundance estimation techniques suggest that this approach could potentially be a useful tool for monitoring populations at large spatial scales and such use has been strongly advocated (Royle 2004, Kery 2008). Yet, BMM have, for some species, provided biologically unrealistic estimates of abundance with inflated estimates of error (Dodd and Dodd and Dorazio 2004, Kery et al. 2005, Joseph et al. 2008), thus continued reassessment of the reliability of this technique is warranted.

Spot-mapping is an established method used to estimate the territory density of breeding birds by mapping territories within a designated plot (Bibby et al. 1992). This technique has long been considered the standard by which all other avian survey methods are compared (Szaro and Jakle 1982, Verner and Ritter 1988, Verner and Milne 1990, Bibby et al. 1992). However, spot-mapping fails to account for imperfect detection, as does occupancy and BMM; moreover, accurate delineation of territories is a function of sample effort, and delineating territories of individual birds that cannot be uniquely identified can be challenging (Verner and Milne 1990). Additionally, spot-mapping does not provide estimates of error. Nevertheless, comparisons of spot-mapping results to estimates of occupancy and abundance adjusted for imperfect detection demands close scrutiny and under conditions where spot-mapping results are considered robust and reliable, spot-mapping results may be used to test the reliability of established occupancy and abundance estimators.

When evaluating the reliability of survey techniques, one issue to consider is the effect of area surveyed on estimates of population parameters. For logistical reasons, surveys typically only sample a small portion of the area occupied by a population (MacKenzie 2005). Under these circumstances, it is usually of interest to make inferences regarding population parameters at spatial scales larger than the area surveyed. However, abundance estimates can be positively biased when an insufficient amount of area is surveyed, thus estimates of population size may be scale dependent (Jablonski 1976, Franklin et al. 1990, Pettorelli et al. 2009). Occupancy estimates are also scale dependent, given that a larger survey area will likely result in a higher probability of occupancy (MacKenzie et al. 2006). Ignoring the influence of area surveyed may result in population estimates that do not accurately reflect the actual population state.

Herein, I investigated the utility of occupancy and BMM as a feasible and reliable monitoring approach for monitoring the federally endangered golden-cheeked warbler (GCWA, *Dendroica chrysoparia*) by comparing parameter estimates from these models to territory densities estimated using a more labor-intensive spot-mapping method. The golden-cheeked warbler (GCWA) is a Neotropical migrant songbird with a breeding range restricted to central Texas (Pulich 1976). The Balcones Canyonlands Preserve (BCP) is a collection of properties managed for the GCWA and other endangered species (Becker and Koehler 2004). Since 1998, GCWA populations on the BCP have been monitored using the spot-mapping method, which has entailed estimating territory density within 40.5 ha plots at seven locations throughout the preserve. One goal of the BCP is to maintain and increase the GCWA population on the preserve (Becker and Koehler 2004). Effective management of GCWA on this preserve depends on reliable tracking of spatial and temporal variation in population dynamics.

There were four objectives for this study. First, I evaluated potential covariates influencing detection of GCWA. Second, I estimated occupancy at each of the seven BCP plots surveyed and evaluated the influence of spatial scale on estimates of occupancy. Third, I estimated abundance at each BCP plot surveyed using both BMM and by using the equation $C/p = N$. Fourth, we compared my estimates of GCWA abundance with estimates of territory density independently derived from spot-mapping on multiple sites.

Methods

The 5,365- ha BCP consists of a discontinuous collection of properties in Travis County, Texas. The City of Austin (COA) annually monitors GCWA populations on the

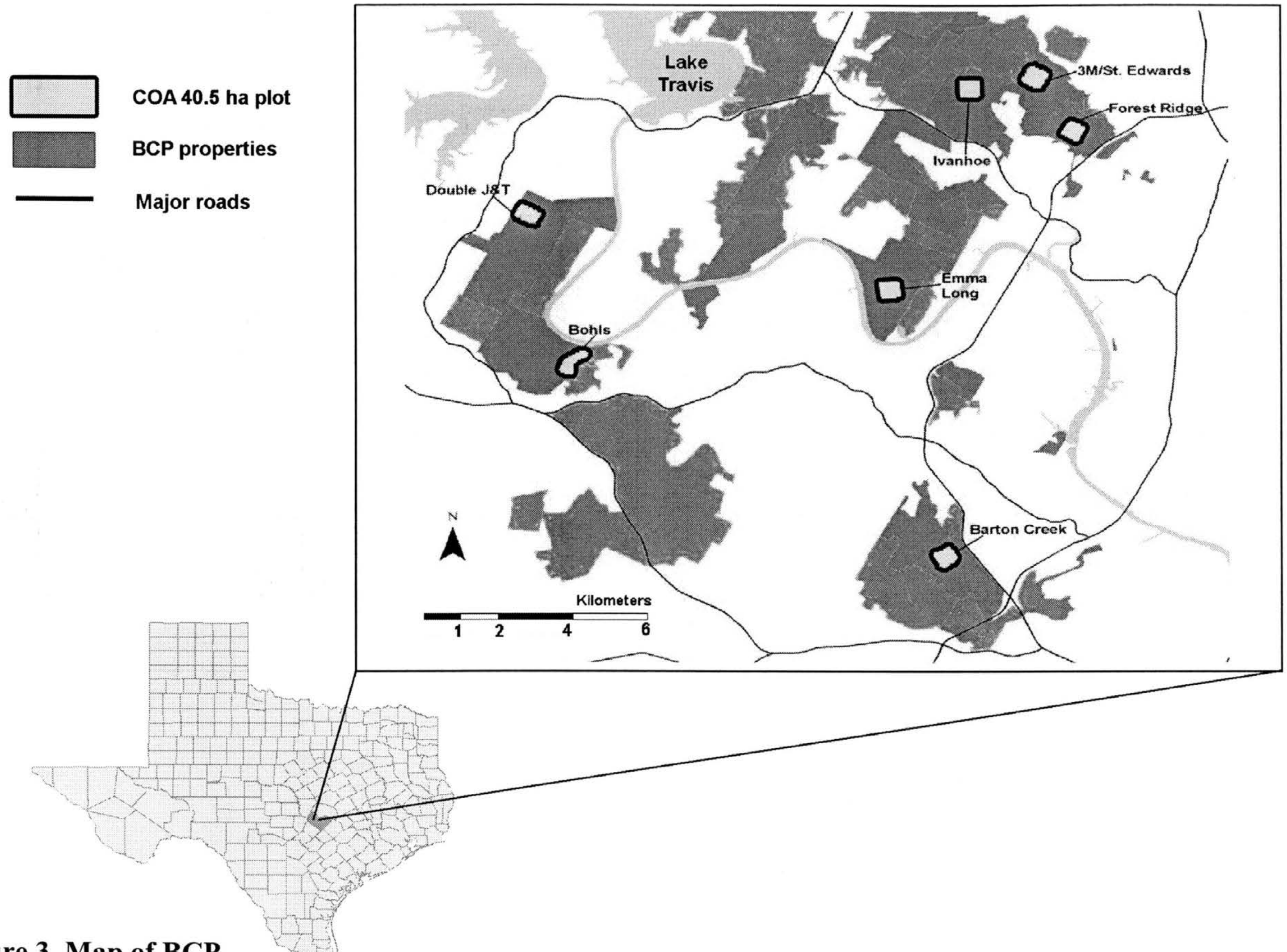

Figure 3. Map of BCP.
Map of the Balcones Cayonlands Preserve in Travis County, Texas. The 40.5 hectare plots used by the City of Austin (COA) for estimating GCWA territory density are indicated.

preserve by conducting spot-mapping surveys on seven different sites (Figure 3). Five of these sites (Ivanhoe, Forest Ridge, St. Edwards, Emma Long, and Barton Creek) are considered areas of prime GCWA habitat, which consists of mature ash-juniper (*Juniperus ashei*) and oak (*Quercus spp.*) forest with at least 75 percent of the area containing more than 70 percent canopy cover (Abbruzzese and Koehler 2002). Two plots (Bohls and Double J&T) were established in transitional GCWA habitat, which was defined as areas with noticeably less than 75 percent prime habitat (Abbruzzese and Koehler 2002). Square-shaped 40.5 ha plots were established on six of theses sites, while a polygon-shaped plot was established on the Bohls plot, due to topography. Territory densities have been estimated annually by the COA on the prime habitat plots and biannually on the transitional plots. Spot-mapping consists of six hour surveys conducted over ten weeks, for a total of 60 hours of survey effort per plot (Becker and Koehler 2004).

On each of these seven sites, a grid consisting of 36 detection stations was established to provide the framework for conducting point-count surveys. Each detection grid encompassed an area of approximately 100 ha and overlaid the 40.5 ha spot-mapping plot on each site. As previous studies indicated that the mean diameter of GCWA territories is 143 m, detection stations were located 200 m apart to insure that detections were independent (Ladd and Glass 1999, DeBoer and Diamond 2006). Point count surveys consisted of an observer recording all GCWA detected by sight or sound during a 5 minute interval at each point. For the purposes of this study, only male GCWA were considered in the subsequent data analysis, although females were noted when detected during the 5 minute intervals at each point. The compass direction of each bird detected was recorded and observers estimated and recorded the distance of the bird from the survey point to one of three categories: immediate proximity (0-20 m), moderate to distant (20-100 m), and far away (>100m). Surveys began shortly after sunrise under appropriate weather conditions for detecting GCWA (U.S. Fish and Wildlife Service 1992). The order in which points 1-36 were surveyed in each grid was reversed for each successive visit to reduce time of day bias. Each site was surveyed approximately weekly, four times from late March to early April, 2008-2009. Five sites were surveyed in both 2008 and 2009 and two sites were surveyed only in 2009.

Survey data were analyzed by means of both single-season occupancy models and BMM using program PRESENCE 2.2 (MacKenzie et al. 2002). Each year was analyzed separately in both types of models. Single-season occupancy models included parameters for occupancy (ψ) and probability (p) of detecting the species (MacKenzie et al. 2002), whereas BMM included parameters for abundance (λ) and probability (p) of detecting individuals (Royle 2004). The abundance parameter λ represents the average number of animals per point, and is used herein to make inferences regarding the number of male GCWA on each 100 ha detection grid.

The essential first step in estimating occupancy or abundance was to determine the covariates that influence detection of GCWA at both the species and the individual level. Covariates of detection considered in this first step of model selection included site, survey week (season), and time of day with a linear relationship (time/linear), or time of day with a quadratic relationship (time /quadratic). Additionally, a covariate for observer was included in the BMM due to previously described significant differences in probability of detecting individuals among the surveyors involved in this study (Figure

2). The covariates site, season, and observer were considered discrete variables, whereas time of day (referring to the minutes after sunrise that a detection was recorded) was considered a continuous variable. I considered both linear and quadratic time of day covariates in model selection because the exact relationship between detection of GCWA and time of day was unknown. Since this first stage of model selection examined only covariates influencing detection, both occupancy and abundance were set as constants. Model selection was conducted using the information-theorectical approach, with Akiaike Information crieterion corrected for small sample size (AIC_c) (Akaike 1973).

The next step of model selection for both single season occupancy models and BMM focused on selecting models to directly estimate occupancy and abundance at each BCP site. Models considered in this analysis included a site covariate for either occupancy or abundance, as well as the covariates for detection selected in the first step of model selection. In cases where multiple models had equally competitive AIC_c values ($\leq$4 AIC_c units) model averaging was used to obtain parameter estimates to account for uncertainty in model selection (Burnham and Anderson 2004).

To evaluate the effect that spatial scale had on estimates of occupancy, I randomly selected contiguous sections for each detection grid, representing the following spatial scales: 25 ha (9 detection stations), 50 ha (18 detection stations), 75 ha (27 detection stations). Occupancy was estimated at each scale using the survey data from the selected stations. The influence of spatial scale on estimates of abundance was not considered in this study due to difficulties encountered using the BMM.

Following inspection of estimates of abundance based on BMM, I developed an alternative estimate of abundance using equation (2). I obtained C by calculating the average number of GCWA detected at each site across the four week sampling period. The estimate of p was obtained from single season occupancy models using survey data only from those survey stations at which GCWA were detected. Thus, for this estimator, occupancy was fixed at 1 (i.e. 100% of detection stations occupied) for each site. When only one individual is available to be detected at each sampling unit, p estimates the probability of detecting individuals (MacKenzie et al. 2002). The results of this study, however, suggested that multiple birds were often available at detection stations. I therefore assumed that detection is positively correlated to GCWA population density at each site, which is a reasonable assumption (Watson et al. 2008). If this is true, then the site covariates used in my models should accommodate the possibility of multiple birds in estimates of detection. Covariates of detection considered in this analysis, as before, included site, season, time/linear, and time/quadratic. Estimates of p for each site were then obtained from models with the smallest AIC_c, and averaged across each day and week.

Finally estimates of abundance from both the BMM and the C/p estimator were compared with territory densities independently estimated in each respective site during 2008 and 2009 at the same time and during the same breeding season. Territory density was initially estimated on 40.5 ha plots, thus comparisons were made to territory densities extrapolated to 100 ha.

Results

Nearly all detections (99%) of GCWA during this study were aurally based. Naïve occupancies (proportion of stations where GCWA were detected) per site ranged from 0.43 (Bohls) to 1.0 (Ivanhoe and St. Edwards) in 2008 and 0.45 (Bohls) to 1.0 (Emma Long, Barton Creek, Ivanhoe) in 2009. Among both years there were 5 sites with an occupancy of 1.0 (i.e. 100% of the stations occupied by GCWA). Among stations where GCWA were detected, the majority of stations had ≥2 individuals detected across the four week sampling season (Figure 4). An analysis of the distribution of detections as a function of distance, revealed that most detections (88 % in 2008 and 87% in 2009) were estimated by surveyors as being within 20 to 100 meters from the survey point (Figure 5).

Model selection examining covariates of detection indicated two equally competitive single-season occupancy models in each year that were superior to all other candidate models considered in this analysis (Table 3). Both models contained site and season covariates for detection, while one model contained the covariate time/linear and the other contained time/quadratic. These results indicate that the probability of detecting GCWA is influenced by time of day, time of season, and site. I found differences in detection probabilities among the seven sites in each year ranging from 0.29 to 0.81 in 2008 and 0.19 to 0.70 in 2009 (Figure 6). Furthermore, detection probabilities for each site were consistent across the two years and the ranking of order among sites (from lowest to highest probabilities) was identical in each year, indicating that the estimation of detection probabilities accurately accounted for important covariates influencing detection of GCWA. Seasonal variation in detection showed a consistent pattern among all sites with the first survey week each year having the highest detection probabilities and detection probabilities declining consistently across the four week sampling period

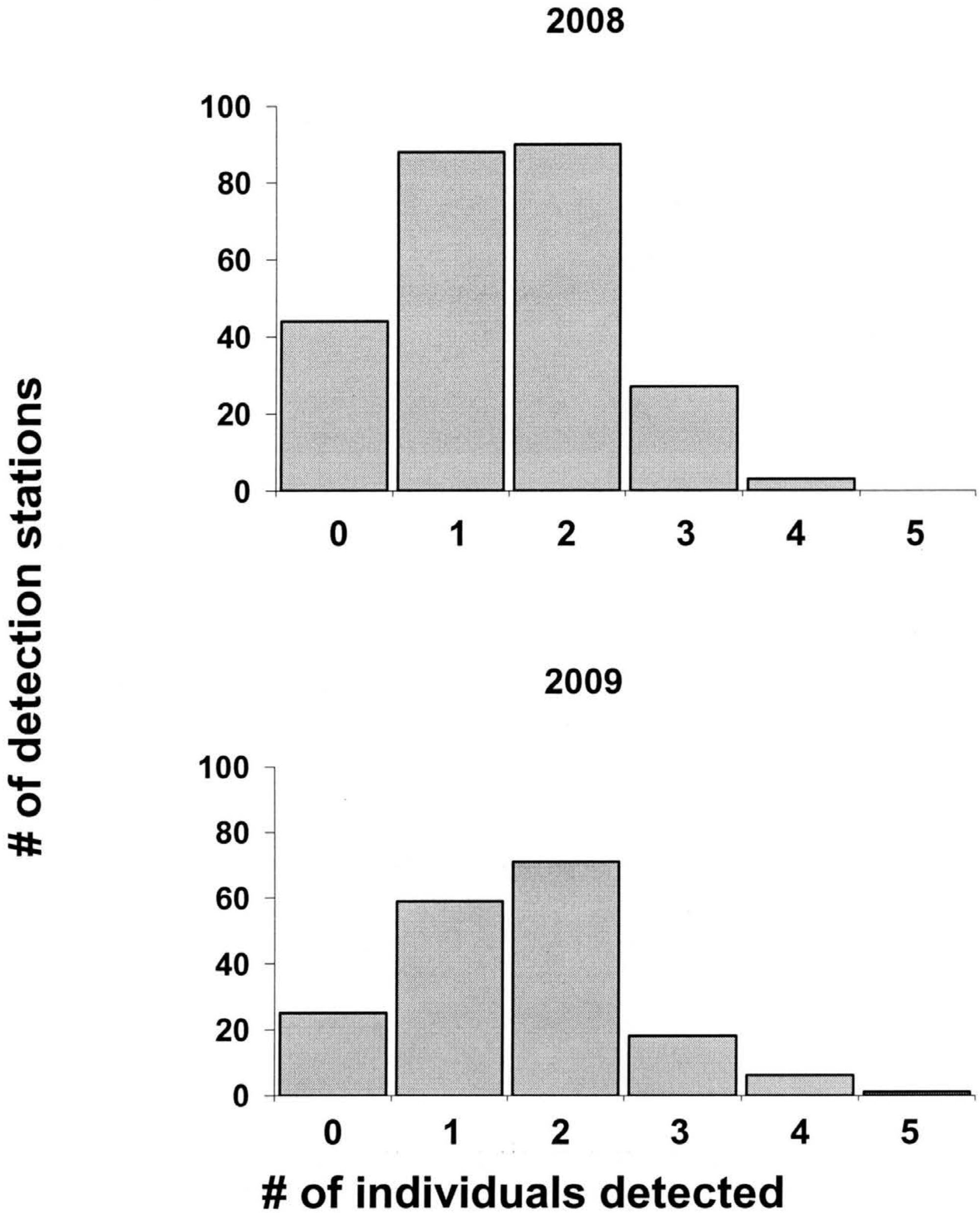

Figure 4. Number of GCWA Detected.
The maximum number of GCWA individuals detected across the four week sampling period for detection stations across all sites, in both 2008 and 2009. The number of individuals detected per station ranged from 0 to 5.

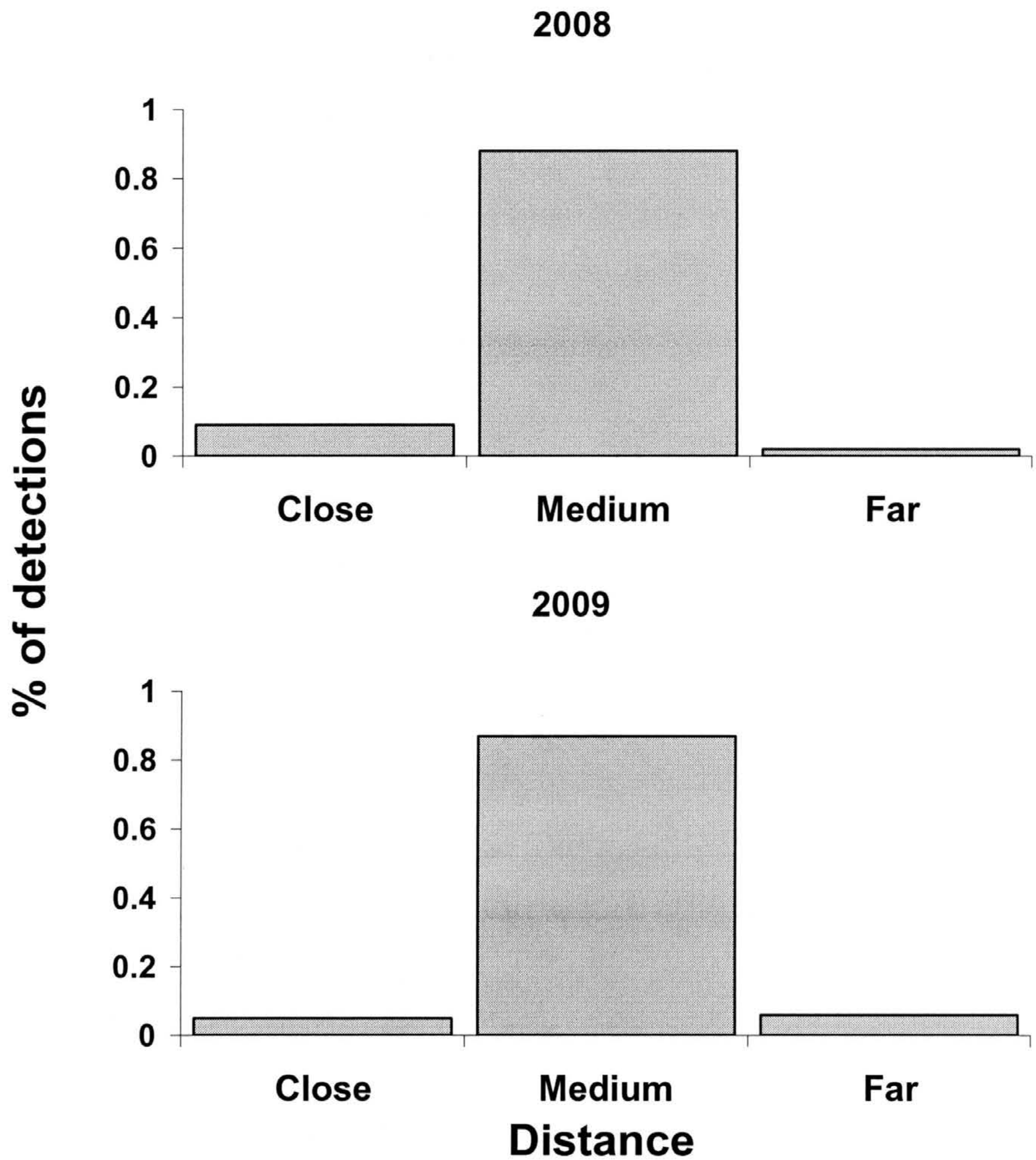

Figure 5. Detection Distances.
The percentage of total detections across all sites, in both 2008 and 2009, as a function of distance from the survey point. The distance of each GCWA detected as estimated by surveyors into one of three categories: 0-20 m (Close), 20-100 m (Medium), >100m (Far). The total number of detections were 623 and 722 for 2008 and 2009, respectively.

Table 3. Model Selection Summary (Covariates of Detection).
Summary of model selection for the single-season occupancy models in 2008 and 2009, showing covariates influencing the probability of detecting GCWA. Parameters estimated in these models were occupancy (ψ) and probability of detection (p). Covariates examined included site, season, time of day with a linear effect (time/linear) and time of day with a quadratic effect (time/quadratic), and no influence of a covariate (.). Model selection statistics presented are Akaike information criterion value corrected for small sample size (AIC$_c$), AIC$_c$ weight (w), number of parameters (N. par.) and twice the log likelihood (-2 LL). Sample sizes (number of point-count surveys across all sites) were 180 and 252 for 2008 and 2009, respectively. Selected models are indicated in bold font.

	2008				2009			
Model	AIC$_c$	w	N. par.	-2LL	AIC$_c$	w	N. par.	-2LL
ψ (.) p(site, season, time/quadratic)	**835.61**	**0.573**	**8**	**818.77**	**1204.62**	**0.436**	**10**	**1183.71**
ψ (.) p(site, season, time/linear)	**836.20**	**0.428**	**8**	**819.36**	**1204.13**	**0.557**	**10**	**1183.22**
ψ (.) p(site, season)	855.65	<0.001	7	841.00	1216.71	<0.001	9	1197.97
ψ (.) p(site, time/quadratic)	856.42	<0.001	7	841.77	1214.83	<0.001	9	1196.09
ψ (.) p(site, time/linear)	857.29	<0.001	7	842.64	1214.35	<0.001	9	1195.61
ψ (.) p(site)	875.59	<0.001	6	863.10	1226.80	<0.001	8	1210.21
ψ (.) p(.)	909.44	<0.001	2	905.37	1325.66	<0.001	2	1321.61

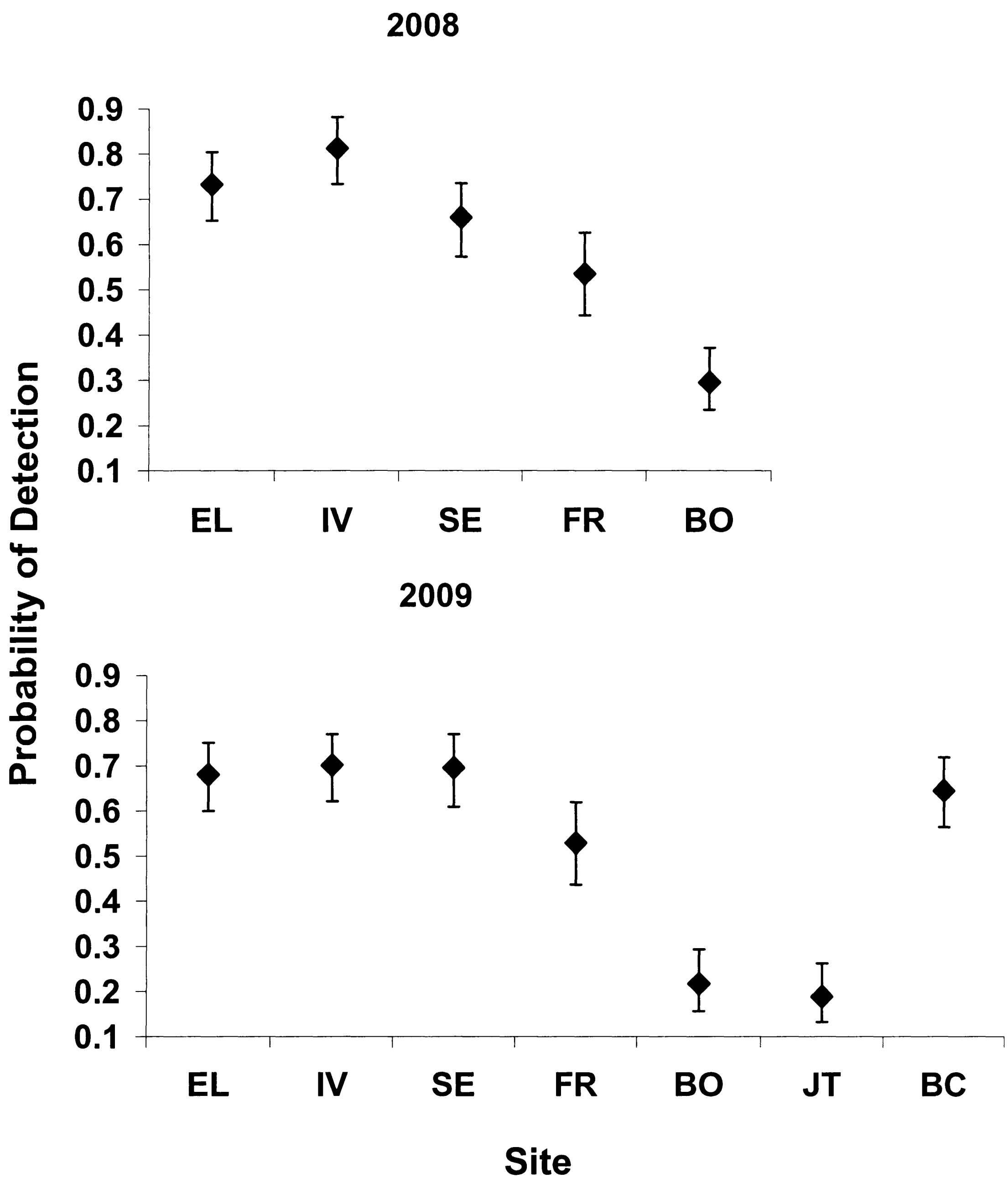

Figure 6. Detection Probabilities per Site.
Average probabilities of detection among the four week sampling period for each site in 2008 and 2009. Error bars represent 95% CI.

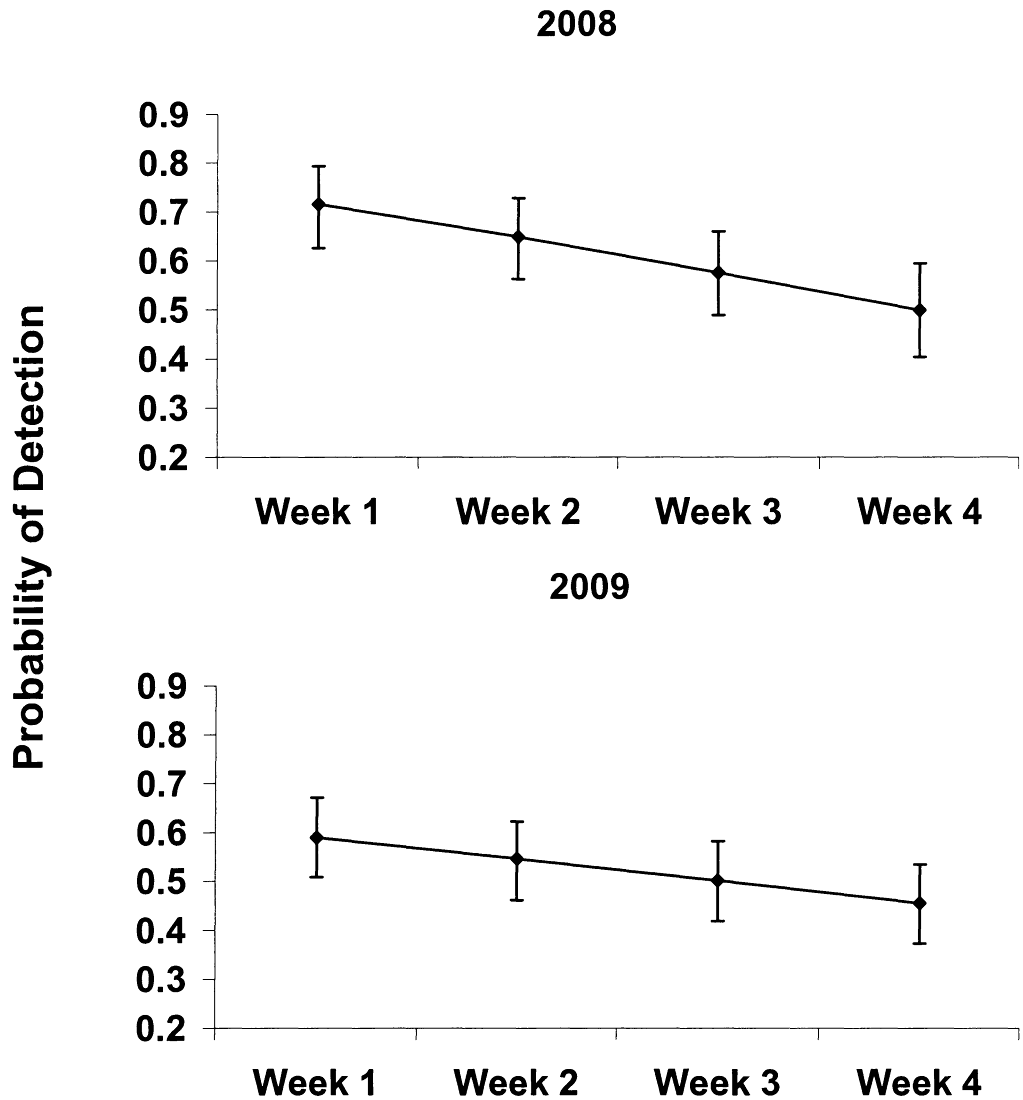

Figure 7. Detection Probabilities per Week.
Average detection probability of GCWA for all sites across the four week sampling season in 2008 and 2009. Error bars represent 95% CI.

(Figure 7). Although this pattern was evident in both years, detection probabilities for each week in 2008 were comparatively higher than estimates in 2009. Both time of day covariates (linear, quadratic) revealed that the probability of detecting GCWA gradually declined throughout a day (Figure 8).

Two single-season occupancy models containing the selected covariates of detection as well as a site covariate for the occupancy parameter ψ were equally competitive in both 2008 and 2009 (Table 4). The inclusion of a site covariate for ψ produced models that fit the survey data better (i.e. smaller AIC_c values) relative to models where ψ was set as a constant, indicating that estimates of occupancy were strongly influenced by site (Table 5). Model-averaged estimates of occupancy adjusted for imperfect detection for each site ranged from 0.48 (Bohls) to 1.0 (Ivanhoe and St. Edwards) in 2008 and 0.52 (Bohls) to 1.0 (Emma Long, Barton Creek, Ivanhoe) in 2009 (Figure 9). With the exception of sites with $\psi = 1$, occupancy estimates from the single-season models were higher than naïve occupancy at each site. For the five sites surveyed in both years, estimates of occupancy did not differ significantly between years.

Estimates of occupancy (± 95% CI) at smaller spatial scales within the detection grids suggested that there were no substantial differences in estimating occupancy at spatial scales ranging from 25 to 100 ha (Figure 10). At sites with lower occupancy estimates based on the 100 ha scale (Bohls and Double J&T), there appeared to be more variation at smaller scales, however 95 % CI for these estimates were large and overlapping indicating that there were no substantial differences in estimates even at these low density sites.

Model selection for the BMM, containing potential covariates influencing detection of GCWA individuals, revealed four models in each year which were equally competitive (Table 6). All four models included covariates for site, season, and either the time/linear or time/quadratic, and two models included an observer covariate. Since each of the four models were equally competitive in model selection, we concluded that each combination of covariates represented in these models strongly influenced detection of GCWA on the individual-level. The subsequent inclusion of a site covariate for the abundance parameter λ in BMM containing these four combinations of covariates of influencing detection of individuals, once again led to each model being equally competitive in both years (Table 7). Additionally, models including a site covariate for abundance fit the survey data better (i.e. smaller AIC_c) relative to models where abundance was set to be constant, indicating that estimates of abundance were strongly influenced by site (Table 8). Model-averaged estimates of λ per site, which for this study represented the average number of male GCWA per point, ranged from 1.2 (Bohls) to 3.6 (Ivanhoe) in 2008 and 2.2 (Double J&T) to3.6 (Ivanhoe) in 2009. Estimates of λ extrapolated across all 36 points per site (λ multiplied 36) revealed estimates of the total number of male GCWA for each 100 ha site, and rounded to the nearest whole number, these estimates ranged from 64 (Bohls) to 142 (Ivanhoe) in 2008 and 96 (Double J&T) to 225 (Ivanhoe and St. Edwards) in 2009 (Figure 11). Although the ranking of the sites, from lowest to highest abundance, was consistent between years, estimates were considerably higher in 2009. Estimates of error, represented by 95 % CI, were very large for these abundance estimates, especially in 2009, when the upper limit of the CI extended to at least 700 for five sites (EL, IV, SE, FR, BC).

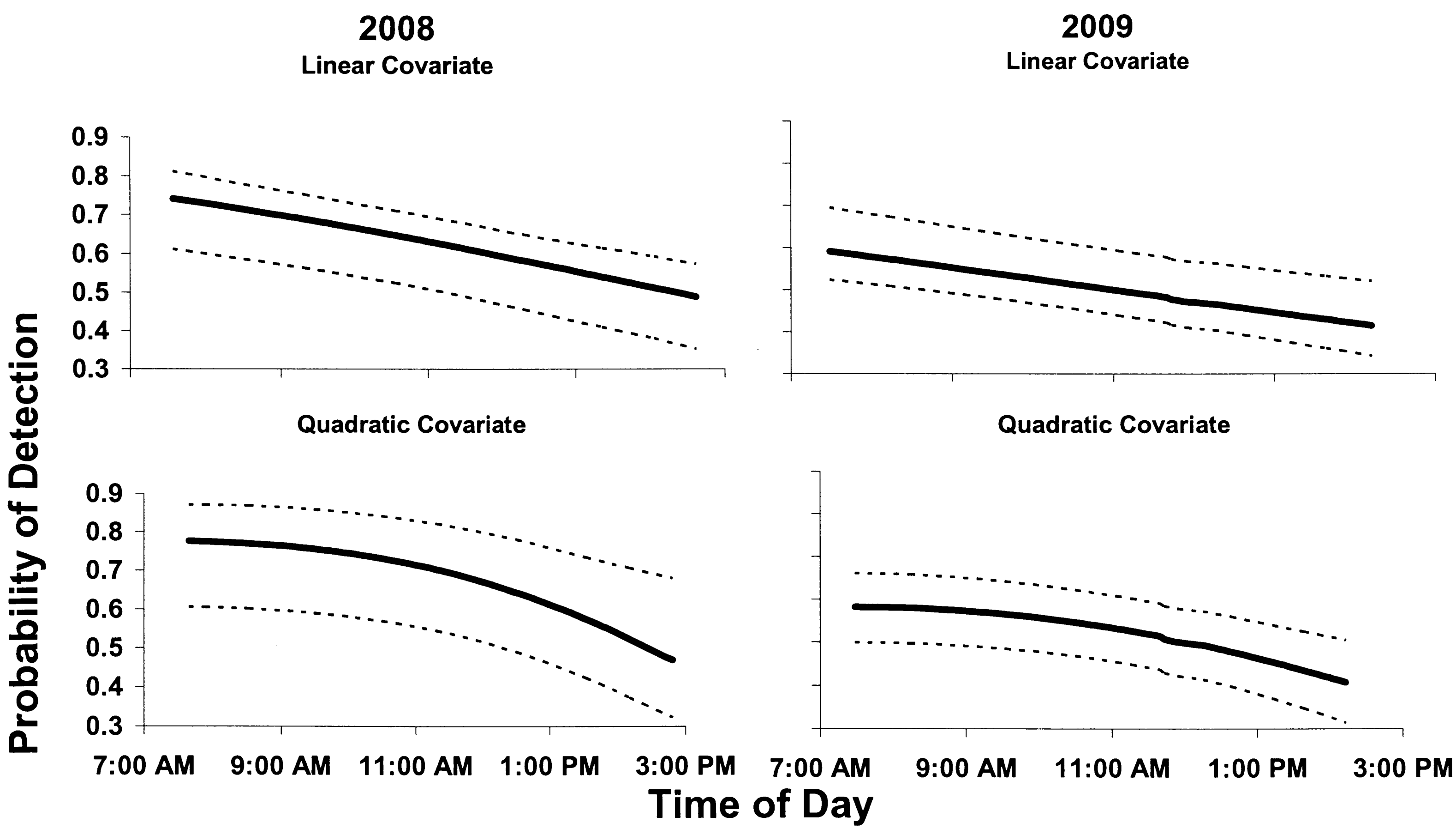

Figure 8. Detection Probabilities for Single Survey.
Detection probabilities of GCWA over the course of a single survey among all sites in 2008 and 2009. Both the linear and quadratic time of day covariates are shown. The solid line represents the probability of detection, while the dotted lines represent the upper and lower limits of the 95% CI.

Table 4. Model Selection Summary (Estimating ψ).
Summary of model selection for the single-season occupancy models in 2008 and 2009, showing selected covariates for probability of detection (p) and a site covariate for occupancy (ψ).

	2008				2009			
Model	AIC_c	w	N. par.	-2LL	AIC_c	w	N. par.	-2LL
ψ (site) p (site, season, time/quadratic)	**805.09**	**0.633**	**12**	**779.14**	**1192.79**	**0.625**	**16**	**1158.47**
ψ (site) p (site, season, time/linear)	**806.10**	**0.367**	**12**	**780.23**	**1193.81**	**0.375**	**16**	**1159.49**

Table 5. Model Selection Summary (Inclusion of Site Covariate).
Summary of model selection comparing single-season occupancy models with and without site covariates for occupancy (ψ) in 2008 and 2009. Selected models are indicated in bold font.

	2008				2009			
Model	AIC_c	w	N. par.	-2LL	AIC_c	w	N. par.	-2LL
ψ (site) p(site, season, time/quadratic)	**805.09**	**0.633**	**12**	**779.14**	**1192.79**	**0.625**	**16**	**1158.47**
ψ (site) p(site, season, time/linear)	**806.10**	**0.367**	**12**	**780.23**	**1193.81**	**0.375**	**16**	**1159.49**
ψ (.) p(site, season, time/quadratic)	835.61	<0.001	8	818.77	1204.62	<0.001	10	1183.71
ψ (.) p(site, season, time/linear)	836.20	<0.001	8	819.36	1204.13	<0.001	10	1183.22

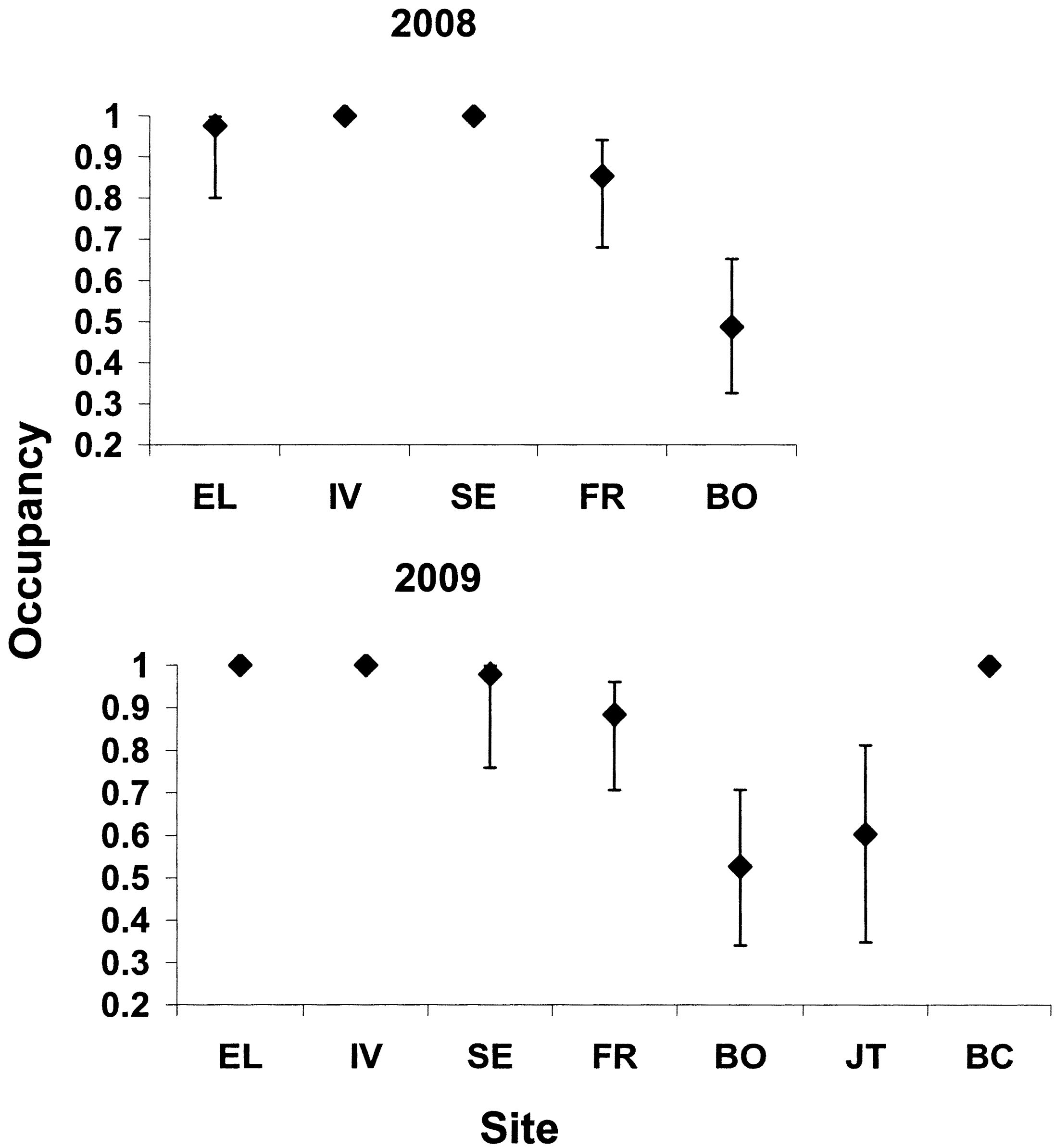

Figure 9. Estimates of Occupancy.
Estimates of occupancy (proportion of 36 stations occupied by ≥1 GCWA) for each site surveyed in 2008 and 2009. Error bars represent 95% CI and are indicated only for sites with $\psi \neq 1$.

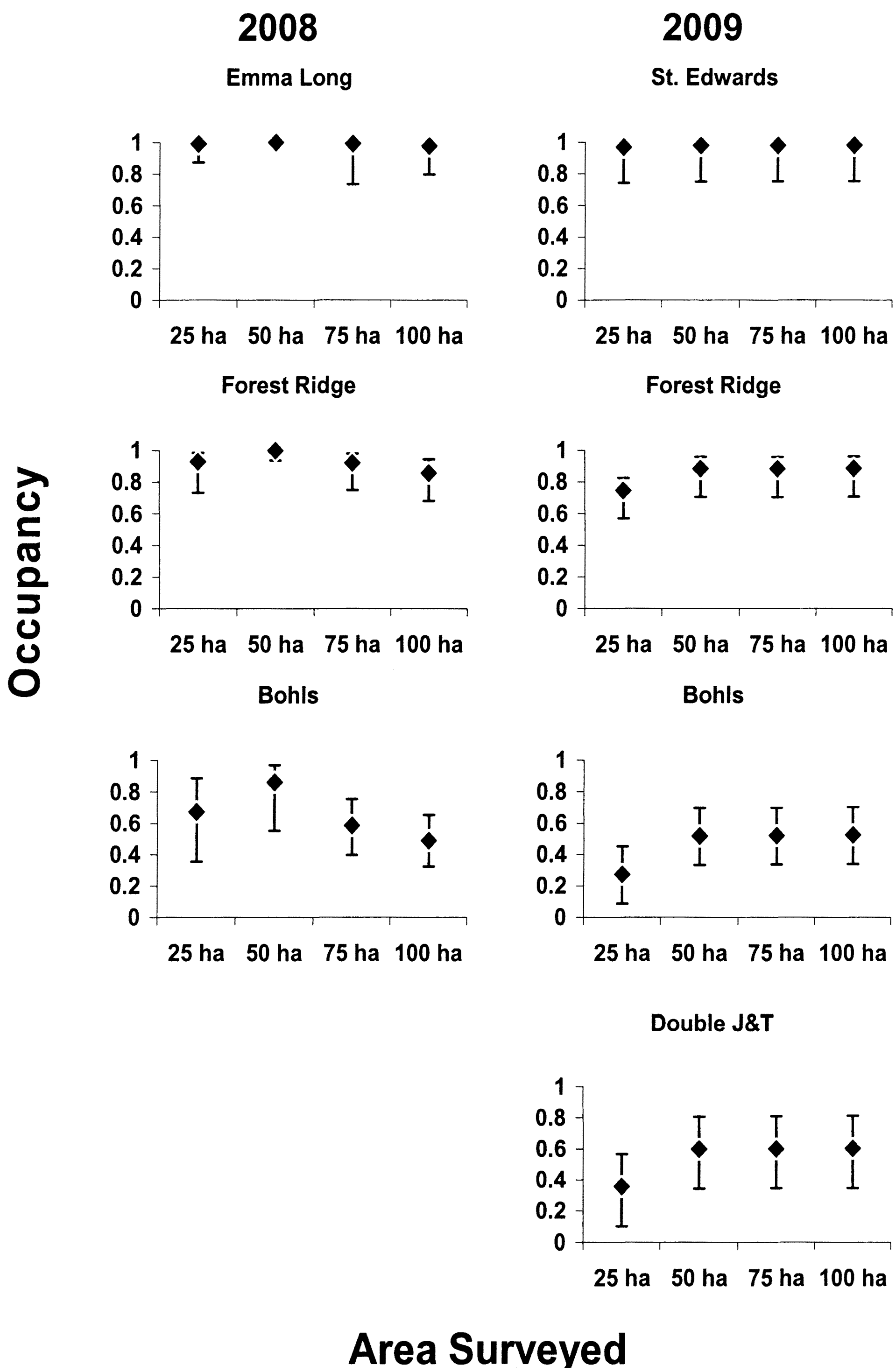

Figure 10. Estimates of Occupancy and Spatial Scale.
Estimates of occupancy for each site at different spatial scales in 2008 and 2009. Error bars represent 95% CI. Two sites in 2008 (IV and SE) and three sites in 2009 (IV, EL, and BC) are excluded due to naïve occupancy estimates of 1 at 100 ha, which negates any potential variability at the smaller spatial scales.

A comparison between BMM estimates of abundance to territory densities estimated from spot-mapping revealed a large discrepancy in the number of male GCWA estimated at each 100 ha site. Spot-mapping estimates of the number of GCWA territories per 100 ha site ranged from 7 (Bohls) to 54 (Ivanhoe) in 2008 and from 6 (Double J&T) to 44 (Ivanhoe and St. Edwards) in 2009 (Figure 11). The ranking of the sites, from lowest to highest number of territories, is consistent with ranking estimates of abundance from the BMM; however, BMM estimates of abundance were on average four and six times higher than territory density in 2008 and 2009, respectively. In most cases, the degree of discrepancy between abundance and territory density was greatest at the low density sites and smallest at the higher density sites. This pattern was evident in both years, with the only exception being Barton Creek (BC) in 2009, which showed the greatest discrepancy among all sites, despite being ranked among the higher density sites. Both the disparity with territory density and inflated 95 % CI, led me to conclude that the BMM estimates of GCWA abundance were biologically unrealistic for each of these sites.

The alternative abundance estimator, using the equation C/p, provided reasonable estimates of GCWA abundance for each site. The average number of GCWA detected during each survey of 36 detections stations (C) varied among sites, ranging from 12 (Bohls) to 39 (Ivanhoe) in 2008 and from 8 (Double J&T) to 38 (Ivanhoe) in 2009. Model selection for the single-season occupancy models fixed at 1.0, resulted in two models competitively superior in both years, each containing the same covariates of p selected in modeling detection probabilities (Table 3). Model-averaged estimates of p were obtained from these two models and subsequently used in the C/p estimator.

Table 6. Model Selection Summary (Covariates of Detection).
Summary of model selection for the binomial mixture models in 2008 and 2009, showing covariates influencing the probability of detecting GCWA individuals. Parameters estimated in these models were abundance (λ) and probability of detection for individuals (p). Covariates examined included site, season, observer, time of day with a linear effect (time/linear) and time of day with a quadratic effect (time/quadratic), and no influence of a covariate (.). Model selection statistics presented are Akaike information criterion value corrected for small sample size (AIC_c), AIC_c weight (w), number of parameters (N. par.) and twice the log likelihood (-2 LL). Sample sizes were 180 and 252 for 2008 and 2009, respectively. Selected models are indicated in bold font.

	2008				2009			
Model	AIC_c	w	N. par.	-2LL	AIC_c	w	N. par.	-2LL
λ (.) p(site, season, time/linear)	**1577.07**	**0.401**	**8**	**1560.23**	**2045.84**	**0.289**	**10**	**2024.54**
λ (.) p(site, season, time/quadratic)	**1577.34**	**0.351**	**8**	**1560.50**	**2044.88**	**0.467**	**10**	**2023.58**
λ (.) p(site, season, time/linear, observer)	**1579.29**	**0.132**	**9**	**1560.23**	**2048.11**	**0.093**	**11**	**2024.54**
λ (.) p(site, season, time/quadratic, observer)	**1579.56**	**0.116**	**9**	**1560.50**	**2047.15**	**0.150**	**11**	**2023.58**
λ (.) p(site, time/quadratic)	1598.99	<0.001	7	1584.34	2058.30	<0.001	9	2039.24
λ (.) p(site, time/linear)	1599.19	<0.001	7	1584.54	2059.37	<0.001	9	2040.31
λ (.) p(site, season)	1601.12	<0.001	7	1586.47	2058.39	<0.001	9	2039.33
λ (.) p(site)	1621.75	<0.001	6	1609.26	2074.64	<0.001	8	2057.80
λ (.) p(site, observer)	1623.91	<0.001	3	1659.27	2076.86	<0.001	9	2057.80
λ (.) p(observer)	1665.41	<0.001	3	1659.27	2183.51	<0.001	3	2177 37
λ (.) p(.)	1669.89	<0.001	2	1665.82	2181.92	<0.001	2	2177.85

Table 7. Model Selection Summary (Estimating λ).
Summary of model selection for the binomial mixture models in 2008 and 2009, showing selected covariates for probability of detection for individuals (p) and a site covariate for abundance (λ).

	2008				2009			
Model	AIC_c	w	N. par.	-2LL	AIC_c	w	N. par.	-2LL
λ (site) p(site, season, time/quadratic)	**1568.98**	**0.336**	**8**	**1552.14**	**2039.45**	**0.391**	**10**	**2018.15**
λ (site) p(site, season, time/quadratic, observer)	**1569.21**	**0.300**	**8**	**1552.37**	**2045.84**	**0.225**	**11**	**2016.99**
λ (site) p(site, season, time/linear)	**1570.11**	**0.191**	**9**	**1551.05**	**2040.40**	**0.243**	**10**	**2019.10**
λ (site) p(site, season, time/linear, observer)	**1570.32**	**0.172**	**9**	**1551.26**	**2041.49**	**0.141**	**11**	**2017.92**

Table 8. Model Selection Summary (Inclusion of Site Covariate).
Summary of model selection comparing binomial mixture models with and without site covariates for abundance (λ) in 2008 and 2009

	2008				2009			
Model	AIC_c	w	N. par.	-2LL	AIC_c	w	N. par.	-2LL
λ (site) p(site, season, time/quadratic)	**1568.98**	**0.336**	**8**	**1552.14**	**2039.45**	**0.391**	**10**	**2018.15**
λ (site) p(site, season, time/quadratic, observer)	**1569.21**	**0.300**	**8**	**1552.37**	**2045.84**	**0.225**	**11**	**2016.99**
λ (site) p(site, season, time/linear)	**1570.11**	**0.191**	**9**	**1551.05**	**2040.40**	**0.243**	**10**	**2019.10**
λ (site) p(site, season, time/linear, observer)	**1570.32**	**0.172**	**9**	**1551.26**	**2041.49**	**0.141**	**11**	**2017.92**
λ (.) p(site, season, time/linear)	1577.07	<0.001	8	1560.23	2045.84	<0.001	10	2024.54
λ (.) p(site, season, time/quadratic)	1577.34	<0.001	8	1560.50	2044.88	<0.001	10	2023.58
λ (.) p(site, observer, season, time/linear)	1579.29	<0.001	9	1560.23	2048.11	<0.001	11	2024.54
λ (.) p(site, observer, season, time/quadratic)	1579.56	<0.001	9	1560.50	2047.15	<0.001	11	2023.58

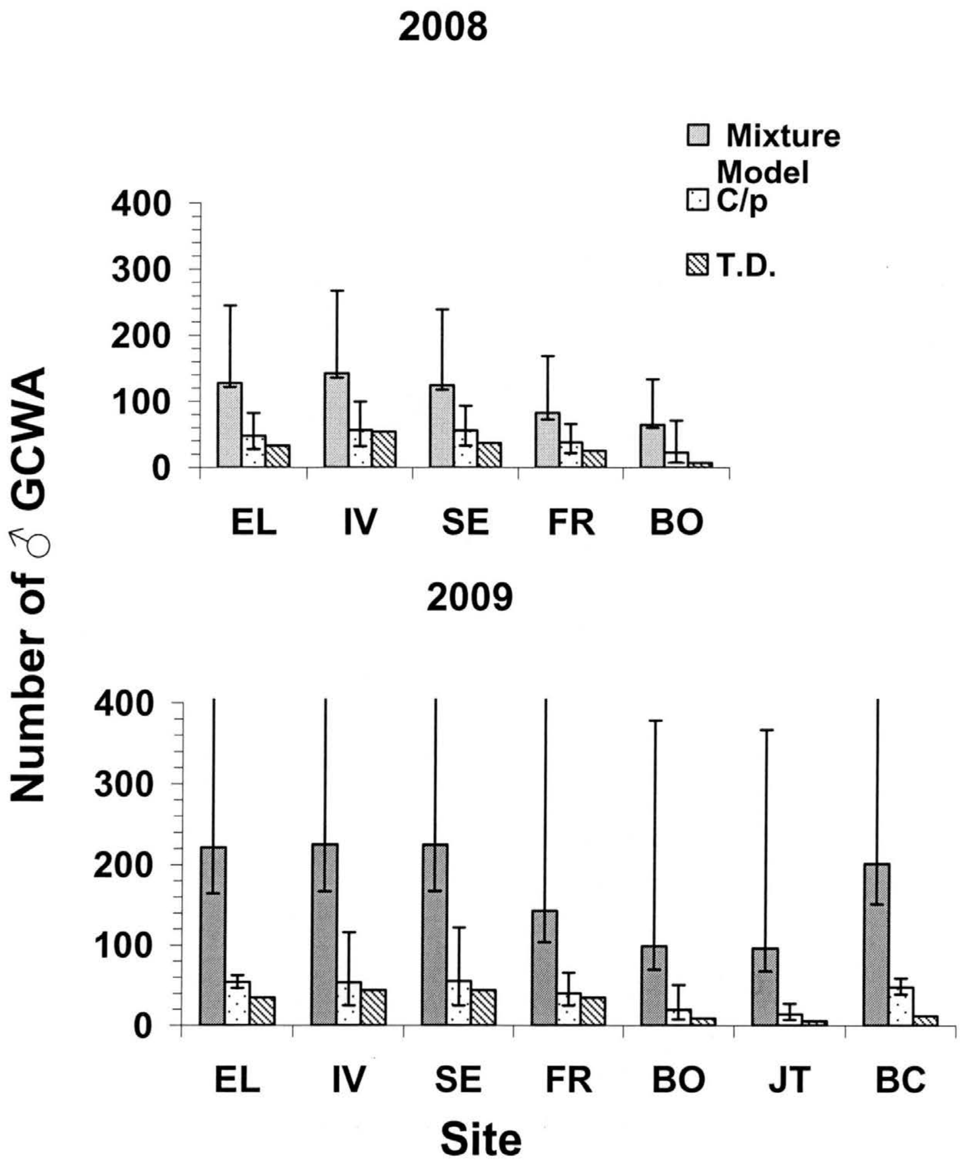

Figure 11. Estimates of Abundance.

Estimates of number of male GCWA per 100 hectares for each of five sites in 2008 and seven sites in 2009, inferred from binomial mixture models, C/p estimator, and territory density assessed by spot-mapping. Error bars represent 95% CI. The upper limits of confidence intervals in 2009 extended to at least 700 for five sites (EL, IV, SE, FR, BC) in 2009.

Estimates of abundance using the C/p estimator were significantly lower than the BMM's estimates and also had smaller 95 % CI (Figure 11). These abundance estimates ranged from 23 to 56 in 2008 and 16 to 58 in 2009. In most cases, the lower limit of the 95 %CI, included the territory density estimated at each site. Among both years there were four sites with a C/p estimate that was significantly higher than territory density.

Discussion

This study demonstrates that using point-count surveys in conjunction with a model-based approach that estimates population parameters adjusted for imperfect detection is a reliable and feasible approach to monitoring GCWA. The spot-mapping method, while considered the most reliable of avian survey techniques for estimating density of breeding birds (Szaro and Jakle 1982, Verner and Ritter 1988, Verner and Milne 1990, Bibby et al. 1992), is limited by its labor-intensive approach in the amount of area that can be surveyed. Spot-mapping plots typically do not exceed 40 ha in size, thus restricting the area at which density can be estimated (Bibby et al. 1992). The study design for this project allowed for a much larger area to be surveyed (100 ha) by collecting survey data using the point count method. Furthermore, considerably less time was required to conduct point count surveys (four weeks) compared to spot-mapping (ten weeks). Abundance estimated from point count data that incorporated a novel approach to estimating p, provided estimates that were largely in agreement with territory densities obtained from the spot-mapping method. The agreement between the C/p estimator and spot-mapping suggests that using a model-based approach to estimating abundance is a reliable technique for monitoring GCWA. When spot-mapping is relied upon as a means of monitoring avian populations, I advocate, based on the results of this study, that a more efficient monitoring approach that estimates detectability-adjusted population parameters based on point count data be considered as a feasible alternative.

I found that detection probabilities varied among sites, and showed temporal variation across the day and during the survey season. The sources of variability in detection among sites was not directly investigated in this study. Although there were habitat differences among the sites, prior research indicates that detection of GCWA is not greatly influenced by variation in habitat characteristics (Watson et al. 2008). One possible explanation for the variability among sites in this study is that population density is influencing probabilities of detection. Detection probabilities for each site ranged from 0.18 to 0.70, and the order of ranking from lowest to highest also coincides with the order of ranking for site abundance. This pattern suggests a possible correlation between population density and detection, and future studies should directly investigate this relationship and its implications on avian survey design.

Estimates of occupancy showed no significant differences among the spatial scales considered (25 ha -100 ha). This indicates that a study area within this size range would be sufficient for obtaining reliable estimates of occupancy. Investigating the influence of spatial scale on estimates of abundance was prohibited due to the failure of the BMM in providing reliable estimates. Additionally, spatial scale was not evaluated for the C/p estimator because survey data was already truncated (i.e. discounted stations where birds were not detected) to obtain an estimate of detecting individuals, thus removing additional stations would have been problematic, especially for sites with few detections. For territorial species like GCWA, however, occupancy and abundance should be strongly correlated, thus conclusions regarding the influence of spatial scale on occupancy would also give insight into estimating abundance (He and Gaston 2000). The results of this analysis indicate that a study area as small as 25 ha would provide reliable estimates of occupancy; however, an area of this size would severely restrict the number of independent sampling units for avian point count surveys (Hutto et al. 1986). Additionally, surveying over a larger area, when logistically feasible, provides more survey data and thus improves precision of population estimates (MacKenzie et al. 2006).

My estimates of GCWA abundance from BMM consistently exceeded territory densities estimated on these same plots by independent researchers using spot-mapping techniques and were on average five times higher than territory densities among both years (Figure 11). Moreover, the degree of difference between BMM estimates and territory density varied among sites, with the greatest discrepancies noted at the lowest density sites. Estimates of abundance from BMM's were not only significantly higher than the COA's territory density estimates, but also exceeded the upper limit of observed GCWA territory density (63 territories/100 ha) found by other researchers throughout central Texas (Wahl et al. 1990). Thus, I concluded that my estimates of abundance were ecologically unrealistic.

The limited application of BMM in published studies has revealed this technique can generate reliable estimates under simulated conditions, and in some cases provide reasonable estimates of abundance for some species (Dodd and Dorazio 2004, Royle 2004, Kery et al. 2005, Wenger and Freeman 2008). However, the ability of BMM to provide unbiased estimates of abundance under field conditions is difficult to assess when there is no available information on the true population size (Royle 2004, Kery et al. 2005). To date, only one additional study compares BMM estimates of abundance to independently derived estimates of territory density obtained from spot-mapping (Kery et al. 2005). Kery et al. (2005) compared BMM estimates to territory densities for eight avian species and found that the abundance estimates from this model were higher than estimates based on territory mapping. Most of the species considered in that study had abundance estimates that were about twice as high as territory density, while one species had an abundance estimate that was 8.9 times greater than territory density. Determining the source of bias in discrepancies of this magnitude requires a close examination of the assumptions inherent in both of these sampling approaches.

There are a number of possibilities to explain the large discrepancy between the BMM estimates and territory density estimates based on spot-mapping. For the purposes of this study territory densities obtained from spot-mapping were used as a base line comparison to evaluate the reliability of detectability-adjusted estimates of abundance obtained from point count data. Estimates of abundance based on point count data may be biased high, compared to spot-mapping, due to systematic detection of birds outside the 100 ha grid when surveyors are on points along the perimeter of the detection grid. Thus, when territory density is extrapolated to 100 ha, there is certainly some inherent bias in the study design for estimates of abundance to be higher than territory density. However, the degree of overestimation by the BMM suggests that one or more assumptions of this model may have been violated, thus leading to biased estimates of abundance.

A fundamental assumption of BMM is that the population within the surveyed area is closed during the total sampling season (Royle 2004). I choose a survey season of four weeks, lasting from late March to early April, to coincide with the beginning of the

GCWA breeding season. Population closure for a period of four weeks during this time of year is likely to be met for this species (Watson et al. 2008). The assumption that the distribution of the population across the surveyed area fits some prior statistical distribution is difficult to assess in this study. Estimates from BMM and their associated estimates of error appear to be sensitive to the type of statistical distribution used to model the population's spatial distribution (Kery et al. 2005, Joseph et al. 2009). I choose to model abundance using the Poisson distribution, which assumes that the true abundance at each point is random, and independent of the number of individuals at any other point (Kery et al. 2005). Independence between survey points is likely to be met for this species when points are at least 200 m apart (Ladd and Glass 1999, DeBoer and Diamond 2006, Watson et al. 2008). Additionally, survey data from our study suggests that the majority of birds were detected within 100 m of each point (Figure 5). However, considering the variability in both population density and territory size of individual males noted for this species across its range, it is unclear if the Poisson distribution is an appropriate assumption for the GCWA (Ladd and Glass 1999, Wahl et al. 1990). The negative binomial distribution has also been considered for modeling abundance, and is appropriate when there is significant variation in parameter estimates (Wegner and Freeman 2008). Yet, several studies have demonstrated the negative binomial distribution often results in not only poorer fit to survey data (i.e. larger AIC) compared to models with Poisson distribution, but unreasonable estimates of abundance with inflated error estimates as well (Wenger and Freeman 2008, Joseph et al. 2009). The zero-inflated variants of both the Poisson and negative binomial BMM show great potential, in that these models simultaneously estimate probability of detection, abundance, and occupancy (Joseph et al. 2009). While, these models appear to be appropriate for data sets that are truly “zero-inflated”, my GCWA survey data contained numerous detections, often involving multiple individuals, thus the zero-inflated distribution was likely not a strong candidate for modeling abundance for this study. Additionally, failure of BMM could also be due to the absence of ecological covariates that influence local abundance within the population (Royle 2004, Joseph et al. 2009). Models not containing such covariates would be unlikely to account for heterogeneity in count data resulting from ecologically mechanisms, such as habitat characteristics (Royle 2004). While I did not directly include habitat as a covariate for abundance in my analysis, the site covariates considered in these models reflected a broad range of habitat features.

The alternative approach used in this study to estimate GCWA abundance using the C/p estimator provided lower estimates of abundance, with smaller 95% CI. This estimator, unlike BMM, is not constrained by the assumption regarding the population’s spatial distribution. However, obtaining an estimate of the probability of detecting individuals from fixed occupancy models assumes that only one individual is available to be detected at each survey point. There was a clear violation of this assumption, in that most of the points surveyed in each year had ≥ 2 individuals recorded (Figure 4). Despite this violation, estimates of abundance obtained from the C/p estimator provided reasonable estimates, as evidenced by the close agreement with territory density estimates. A comparison of my C/p estimates of abundance to territory densities estimated using spot-mapping revealed that territory density extrapolated to 100 ha was, in most cases, slightly lower than the C/p estimates of abundance. However, for most sites the lower limit of the 95 % CI included the 100 ha territory density estimate, indicating that there was no significant difference between estimates of abundance and territory density. Among both years, there were four sites with territory density estimates outside the 95 % CI for the C/p estimates of abundance (2008:Bohls; 2009: Emma Long, Double J&T, and Barton Creek). The largest discrepancy was at Barton Creek, which had an abundance estimate of 48 male GCWA, yet only 12 territories were estimated in this same 100 ha area. It is unclear whether this discrepancy is associated with error in the C/p estimator or the spot-mapping method, or a combination of errors from both survey techniques. Nevertheless, I believe that the C/p estimator provided more precise and unbiased estimates of GCWA abundance, than did the BMM. I suggest that using this novel approach for estimating the probability of detecting individuals be considered, especially in light of the uncertainty associated BMM estimates (Dodd and Dodd and Dorazio 2004, Kery et al. 2005, Joseph et al. 2008).

This study demonstrated that monitoring GCWA using point-count surveys to estimate detectability-adjusted population parameters is a feasible alternative to spot-mapping. Evaluating the reliability of survey techniques to estimate unbiased population estimates is difficult without knowledge of the true population size. However, I found that estimates of detectability-adjusted abundance using the C/p equation were largely in agreement with territory densities obtained using the spot-mapping method. Associated error in the form of 95% CI for the population parameters in this study conveys the degree of precision for these estimates. The spot-mapping technique provides an index of population size without any associated error estimate, and thus no means of evaluating precision, a component of reliability. Survey designs that allow for estimation of detection probabilities and either occupancy or abundance should be considered as a feasible monitoring approach for avian species.

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VITA

Jason Hunt was born to Ronnie Odell and Rebecca Ann Hunt on 28 October 1981. He has a younger brother Paul. He grew up in middle Tennessee and graduated from Gallatin High School in 2000. After attending two semesters at Florida College, he transferred to Tennessee Technological University. As an undergraduate, he worked for the Tennessee Cooperative Fishery Research Unit, where he assisted graduate students with research on freshwater fish and mussels. Jason graduated in May 2005 with a Bachelors of Science in Wildlife and Fisheries Science, with an emphasis in Conservation Biology. Upon graduating, he served as a member of the Student Conservation Association, completing internships at the Warm Springs Fish Technology Center in Georgia and the Attwater Prairie Chicken National Wildlife Refuge in Eagle Lake, TX. In the spring of 2008 he enrolled in the Population and Conservation Biology graduate program at Texas State University-San Marcos. Throughout his graduate work, he worked as an instructional assistant teaching the Vertebrate Physiology lab.

Permanent Address: 1126 Douglas Loop
Gallatin, TN 37066

This thesis was typed by Jason W. Hunt