Changes in Occupancy and Relative Abundance of a Southern Population of Spruce Grouse Based on a 25-year Resurvey

Authors: Christopher Gilbert, and Erik Blomberg

Source: Northeastern Naturalist, 26(2) : 275-286

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/045.026.0204

2019 *NORTHEASTERN NATURALIST* 26(2):275–286

Changes in Occupancy and Relative Abundance of a Southern Population of Spruce Grouse Based on a 25-year Resurvey

Christopher Gilbert[1,*] and Erik Blomberg[1]

Abstract - Marginal populations are often distributed throughout fragmented landscapes and experience less optimum conditions compared to central range populations. *Falcipennis canadensis* (Spruce Grouse) inhabit conifer-dominated forests distributed throughout the northern US and Canada, and reach their southeastern range extent in the northeastern US, including Maine. We resurveyed 18 forest stands on Mount Desert Island, ME, that were comprised of *Picea mariana* (Black Spruce) and *Larix laricina* (Tamarack) and which were originally surveyed during 1992–1993. Our goal was to observe changes in Spruce Grouse occupancy and abundance between the 1990s and the present (2017). We conducted repeated callback surveys to detect territorial male Spruce Grouse within each stand during spring 2017, using a systematic survey design that covered the entirety of each stand and replicated methods used during the 1990s. We documented 7 individual Spruce Grouse, including 6 males and a single female. Single-season occupancy models for 2017 predicted Spruce Grouse stand occupancy of 0.226 (±0.100 SE), with a survey-level detection probability for male Spruce Grouse of 0.857 (±0.141 SE). Stand occupancy decreased from 8 stands in 1992–1993 to 4 in 2017, a 50% decline in the proportion of stands occupied. Further, the total number of males observed decreased from 32 (average between 1992 and 1993) to only 6 during our study, a >80% decline in apparent abundance. Our results suggest Spruce Grouse populations on Mount Desert Island have decreased and may be at risk of local extinction.

Introduction

Species are confined to a geographical range with limits imposed by abiotic and biotic factors. In most cases, the center of a species' range contains optimal abiotic conditions and the greatest availability of continuous suitable habitat (Hargrove and Rotenberry 2011). Range margins often occur along ecological gradients, which impose the biotic or abiotic limits that define the boundaries of the species' range (Sagarin and Gaines 2002). A common feature among species in the center of their range are often less sensitive to environmental changes compared to those a the margin because of greater abundance and genetic diversity (Grant and Antonovics 1978). Patches of habitat at range margins are often smaller in area and interspersed within a non-habitat matrix, causing greater isolation compared to habitat within the center of a species' range (Guo et al. 2005). As a result, local populations become smaller and genetically isolated (Grant and Antonovics 1978), increasing the probability of localized extinction due to lower abundance, lack of

---

[1] Department of Wildlife, Fisheries and Conservation Biology, University of Maine Orono, ME 04469. [*] Corresponding author - christopher.gilbert1128@gmail.com.

Manuscript Editor: Peter Paton

genetic diversity, or lower connectivity. These factors may in turn reduce a population's ability to adapt to environmental or land-use changes (Guo et al. 2005). In this study, we conducted a re-survey of *Falcipennis canadensis* L. (Spruce Grouse) stand occupancy and relative abundance for an isolated island population at the southern extent of the species' range.

Spruce Grouse is a northern conifer forest obligate that is often associated with mid-successional forests, although habitat characteristics vary widely across the species' range (Schroeder et al. 2018). Much of Spruce Grouse range is in the boreal forest, the conifer-dominated forests of high northern latitudes (Aldrich and Duvall 1955, Bent 1932, Williamson et al. 2008). These forests are composed primarily of *Pinus* spp. (pines), *Picea* spp. (spruces), or *Larix* spp. (larches) (Kaplan 1996). Spruce Grouse habitat in Maine, at the southeastern extent of the species' range, is primarily forested wetlands composed of *Picea rubens* Sarg. (Red Spruce), *Picea mariana* (Mill.) Britton, Sterns & Poggenburg (Black Spruce), *Abies balsamea* (L.) Mill. (Balsam Fir), and *Larix laricina* (Du Roi) K. Koch (Tamarack), with horizontal cover often comprised of ericaceous shrubs (Dunham 2016, Schroder et al. 2018, Whitcomb et al. 1996b).

Since the early 1990s, Spruce Grouse populations have declined at the southeastern extent of their range (Bouta 1991, Ross et al. 2016). The occurrence of conifer forest patches within a deciduous forest matrix has subdivided Spruce Grouse populations making them more prone to localized extinction (Ross et al. 2016). Spruce Grouse are known to have annual home ranges of 4 ha; habitat deemed suitable for Spruce Grouse populations was previously believed to be a minimum of 20 ha in size (Fritz 1979). Prior research on Mount Desert Island, ME, found that Spruce Grouse occurred in habitat patches from 8 ha to 26 ha (Whitcomb et al. 1996b), smaller than the minimum size described by Fritz (1979). Whitcomb et al. (1994) also suggested that Spruce Grouse on Mount Desert possessed characteristics of a spatially structured population, occupying highly fragmented conifer patches isolated within a deciduous forest landscape, which could increase risk of localized extinction.

Whitcomb et al. (1996b) surveyed all stands on Mount Desert Island dominated by Black Spruce and Tamarack, which they presumed to reflect the majority of available Spruce Grouse habitat on the island. Our research objectives were to (1) resurvey these stands 25 y later to determine changes in Spruce Grouse occupancy and relative abundance, and (2) investigate the relationship between Spruce Grouse occupancy and stand size. We hypothesized that Spruce Grouse occupancy and abundance have declined since the Whitcomb et al. (1996b) study based on research from other populations in the northeastern US at the southern extent of the species' range (Ross et al. 2016). We also predicted that larger stands would support a greater number of individuals, increasing the likelihood of persistence, and thus, present occupancy, because risk of local extinction due to demographic stochasticity decreases with increasing population size (Grant and Antonovics 1978).

Field-site Description

We conducted our study on Mount Desert Island (MDI), ME. The island is situated in the Gulf of Maine, approximately 0.6 km from the mainland and has an area of 281 km^2 (Fig. 1). MDI is an island with moderate to steep topography as a result of north-to-south ridges and U-shaped valleys (Patterson et al. 1983). The

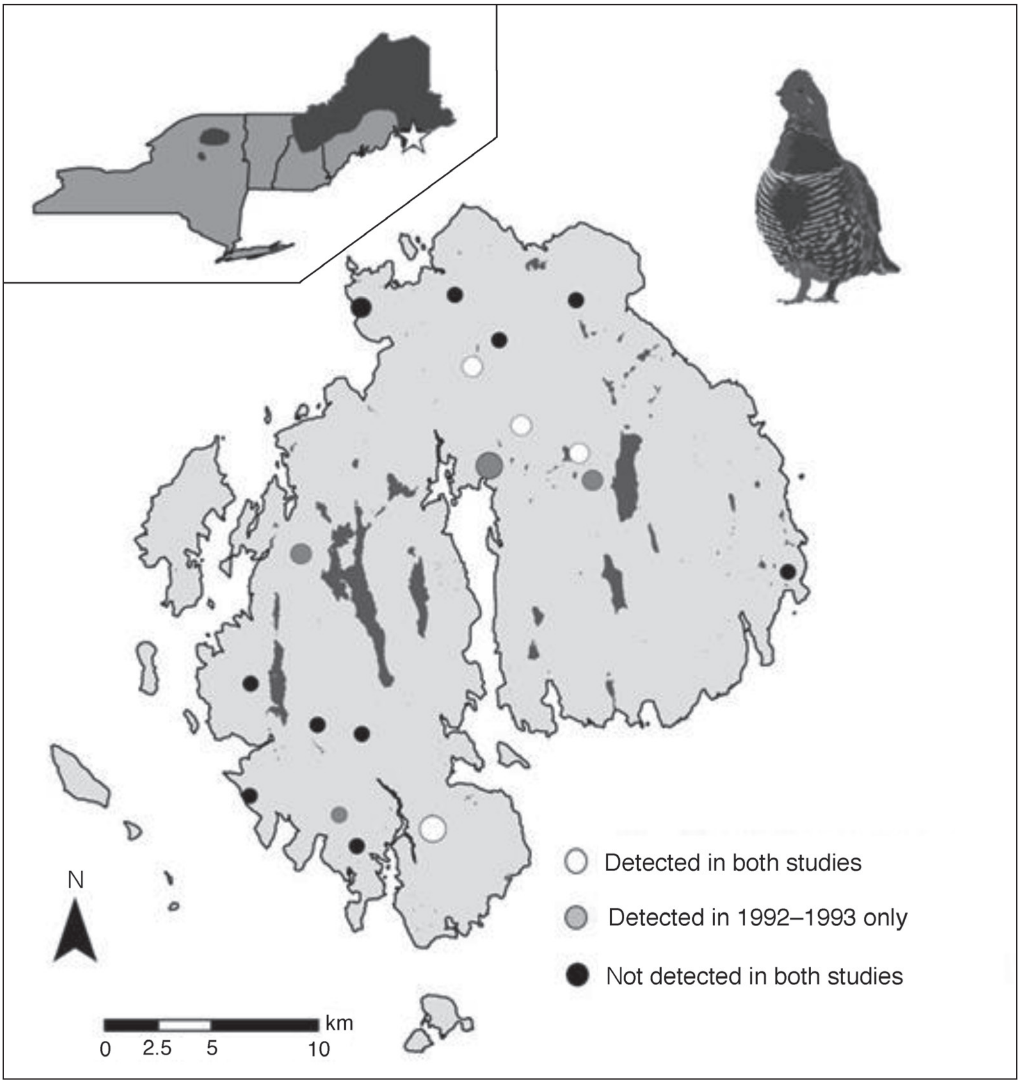

Figure 1. Map of Mount Desert Island, ME, showing the location, relative size, and occupancy status of each Black Spruce–Tamarack stand surveyed for Spruce Grouse occupancy during the spring of 2017. We compared stand occupancy between surveys conducted during 1992–1993 by Whitcomb et al. (1996b) and our surveys of the same stands during 2017. Symbol size is proportional to stand size, and the dark irregular polygons indicate major inland water bodies on Mount Desert Island for spatial reference. The inset map in the upper left provides the approximate current range (dark gray) of Spruce Grouse in the Northeastern US and the location of Mount Desert Island (white star).

landscape on MDI consists of both deciduous and conifer forests with a mix of private ownership and federally managed lands associated with Acadia National Park. We conducted our research at 18 forest stands located throughout MDI that were originally identified and surveyed by Whitcomb et al. (1996b) during 1992 and 1993. These stands occur on poorly drained soils, are dominated by Black Spruce and Tamarack, and are thought to contain the majority of potential habitat for Spruce Grouse on MDI (Whitcomb et al. 1996b). Some stands extend onto adjacent uplands with well-drained shallow acidic soils. Stand structural characteristics were variable. Mid-story cover consisted of dense clusters of Black Spruce and Tamarack saplings, and ericaceous shrubs. Patches of Red Spruce and Balsam Fir, as well as patches of *Alnus incana* (Nutt.) Breitung (Speckled Alder) and *Acer rubrum* L. (Red Maple) were adjacent to many Black Spruce stands. Some sites had intermixed *Thuja occidentalis* L. (Northern White Cedar), which also occurs in areas of poorly drained soils. Some stands near uplands were also bordered by either coniferous forests containing Red Spruce, *P. glauca* (Moench) Voss (White Spruce), Balsam Fir, and *P. strobus* L. (White Pine) or by deciduous forest dominated by *Betula papyrifera* Marshall (White Birch) and *Populus tremuloides* Michx. (Quaking Aspen). Nine of the 18 stands are within the boundaries of Acadia National Park, 7 stands are on private land, and 2 stands are located on both privately-owned and national park lands.

Methods

Breeding patch surveys

We conducted stand occupancy surveys for breeding male Spruce Grouse during the spring of 2017, beginning on 15 April and continuing until 25 May, generally following the same methods used by Whitcomb et al. (1996b). We spaced survey points 150 m apart, following a grid system, such that we surveyed the entire footprint of each stand. To create the gird system, we employed ArcGIS to overlay a 150 m x150 m grid over each of the 18 plots that were designated by Whitcomb et al (1996b). We extracted a UTM coordinate from the center of each grid cell and converted these into latitude–longitude coordinates on a GPS device (GPS-72H; Garmin, Olathe, KS). We began surveys 30 min prior to sunrise and ended them before 1:00 pm. We used a FOXPRO Game Caller (Model NX4; FOXPRO Inc., Lewiston, PA) to play recordings of a female Spruce Grouse aggression or "cantus" call, followed by a recording of a male flutter-flight display. After each sequence of female and male calls, we listened for 1 min for a reciprocal flutter-flight or watched for approaching grouse. We repeated this process twice before moving to the next survey point, and recorded the number of male and female Spruce Grouse observed at each survey point. These survey methods are commonly used for Spruce Grouse studies (Bouta 1991, Dunham 2016, Ross et al. 2016, Whitcomb et al. 1996b). Male Spruce Grouse hold and defend individual territories throughout the breeding season (Schroeder et al. 2018); thus, we assumed that males observed repeatedly at the same location represented the same individual. We also assumed that when we detected males at >1 survey point within a stand, they were unique individuals, due to the territoriality and high site-fidelity of males during the breeding season (Schroeder et al. 2018). In practice, our detections of males were relatively infrequent and not located at immediately adjacent survey points, so we feel this assumption is robust. In addition to survey data, we recorded survey start time and temperature, as well as wind speed using a digital anemometer (Hold Peak, HP-866B). We conducted all research within Acadia National Park under National Park Service permit number ACAD-2017-SCI-0018.

Data analysis

We used single-season stand-occupancy models to evaluate differences in the probability of Spruce Grouse occupancy among stands and also the probability of detection during a single survey (Mackenzie et al. 2002). In order to run the occupancy model, we aggregated point-level survey data into a stand-level history that included the 2 replicated surveys of each stand (see Supplemental Appendix 1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n26-2-N1687-Gilbert-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1687.s1). We believe our sampling protocol meets the general assumptions of the single-season occupancy model (Mackenzie et al. 2002) for closure among repeated surveys and independence among sample stands, particularly because we conducted all surveys within a single Spruce Grouse breeding season, and individual forest stands were spatially distinct and separated by distances that far exceeded male Spruce Grouse territory size. These models also assume homogenous occupancy probability among sites, and detection probabilities among sites and surveys, and we accommodated potential heterogeneity in occupancy and detection by incorporating a number of site- and survey-level covariates (described below).

We tested multiple variables that we hypothesized could affect either occupancy or detection probability. These parameters included wind speed, ordinal day, and start time relative to sunrise as survey-level detection variables, and stand size as a site-level occupancy variable. The ambient noise produced by wind may affect an observer's ability to hear flutter flights and territorial calls (Conway and Gibbs 2001). Prior Spruce Grouse research has shown that males tend to respond more to callbacks during peak breeding season but are less likely to respond to such stimuli later in the season (Robinson 1980). It has been found that Spruce Grouse males tend to be more active during the early morning hours, and their call and display frequency decreases as time approaches noon (Schroeder et al. 2018). Spruce Grouse are commonly found in patches greater than 20 ha (Fritz 1979, Ross et al. 2016), but previous studies on MDI found that Spruce Grouse were also found in patches smaller than 20 ha (Whitcomb et al. 1996b).

We conducted a single-season occupancy analysis (Mackenzie et al. 2002) using the 'unmarked' package in program R (R Core Team 2013). We initially attempted to fit the model under a penalized likelihood (Hutchinson et al. 2015); however, these models would not converge and so we used the more general single-season model. We evaluated each detection variable paired with an intercept-only structure for the occupancy parameter and evaluated the effect of area on occupancy with an intercept-only model for detection probability. We contrasted all of these models' structures against a null model (intercept only on both occupancy and detection). We ranked each of the above models using the Akaike information criterion (AIC), and used ΔAIC to determine the strength of evidence for each model (Burnham and Anderson 2002), using a criterion of $\Delta\text{AIC} < 2.0$. Based on results of initial model evaluation, we also tested wind as a detection covariate paired with stand size (ha) as an occupancy covariate, as well as ordinal day as a detection covariate paired with stand size (ha) as an occupancy covariate. We further evaluated 95% confidence intervals of the Beta coefficients to see whether they overlapped 0.

Following occupancy analysis, we calculated p^*, which provides an estimate of the probability that an animal was detected at least once during n number of repeated surveys, where $p^* = 1 - (1 - p)^n$, and where p is the probability of detecting a Spruce Grouse during a single survey. Using p^* allowed us to evaluate the probability that we failed to detect Spruce Grouse presence within all truly occupied stands, given the modeled detection probability from our occupancy analysis and the number of repeated surveys we conducted. This step was necessary for comparison with the results of Whitcomb et al. (1996b), who conducted 3 repeated surveys compared to our 2 surveys.

We did not attempt to model individual abundance within each stand or at each survey point, such as using the N-mixture approach (Royle 2004). Generally, our observations of individual Spruce Grouse were infrequent, and we considered our counts too sparse for this approach. As such, our counts of territorial males represent relative abundances that are not corrected for imperfect detection, and we include them largely for comparison with similar values reported by Whitcomb et al. (1996b). To give context to differences in counts of males between the early 1990s and our study, we approximated individual male detection rates during our study based on repeated observations at survey points with known territorial males. We calculated the binomial probability of detection for individual territorial males that were observed during either 1 or both repeated surveys as $p = c / n$, where c is the count of total detections at survey points where a territorial male was observed, and n is the number of survey points where a male was observed at least once. The standard error (SE) for the maximum likelihood estimate of p is then given as $\text{SE} = (p\ [1 - p] / n)^{0.5}$. Using this estimate of p, we then calculated p^* for individual territorial male Spruce Grouse, as described above.

Results

We conducted callback surveys twice at 227 survey points spanning 18 stands, totaling 454 individual callback surveys. We detected Spruce Grouse in 4 of the 18 stands (Fig. 1), and observed 7 unique individuals, including 6 males and 1 female (Table 1). The mean area of stands where we detected Spruce Grouse was 82.2 ha (±107.5 SD), and was 14.0 ha (±18.4 SD) for stands where we did not detect Spruce Grouse.

Naïve occupancy (proportion of stands where we detected Spruce Grouse) during our surveys was 0.222. Based on our occupancy models, the average detection probability (p) during a single survey was 0.857 (±0.141 SE), and the estimated occupancy probability (ψ) was 0.226 ± 0.100 SE. Four models were competitive based on ΔAIC (Table 2) and indicated that wind speed and ordinal day affected detection probability, while occupancy was affected by stand area. However, confidence intervals for each of these effects overlapped 0.0, indicating substantial uncertainty in their support (Table 3). Start time relative to sunrise had no effect on detection probability ($\beta = 0.00 \pm 0.01$ SE; Table 4). Based on a detection probability of 0.857 ± 0.141 SE and each stand being surveyed twice, $p^* = 0.980$,

Table1. Differences in observed Spruce Grouse abundance by sex from surveys on Mount Desert Island, ME, during the 1992, 1993, and 2017 field seasons. The data from the 1992 and 1993 field seasons were obtained from Whitcomb et al. (1996b).

	1992		1993		2017	
Site	Males	Females	Males	Females	Males	Females
Aunt Betsy Brook (ABB)	4	0	3	1	2	0
Aunt Betty Pond (ABP)	4	2	6	4	1	0
Bernard (B)	0	0	0	0	0	0
China Hill (CH)	3	0	2	0	0	0
Dodge Point Road (DPR)	0	0	0	0	0	0
Eagle Lake (EL)	3	1	3	1	0	0
Fresh Meadow (FM)	0	0	0	0	0	0
French Pond (FP)	0	0	0	0	0	0
Hio Bridge (HB)	9	3	5	2	2	1
Jones Marsh (JM)	0	0	0	0	0	0
Pretty Marsh (PM)	3	1	0	0	0	0
Saint Andrews (SA)	0	0	0	0	0	0
Sand Beach (SaB)	0	0	0	0	0	0
Stony Brook (SB)	0	0	0	0	0	0
Southern Heath (SH)	2	1	2	0	1	0
Whalesback (W)	8	6	7	3	0	0
West Mountain East (WME)	0	0	0	0	0	0
West Mountain West (WMW)	0	0	0	0	0	0
Total	36	14	28	11	6	1

Table 2. Model selection statistics for single season occupancy models of Spruce Grouse on Mount Desert Island, ME, based on repeated male callback surveys conducted during spring 2017. Ψ = probability of occupancy, p = probability of detection, (.) = y-intercept only, Wind = average wind speed during a survey, Day = ordinal day of survey, Start = time of survey relative to minutes before sunrise, and Area = size of stand (ha)

Model	K	AIC	ΔAIC	AIC*wt*
pWind,ψArea	4	23.57	0.00	0.3456
pDay,ψArea	4	24.29	0.72	0.2414
pWind,ψ(.)	3	25.07	1.50	0.1633
pDay,ψ(.)	3	25.24	1.66	0.1506
p(.),ψArea	3	27.47	3.90	0.0492
p(.),ψ(.)	2	28.95	5.38	0.0235
pStart,ψ(.)	3	30.83	7.26	0.0092

indicating a ~2% chance that we failed to detect Spruce Grouse presence within a truly occupied stand.

We detected individual males 8 times during 12 point-level surveys where a male was known to be present based on detection during 1 or more surveys. These detections yielded an individual detection probability of 0.667 ± 0.137 SE during a single survey, and an associated estimate of $p^* = 0.889$ for 2 repeated surveys. Thus, there was an approximately 11% chance that we failed to detect an individual male Spruce Grouse during our 2 repeated surveys, given that it was present and available for detection.

Discussion

There was a decrease in stand occupancy as well as apparent abundance of Spruce Grouse on MDI between our 2017 surveys and those conducted in the early 1990s. During the 1990s, Whitcomb et al. (1996b) documented 36 (1992) and 28 (1993) male Spruce Grouse across 8 occupied stands, while in contrast we only observed 6 males located in 4 stands. This change reflects a 50% reduction in patch occupancy and a >80% reduction in apparent abundance of Spruce Grouse compared with the early 1990s. These results are similar to those observed for Spruce Grouse in the Adirondack Mountains of New York, where habitat extent declined by 70% and the number of occupied patches declined by 25%, based on resurvey work conducted over a 40-y period (Ross et al. 2016). Although our study included only 1 y of survey data (discussed below), we nevertheless conducted a comprehensive survey of all stands surveyed by Whitcomb et al. (1996b). Thus, the change in both occupancy and apparent abundance we observed reflects a true change during the 25-y interval between the 2 surveys.

Whitcomb et al. (1996b) found that patch size was a primary predictor of Spruce Grouse presence in the 1990s, where patches >11 ha in size were normally occupied and smaller patches unoccupied. During our study, all small stands that were previously unoccupied remained unoccupied; however, some previously occupied stands, classified as medium and large by Whitcomb et al. (1996b), were now unoccupied. With only a small number of occupied stands (*n* = 4), our data likely lacked power to detect covariate effects on stand occupancy probability. Of the 4 remaining occupied stands, only 1 stand was smaller than 20 ha, however, we also failed to detect Spruce Grouse in the second largest stand (77 ha). So, while it is

Table 3. Estimates of parameter coefficients (β) from site-occupancy models of male Spruce Grouse on Mount Desert Island, ME, based on data obtained from callback surveys conducted during April and May 2017.

				95% Confidence interval	
Covariate	Parameter tested	Estimate (β)	SE	Upper	Lower
Stand size (ha)	Occupancy	0.02	0.02	0.07	-0.02
Wind speed	Detection	-6.03	11.60	16.71	-28.77
Ordinal day	Detection	1.00	1.01	2.98	-0.98
Start time after sunrise	Detection	0.00	0.01	0.02	-0.02

true that only larger stands remained occupied, apparent loss of Spruce Grouse from some large stands also suggests that factors other than stand size may be driving local population dynamics. It is possible that other habitat metrics that we did not measure affected the decline in occupancy we observed, such as changes in forest stand characteristics (Dunham 2016) associated with forest succession during the past 25 y (e.g., Ross et al. 2016), anthropogenic developments occurring outside of Acadia National Park, or climate change. The patterns could also be due to demographic stochasticity coupled with low connectivity among stands. Each previously occupied stand that was unoccupied during our study fell within Spruce Grouse dispersal distance (Whitcomb et al. 1996a) from an occupied stand, but it is possible that recruitment rates within the system are insufficient to maintain local patches through immigration/emigration dynamics.

Although we attempted to replicate Whitcomb et al.'s (1996b) methods as closely as possible, there were some small differences that we acknowledge may affect our comparison with their results. We conducted 2 rounds of callback surveys, while Whitcomb et al. (1996b) conducted 3 rounds, and we also ran an occupancy analysis accounting for detection probability, while Whitcomb et al. (1996b) used a naïve occupancy rate without a formal occupancy analysis. Our p^* value of 0.980 implies that if we were to conduct a 3rd survey, Spruce Grouse stand occupancy would remain at 4 out of 18 stands. If detection probability was similar during the study of Whitcomb et al. (1996b), they too would have observed all occupied stands (8) during 3 repeated surveys. However, if detection probability was lower during their study, then differences in stand occupancy probability between 1992–1993 and 2017 would be greater than we have shown. Our survey design had a ~11% chance of failing to detect an individual territorial male during 2 repeated surveys, given that it was available for detection. It is therefore possible that we undercounted the total number of males present by a few birds due to imperfect detection. Overall, our results show that potential differences in detection probability, both for occupied stands and individual males, are relatively small when compared with the large differences in occupancy and apparent abundance between our surveys versus those of Whitcomb et al. (1996b).

During our surveys, we only detected a single female Spruce Grouse, while Whitcomb et al. (1996b) observed substantially more females in the same stands. Our callback surveys were designed to elicit responses from male Spruce Grouse specifically, and so our sampling methods were not tailored to detecting females. Differences in the ratio of male to female Spruce Grouse observed between the 2 surveys may reflect true decline in female abundance, which could in turn provide a demographic mechanism for the overall population declines we observed. However, given that we did not survey female Spruce Grouse explicitly, we cannot account for detection probability of females during our surveys, and therefore our reported count of females should be interpreted cautiously.

Based on our research, Spruce Grouse that inhabit Black Spruce–Tamarack forests on MDI have declined substantially since the 1990s, and may be at risk of local extirpation. We conducted our surveys only in lowland Black Spruce–Tamarack forests; these forest types are generally considered to be the primary habitat of Spruce Grouse in the region (Ross et al. 2016, Whitcomb et al. 1996b). Spruce Grouse are conifer-forest obligates and do not regularly occur in forests that are not dominated by conifers (Schroeder et al. 2018). On MDI, it is possible that the species also occupies upland conifer forests dominated by Red Spruce, White Spruce, and Balsam Fir (hereafter, upland spruce–fir), which we did not survey for this study. In the early 1990s, Whitcomb et al. (1994) found that Spruce Grouse rarely occurred in these upland spruce–fir forests, and only when adjacent to occupied lowland Black Spruce–Tamarack forests. Future monitoring of Spruce Grouse on MDI should explore present-day occupancy of upland spruce–fir stands.

The degree to which MDI Spruce Grouse are isolated (both demographically and genetically) from mainland populations is also unknown. Mainland Spruce Grouse are found on the Schoodic Peninsula within ~15 km of the nearest occupied stand on MDI. Whitcomb et al. (1996a) observed a maximum dispersal distance of juvenile Spruce Grouse on MDI of 7.2 km (Whitcomb et al. 1996a), while other research has found individuals able to travel up to 11 km (Schroeder 1985). However, Spruce Grouse are not known to cross large water bodies, and dispersal to or from the mainland would require their crossing of Frenchman Bay with an overwater distance >6 km. Geographic isolation, coupled with increased risk of stochastic events due to low population size (Diamond 1984), suggest that Spruce Grouse on MDI may be at heightened risk of extirpation. It is possible that we surveyed the population during a period of short-term population decline, and longer-term monitoring may reveal a less dramatic pattern. Thus, we recommend further monitoring of this population to confirm long-term declines and assess the future viability of the population. A dynamic occupancy modelling approach (MacKenzie et al. 2003) may be useful for systematic long-term monitoring. If maintenance of Spruce Grouse populations at their southern range margins is a conservation priority, additional research is likely needed to identify the causal factors associated with population declines in this and other systems.

Acknowledgments

We thank Acadia National Park, B. Connery, and K. Anderson for granting access to our study sites and for field housing. We are grateful to S. Whitcomb and F. Servello for their input on the project. We thank the University of Maine Honors College and Downeast Audubon Chapter for financial support. We appreciate A. Mortelliti, A. Calhoun, D. Levesque, and M. Ladenheim, as well as 2 anonymous reviewers, for helpful comments on earlier versions of this work. This project was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis project #ME041602 through the Maine Agricultural and Forest Experiment Station. This is Maine Agricultural and Forest Experiment Station Publication no. 3637.

Literature Cited

Aldrich, J.W., and A.J. Duvall. 1955. Distribution of American gallinaceous game birds. US Department of the Interior, Fish and Wildlife Service Circular No. 34. Washington, DC. 23 pp.

Bent, A.A. 1932. Life histories of North American gallinaceous birds. US National Museum Bulletin No. 162. Washington, DC. 490 pp.

Bouta, R.P. 1991. Population status, historical decline, and habitat relationships of Spruce Grouse in the Adirondacks of New York. M.Sc. Thesis. State University of New York College of Environmental Science, and Forestry, Syracuse, NY. 117 pp.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Theoretic Approach. 2nd Edition, Springer-Verlag, New York, NY.

Conway, C.J., and J.P. Gibbs. 2011. Summary of intrinsic and extrinsic factors affecting detection probability of marsh birds. Wetlands 31:403–411.

Diamond, J.M. 1984. "Normal" extinctions of isolated populations. Pp. 191–246, *In* M.H. Nitecki (Ed.). Extinctions. University. of Chicago Press, Chicago, IL. 354 pp.

Dunham, S.W. 2016. Spruce Grouse habitat ecology in Maine's commercially managed Acadian forest. M.Sc. Thesis. University of Maine, Orono, ME. 87 pp.

Fritz, R.S. 1979. Consequences of insular population structure: Distribution and extinction of Spruce Grouse populations. Oecologia 42:57–65.

Grant, M.C., and J. Antonovics. 1978. Biology of ecologically marginal populations of *Anthoxanthum odoratum.* I. Phenetics and dynamics. Evolution 32:822–838.

Guo, Q., M. Taper, M. Schoenberger, and J. Brandle. 2005. Spatial–temporal population dynamics across species range: From center to margin. Oikos 108:47–57.

Hargrove, L., and J.T, Rotenberry. 2011. Spatial structure and dynamics of breeding bird populations at a distribution margin, southern California. Journal of Biogeography 38:1708–1716.

Hutchinson, R.A., J.J. Valente, S.C. Emerson, M.G. Betts, and T.G. Dietterich. 2015. Penalized likelihood methods improve parameter estimates in occupancy models. Methods in Ecology and Evolution 6:949–959.

Kaplan, E. 1996. The Taiga (Biomes of the World). Benchmark Books, New York, NY. 64 pp.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D.I., J.D. Nichols, J.E. Hines, M.G. Knutson, and A.B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 2200–2207.

Patterson, W.A., III., K.E. Saunders, and L.J. Horton. 1983. Fire regimes of coastal Maine forests of Acadia National Park. Scientific Study No. OSS-83-3. US National Park Service, North Atlantic Regional Office, Boston, MA.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.Available online at http://www.R-project.org/.

Robinson, W.L. 1980. Fool Hen: The Spruce Grouse on the Yellow Dog Plains. University of Wisconsin Press, Madison, WI. 221 pp.

Ross, A.M., G. Johnson, and J.P. Gibbs. 2016. Spruce Grouse decline in maturing lowland boreal forests of New York. Forest Ecology and Management 359:118–125.

Royle, J.A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Sagarin, R.D., and S.D. Gaines. 2002. The "abundant centre" distribution: To what extent is it a biogeographical rule? Ecology Letters 5:137–147.

Schroeder, M.A., E.J. Blomberg, D.A. Boag, P. Pyle, and M.A. Patten. 2018. Spruce Grouse (*Falcipennis canadensis*). *In* P.G. Rodewald (Ed.). The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY. Available online at https://doi.org/10.2173/bna.sprgro.02. Accessed 11 February 2018.

Whitcomb, S.D., F.A. Servello, and A.F. O'Connell Jr. 1994. Population and habitat assessment for Spruce Grouse in Acadia National Park and on Mount Desert Island, Maine. National Park Service Technical Report NPS/NAROSS/NRTR-94/23. Boston, MA. 54 pp.

Whitcomb, S.D., A.F. O'Connell Jr., and F.A. Servello. 1996a. Productivity of the Spruce Grouse at the southeastern limit of its range. Journal of Field Ornithology 67:422–427.

Whitcomb, S.D., F.A. Servello, and A.F. O'Connell Jr. 1996b. Patch occupancy and dispersal of Spruce Grouse on the edge of its range in Maine. Canada Journal of Zoology 74:1951–955.

Williamson, S.J., D.M. Keppie, R. Davison, D. Budeau, S. Carriere, D. Rabe, and M.A. Schroeder. 2008. Spruce Grouse continental conservation plan. Association of Fish and Wildlife Agencies, Resident Game Bird Working Group, Washington, DC. 60 pp.