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Twenty-Five Years of Change in Spruce Grouse Occupancy at Their Southern Range Margin in Maine, USA

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TWENTY-FIVE YEARS OF CHANGE IN SPRUCE GROUSE OCCUPANCY AT THEIR SOUTHERN RANGE MARGIN IN MAINE, USA

by

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ABSTRACT

Species at their southern range margin are often dispersed throughout fragmented populations where they experience less optimum conditions compared to their central range. Spruce Grouse (*Falcipennis canadensis*) are boreal forest obligates distributed throughout the Northern United States and Canada and reach their southeastern range extent in Maine. I resurveyed 18 Black Spruce (*Picea mariana*) – Tamarack (*Larix laricina*) stands on Mount Desert Island, Maine, to observe changes in Spruce Grouse occupancy and abundance between the early 1990s (Whitcomb et al. 1996) and present day. I conducted two rounds of call back surveys within each stand from April to May, 2017. I used iButton units to collect stand-level temperature and humidity data for a three-week period starting July 25th, at the 18 sites to examine relationships between these variables and stand occupancy. Single-season occupancy models predicted that Spruce Grouse would occupy 0.226 (±0.100 SE) of stands with a detection probability of 0.857 (±0.141 SE). I only found 7 individuals. I found that stands which remained occupied were larger ($\bar{x}$ = 82.8ha) than unoccupied stands ($\bar{x}$ = 14.0ha), however, there was limited statistical support for this difference. There was no relationship between average daily maximum temperature and average daily humidity per stand and Spruce Grouse occupancy. Stand occupancy decreased from 8 stands to 4 when compared to the Whitcomb et al. (1996) study, and the number of individuals observed decreased from 39 individuals in 1993 to 7 individuals in 2017. My results suggest that over a span of 25 years Spruce Grouse populations on Mount Desert Island have decreased. Potential reasons for decline include habitat loss to development and loss of horizontal cover within stands due to forest succession.

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INTRODUCTION

Species are confined to geographical 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 & Rotenberry 2011). A species' range margin is defined as a geographic area that is occupied by a species which is adjacent to areas that are absent of that species. These range margins often occur along ecological gradients, which impose the biotic or abiotic limits that prevent species from occurring beyond their already defined range (Sagarin & Gaines 2002). A common feature among species is that central populations are often less sensitive to environmental changes compared to marginal populations, as a result of their larger population sizes and greater genetic diversity (Grant and Antonovics 1978). Patches of habitat at a species' range margins are often smaller in area and are more-commonly fragmented by a non-habitat matrix, resulting in 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 for spatially structured populations (SSP) to occur. SSPs can be a set of local populations that interact through individual dispersal (Revillaa & Wiegand. 2008). With SSPs, isolated stands often have high rates of inbreeding, with occasional interactions with other patch-level populations, often occurring at a species range margins (Revillaa & Wiegand. 2008). As a result, marginal range species are more prone to localized extinction due to lower abundance, lack of genetic diversity, or lower connectivity, which may in turn reduce a

population's ability to adapt to environmental or land use changes (Guo et al. 2005). Such outcomes can occur in avian species like the Spruce Grouse.

The Spruce Grouse (*Falcipennis canadensis*) is a northern conifer forest obligate that is often associated with mid-successional forests (Dunham 2016) although habitat characteristics may vary across the species' range. Much of the Spruce Grouse's range is in the boreal forest (i.e., taiga or snow forest); the conifer-dominated forests (often wet) of high northern latitudes (Bent 1932; Aldrich & Duvall 1955; Williamson et al. 2008). These forests are composed of pines (*Pinus* spp.), spruces (*Picea* spp.) or larches (*Larix* spp.) (Kaplan 1996). Over portions of their boreal range, Spruce Grouse habitat is regulated by fires and is dominated by Jack Pine (*P. banksiana*) and Lodgepole Pine (*P. contorta*). In Alaska, spruces dominate the forest landscape (Ellison 1966). Spruce Grouse habitat in New England, Maritime Canada, and the upper Midwestern U.S. more closely resembles the Acadian forest, an ecoregion characterized by patches of coniferous forests intermixed with temperature broadleaf forests (Whitcomb et al. 1996; Dunham 2016). These conifer patches that are occupied by Spruce Grouse in Michigan and parts of Minnesota are dominated by Jack Pine (Robinson 1969; 1980), while Black Spruce (*P. mariana*) is dominant in Spruce Grouse habitat in New York (Ross et al. 2016), other portions of Minnesota (Anderson 1973; Zlonis et al. 2017), and Wisconsin (Anich et al. 2013). Spruce Grouse habitat in Maine, at the southeastern extent of its range, is primarily forested wetlands composed of Red Spruce (*P. rubens*), Black Spruce, Balsam Fir (*Abies balsamea*) and Tamarack (*L. laricina),* with horizontal cover often comprised of ericaceous shrubs (Whitcomb et al. 1996; Dunham 2016; Schroder et al. 2018).

Since the early 1990's, Spruce Grouse populations have declined at the southeastern extent of their range (Bouta 1991). The occurrence of coniferous forest patches (mostly sub-boreal or temperate in Maine) 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, and 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, Maine, found that Spruce Grouse occurred in habitat patches from 8-26 ha (Whitcomb et al. 1996), smaller than the minimum size described by Fritz (1979). Whitcomb et al. (1996) also suggested that Spruce Grouse on Mount Desert possessed characteristics of a spatially structured population, occupying a highly fragmented and isolated landscape amongst deciduous forest, making them more prone to localized extinction as a result of environmental and land use change. This population also occurs at the southeastern extent of the Spruce Grouse's range and could resemble other populations throughout the southeastern extent (Whitcomb et al. 1996, Ross et al. 2016).

During the study by Whitcomb et al. (1996), 18 stands dominated by Black Spruce and Tamarack were surveyed on Mount Desert Island. My research objectives were to (1) resurvey these 18 sites, 25 years later, to determine changes in Spruce Grouse occupancy (number of patches with individuals) and abundance (the total number of individuals), and (2) evaluate factors associated with current stand occupancy. Specifically, I sought to investigate the relationship between Spruce Grouse occupancy, patch size, and stand microclimatic factors (temperature and humidity). I hypothesized that Spruce Grouse occupancy and abundance have declined since the Whitcomb et al.

(1996) study, and I predicted that larger patches would remain occupied by Spruce Grouse. Over a span of twenty-five years development on Mount Desert Island has occurred, and evidence in the Gulf of Maine has shown that the climate has been warming, potentially lowering Spruce Grouse numbers. Larger patches can support a greater number of individuals, increasing the likelihood of a population persisting due lower demographic stochasticity (Grant and Antonovics 1978). I also predicted that occupied patches would be cooler and more humid compared to unoccupied patches. Spruce Grouse prefer cool moist areas, often forested wetlands, and smaller patches may be more prone to edge effects from adjacent developed land or upland habitat causing the patch to be drier and hotter (Matlack 1993).

STUDY AREA

I conducted my study on Mount Desert Island (MDI), Maine. The island is situated in the Gulf of Maine, approximately 0.6 km from the mainland and has an area of 281 km^2 (Figure 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 landscape on MDI consists of both deciduous and coniferous forests with a mix of private ownership and federally-managed lands associated with Acadia National Park. I conducted my research at 18 forest stands located throughout MDI that were originally established by Whitcomb et al. (1996) and surveyed in 1992 and 1993. These stands occur on poorly drained soils and are dominated by Black Spruce and Tamarack. Some stands extended onto adjacent uplands with well-drained shallow acidic soils. Stand structural characteristics such as canopy cover and mid-story composition were variable. Mid-story cover consisted of dense clusters of Black Spruce and Tamarack saplings, and ericaceous shrubs. Canopy cover ranged from 25 to 90%. Adjacent to many of these stands were patches of Red Spruce and Balsam Fir, as well as patches of Speckled Alder (*Alnus incana*) and Red Maple (*Acer rubrum*). Some sites also had intermixed patches of Northern White Cedar (*Thuja occidentalis*), which also occurred in areas of poorly drained soils. Some sites that occurred near uplands were also bordered by either coniferous forests containing Red Spruce, White Spruce (*P. glauca*), Balsam Fir, and White Pine (*P. strobus*), or by deciduous forest dominated by White Birch (*Betula papyrifera*) and Quaking Aspen (*Populus tremulides*). The large majority of deciduous forests bordered stands in the northern third of MDI. Nine of the 18 stands were within

Acadia National Park boundaries and 7 stands were on private land. Two stands, Whalesback and Pretty Marsh were located on both privately owned and National Park lands.

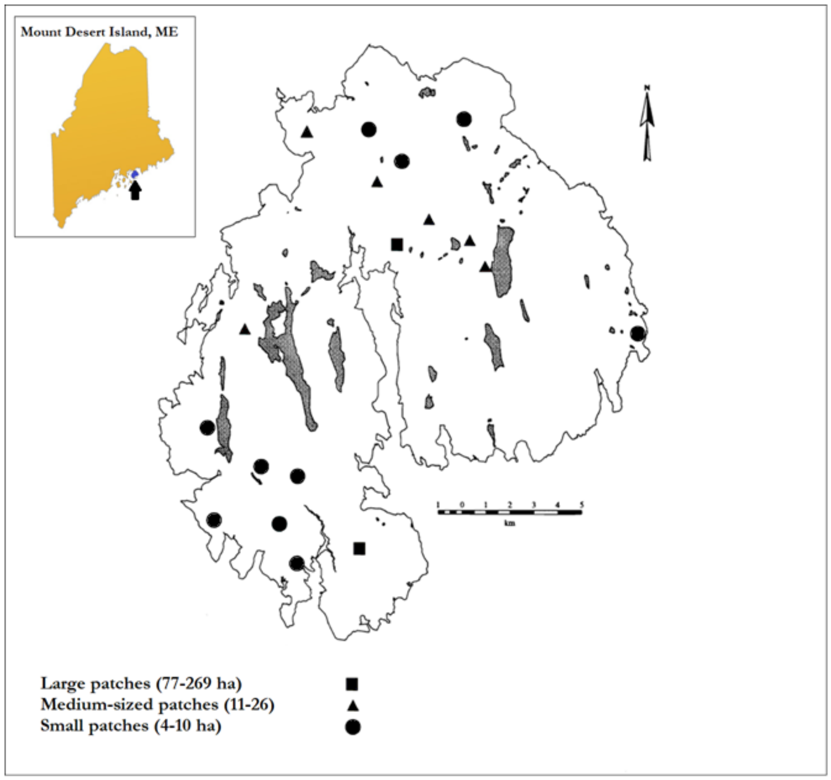

Figure 1. Map of Mount Desert Island, Maine, showing the location and relative size of each Black Spruce – Tamarack stand surveyed for Spruce Grouse occupancy during the spring of 2017. This map was modified from the original map used in Whitcomb et al. (1996).

METHODS

Breeding Patch Occupancy

I established parallel survey transects at each site with 150m spacing, and established survey points along each transects that were also spaced 150m apart. A study done by Fritz (1979) reported that male flutter flight calls can be heard at about 100m away, suggesting that 150m distances lowers the risk of double counting individuals during call-back surveys. Under this assumption, I was able to consider each observed grouse at a different point as a unique individual, given that male spruce grouse maintain fixed breeding territories (Whitcomb et al. 1996; Dunham 2016; Schroeder et al. 2018). These methods also allowed me to cover most of the area of each stand, increasing the likelihood of accounting for each individual. I used ArcGIS software and a 1979 forest cover data layer for MDI to construct a 150 x 150m grid that covered all Black Spruce - Tamarack cover types. The 1979 forest cover data was used by Whitcomb et al. (1996) to establish their sites. I added a center point to each grid cell and created transects by connecting the points in either a North-South or East-West orientation, depending on the specific survey site. I extracted UTM coordinates for each survey point from ArcGIS (Appendix A.). These coordinates were entered into a GPS unit (Garmin, GPS-72H) to locate survey points in the field. I established these survey points to match Whitcomb et al.'s (1996) sampling area as closely as possible.

I conducted patch occupancy surveys for breeding male Spruce Grouse during the spring of 2017, beginning on April 15 and continuing until May 25, generally following the same methods used by Whitcomb et al. (1996). From April 15 through May 12, I

conducted surveys two days/week, after which I conducted surveys every day until May 25. I began surveys 30 minutes prior to sunrise until noon, however during the last 5 days of surveying I extended my ending time until 1pm in order to get a minimum of two surveys per site. At each survey point I recorded the survey start time, as well as temperature and wind speed at the first and last point of each transect using a digital anemometer (Hold Peak, HP-866B). I used a FOXPRO Game Caller (Model NX4, FOXPRO Inc., Lewiston, PA, USA) 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, I would pause for one minute to listen for a reciprocal flutter-flight or to observe any approaching grouse. These survey methods are commonly used for Spruce Grouse studies (Bouta 1991; Whitcomb et al. 1996; Ross et al. 2016; Dunham 2016). I repeated this process twice before moving to the next survey point. I recorded the number of male and female Spruce Grouse observed at each survey point. I conducted all but two days of surveys alone: the other two survey days were conducted with a second observer. I repeated all surveys within each stand, but I alternated the order of points visited on the second round of surveying. In most instances I was able to survey a site in a single day, but occasionally I had to visit a stand on multiple days to survey all points. All research conducted within Acadia National Park was done under National Park Service permit number ACAD-2017-SCI-0018.

<u>Brooding Patch Occupancy</u>

I conducted summertime brood habitat surveys to evaluate the presence of females and broods within the perimeter regions of each breeding site. I began brood surveys on July 15 and continued until August 20. I began surveys thirty minutes before

sunrise and ended no later than 1pm, and I focused these surveys on the 8 sites known to be occupied by males during either the Whitcomb et al. (1996) study or my own. I played a chick distress call every 150m around the perimeter of each stand. I searched the perimeter of the stands because female Spruce Grouse with broods in Maine were observed in areas with more open forest canopies, which often have greater primary production and more food resources such as arthropods and herbaceous forbs (Dunham 2016). I played chick distress calls with one minute of listening before and after each call as described in the methods of Dunham (2016). If a female and/or brood was observed, I recorded the site, date, time, and number of chicks.

iButton Deployment

To characterize micro-climatic conditions within surveyed stands, I collected stand-level temperature data using thermochron data loggers as well as temperature and humidity hydrochron iButton data-loggers (Model DS1923. Dallas Semiconductor, Sunnyvale, CA, USA). I collected black bulb temperature (T_{bb}) by suspending a thermochron data logger within a black bulb apparatus which was constructed of two stainless steel mixing bowls spray-painted flat black (Figure 2). I suspended the data logger by attaching a unit with Velcro to a strip of cardboard, attached to the interior of the mixing bowl with super glue. I fastened two bowls together using bicycle inner tubing, cut to the circumference of the mixing bowl and stretched around the bowl's circumference and secured with two binder clips. T_{bb} is a closer representation of thermal conditions to which organisms are exposed, compared to ambient temperature (Helmuth et al. 2010), because it accounts variation in temperature associated with solar radiation and wind (Porter & Gates 1969; Carroll et al. 2016). Hydrochron data loggers were used

to measure ambient temperature, along with relative humidity in the area. To prevent the data loggers from getting wet and skewing humidity data, I used Velcro to attach them under a small plastic hood that was suspended above the ground on a wooden stake (Figure 2). I used a matched pair of black bulb and humidity-sensing data loggers at each site.

I distributed micro-climate sensors among all 18 stands beginning on July 25th and allowed 3 weeks of data collection. The warmest months in Maine are July and August (Fernandez et al. 2015), so I collected temperature and humidity data during this period to evaluate the maximum thermal environment experienced by Spruce Grouse on MDI. Data loggers were placed at breeding season survey points that fit specific criteria, including: (1) a centralized location within the stand and (2) 75-100% forest canopy cover. Forest patch edges are often hotter, drier and windier compared to forest interiors (Chen et al. 1993), and the interior forests of Spruce Grouse habitat are often dense and well shaded (Whitcomb et al. 1996; Dunham 2016; Schroeder et al. 2018). I used the criteria for data logger placement to best replicate Spruce Grouse habitat and the conditions they may experience during summer months. I avoided placing data loggers in areas of standing water. Each week, I uploaded data from each data logger onto a laptop before moving the data logger to another location within the stand. I collected micro-climatic data from 3 different points in each of the 18 stands.

Figure 2. Thermochron and hydrochron iButton units (data loggers) were used to measure black bulb temperature (T_{bb}), ambient temperature, and relative humidity. T_{bb} was measured using a data logger suspended in a black-bulb apparatus (*left*). Ambient temperature and humidity were measured using data loggers that were protected from rainfall by being secured under a plastic hood raised above the forest floor using a wooden stake (*right*).

Data Analysis

I used single season site-occupancy models to evaluate differences in the probability of occupancy among stands and also the probability of detection among surveys (Mackenzie et al. 2002). In order to run the occupancy model, I aggregated the point-level survey data into a stand level history that included my two replicated surveys of each stand. I tested multiple variables that I hypothesized could affect either occupancy or detection probability. The ambient noise produced by wind may affect an observer's ability to hear flutter flights and territorial calls (Conway & Gibbs 2001), so I tested the effect of wind speed on detection probability using the average of all wind speed measures recorded within a stand during a single day. 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), so I tested the effect of ordinal day on detection probability. I tested the effect of the time of a survey in relation to the time after sunrise on detection probability. 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). I tested the effects of stand size (ha) on occupancy probability. 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 found in patches smaller than 20 ha (Whitcomb et al. 1996). I tested the effect of daily average relative humidity, and average daily maximum temperature (C°) on occupancy probability. I tested these variables to see if there were any major differences in microclimatic factors between occupied and unoccupied stands. I calculated the daily maximum temperature values using the maximum temperature recorded for each day sampled and averaging the daily maximum temperature amongst all days sampled at each stand. I calculated the daily relative humidity by averaging the relative humidity per day sampled, and then averaging the daily averages per stand. T_{bb} was never analyzed because evaluation of a Pearson's Correlation Coefficient between T_{bb} and ambient temperature values (r=0.977) showed that values were nearly identical, likely a result of placing both data loggers in shaded areas.

I conducted a single-season occupancy analysis (Mackenzie et al. 2002) using the *unmarked* package in program R, implemented using RStudio (R Core Team 2003). I initially attempted to fit the model under a penalized likelihood (Hutchinson et al. 2015), however these models would not converge. I paired each detection variable with an intercept only model for occupancy, as well as each occupancy variable with an intercept only model for detection probability. I used a null model (intercept-only on both detection and occupancy) for my initial analysis as well. I ranked each of the above

models using Akaike information criterion corrected for small sample sizes (AICc), and I computed ΔAICc to determine the strength of evidence for each model (Burnham & Anderson 2002), using a criterion of $\Delta AICc < 2.00$. Based off results of initial model evaluation, I also tested wind as a detection covariate paired with site size (ha) as an occupancy covariate, as well as ordinal day as a detection covariate paired with site size (ha) as an occupancy covariate. I further evaluated 95% confidence intervals of the Beta coefficients to see whether they overlap 0.0 (no slope).

Following data collection and analysis, I calculated p*, which provides an estimate of the probability that an animal was detected at least once during a number of repeated surveys. This allowed me to evaluate, based on detection probability and number of surveys conducted, the probability that I missed Spruce Grouse within truly occupied stands. I used the formula $p^* = 1 – (1-p)^n$; where p is the probability of detecting a Spruce Grouse on a single survey, and n is the number of times the stand was surveyed.

RESULTS

I conducted callback surveys twice at 227 survey points spanning 18 stands, totaling 454 individual callback surveys. I detected Spruce Grouse in 4 of the 18 stands (Figure 3), and observed 7 unique individuals, including 6 males and 1 female (Table 1). I collected 159,342 climatic data readings among the 18 stands.

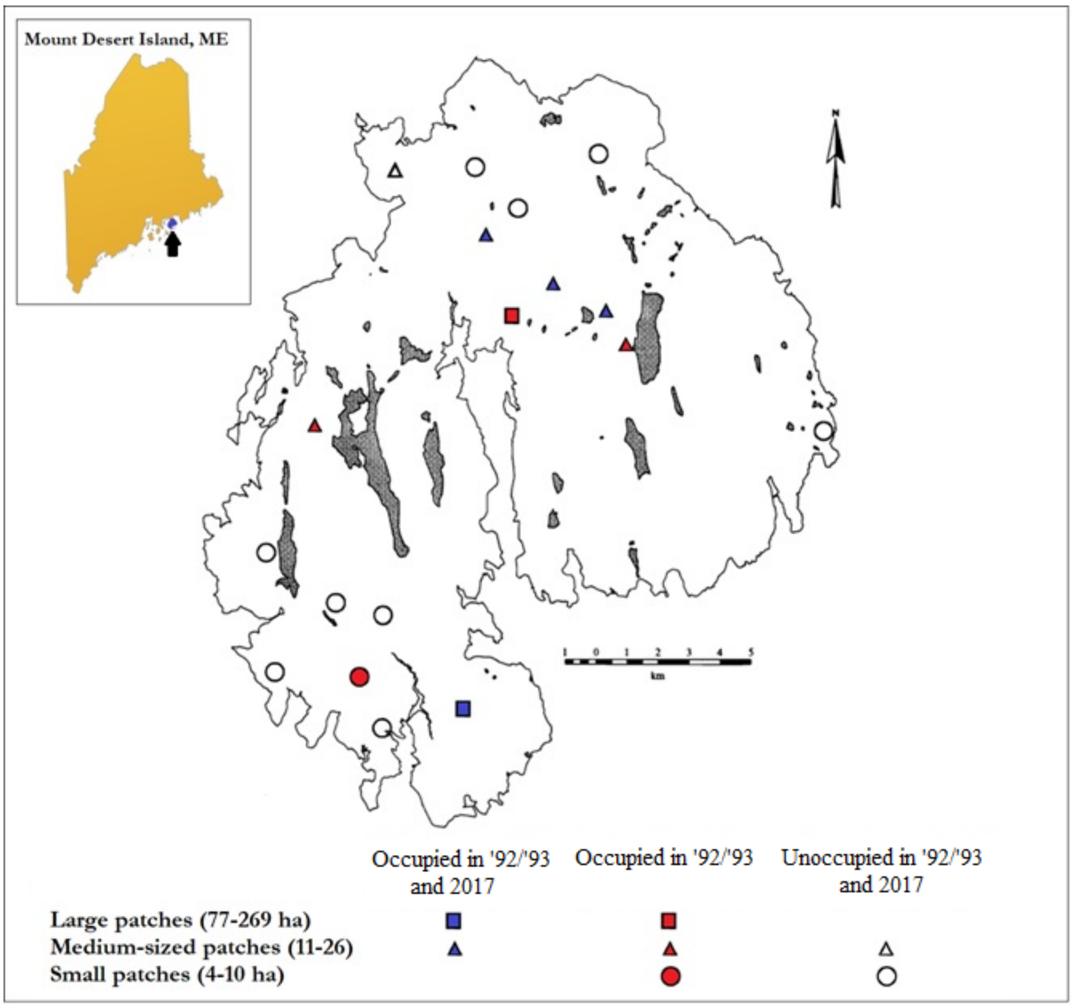

Figure 3. Changes in Spruce Grouse site occupancy on Mount Desert Island, Maine between the 1992/93 field seasons of Whitcomb et al. (1996) and my spring 2017 field season. This map was modified from the original map used in Whitcomb et al. (1996).

Table 1. Differences in observed Spruce Grouse populations from surveys on Mount Desert Island, ME, during the 1992, 1993, and 2017 field seasons. Data from the 1992 and 1993 field seasons were obtained from Whitcomb et al. (1996).

Site	**1992**	**1993**	**2017**
Aunt Betsy Brook (ABB)	4	4	2
Aunt Betty Pond (ABP)	6	10	1
Bernard (B)	0	0	0
China Hill (CH)	3	2	0
Dodge Point Rd (DPR)	0	0	0
Eagle Lake (EL)	4	4	0
Fresh Meadow (FM)	0	0	0
French Pond (FP)	0	0	0
Hio Bridge (HB)	12	7	3
Jones Marsh (JM)	0	0	0
Pretty Marsh (PM)	4	0	0
Saint Andrews (SA)	0	0	0
Sand Beach (SaB)	0	0	0
Stony Brook (SB)	0	0	0
Southern Heath (SH)	3	2	1
Whalesback (W)	14	10	0
West Mountain East (WME)	0	0	0
West Mountain West (WMW)	0	0	0
Total	50	39	7

Table 2. Differences in observed Spruce Grouse population demographics 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. (1996).

	1992		**1993**		**2017**	
Site[a]	Males	Females	Males	Females	Males	Females
ABB	4	0	3	1	2	0
ABP	4	2	6	4	1	0
B	0	0	0	0	0	0
CH	3	0	2	0	0	0
DPR	0	0	0	0	0	0
EL	3	1	3	1	0	0
FM	0	0	0	0	0	0
FP	0	0	0	0	0	0
HB	9	3	5	2	2	1
JM	0	0	0	0	0	0
PM	3	1	0	0	0	0
SA	0	0	0	0	0	0
SaB	0	0	0	0	0	0
SB	0	0	0	0	0	0
SH	2	1	2	0	1	0
W	8	6	7	3	0	0
WME	0	0	0	0	0	0
WMW	0	0	0	0	0	0
Total	36	14	28	11	6	1

[a] Site name abbreviations are given in Table 1.

The naïve occupancy (proportion of sites where individuals were detected) of Spruce Grouse on MDI during my surveys was 0.222. The average detection probability (p) estimate for a single survey was 0.857 (±0.141 SE), and estimated occupancy probability (ψ) was 0.226 (±0.100 SE). Based on AICc, four models that contained effects on detection and probability had ΔAICc < 2 and were competitive (Table 3). Two of these models only contained effects on detection probability and were not used for predictive measurements. A wind speed effect on detection probability was supported based on AICc however, the effect is uncertain due to the confidence intervals overlapping 0 (β = -6.03, ±11.60 SE). An ordinal day effect on detection probability was supported based on AIC_c however, the effect is uncertain due to confidence intervals

overlapping (β = 1.00, ±1.01 SE). Larger stands ($\bar{X}$ = 82.8ha) were more likely to be occupied, while smaller stands ($\bar{x}$ =14.0ha) were vacant; however, the effect of stand size on the probability of occupancy is uncertain as a result of the confidence intervals overlapping 0, despite being supported on AIC_c (Figure 4a; Table 4). Start time relative to sunrise had no effect on detection probability (β = 0.00, ±0.01 SE) (Table 4), and neither maximum stand temperature or average stand humidity appeared to have an effect on stand occupancy on AIC_c (Table 3; Figure 4b, 4c). The values for stand size, daily maximum stand temperature, and daily average stand humidity can be found in Appendix B.

Table 3. AICc assessments of single season occupancy models of Spruce Grouse on Mount Desert Island, Maine, 2017.

Model	nPars	AIC	Delta	AICwt	cumltvWt
pWind,ψArea	4	23.57	0.00	0.3456	0.35
pDay,ψArea	4	24.29	0.72	0.2414	0.59
pWind,ψ(.)	3	25.07	1.50	0.1633	0.75
pDay,ψ(.)	3	25.24	1.66	0.1506	0.90
p(.),ψArea	3	27.47	3.90	0.0492	0.95
p(.),ψ(.)	2	28.95	5.38	0.0235	0.97
pStart,ψ(.)	3	30.83	7.26	0.0092	0.98
p(.),ψTemp	3	30.94	7.37	0.0087	0.99
p(.),ψHumidity	3	30.96	7.39	0.0086	1.00

[a] 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; Area, size of stand (ha); Temp, average daily maximum temperature per stand (°C); Humidity, average daily relative humidity per stand.

Table 4. Estimates for parameters of site-occupancy models of male Spruce Grouse on Mount Desert Island, Maine, based on data obtained from callback surveys conducted during April and May 2017.

Covariate	Parameter Tested	Estimate (β)	SE	95% Confidence Interval Upper	Lower
Stand Size (ha)	Occupancy	0.02	0.02	0.07	-0.02
Avg. Humidity	Occupancy	-0.01	0.20	0.37	-0.40
Avg. Daily Max C°	Occupancy	0.02	0.19	0.39	-0.35
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

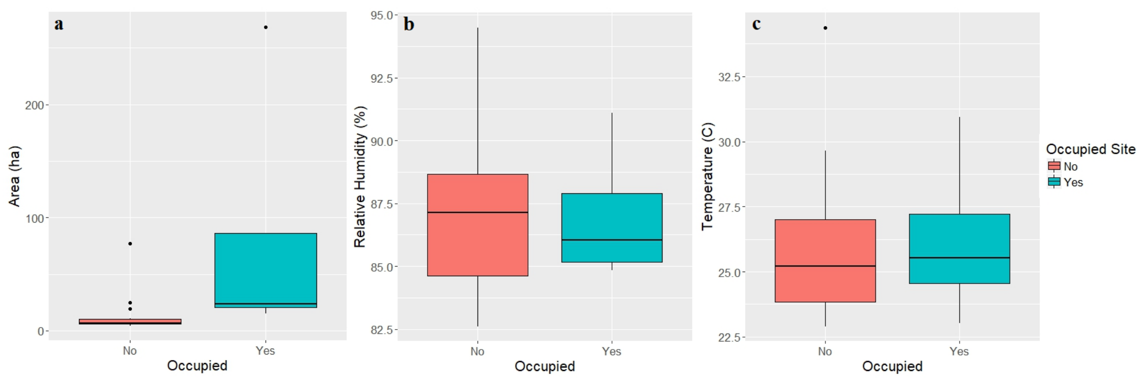

Figure 4. Differences in area (a), relative humidity (b), and average daily maximum temperature °C (c) between stands occupied or unoccupied by Spruce Grouse on Mount Desert Island, Maine, summer 2017

Based on an estimated detection probability of 0.857 (±0.141 SE) and each stand being surveyed twice, I calculated a p* value of 0.980. This value indicated that there was approximately a 2% chance, given my detection probability, I missed any occupied stands by conducting two surveys per stand.

DISCUSSION

There was a decrease in stand occupancy as well as overall abundance of Spruce Grouse on MDI over the 25-year span since Whitcomb et al (1996) conducted their study. Although I attempted to replicate Whitcomb et al.'s (1996) methods as closely as possible, there were some small differences that could have affected the comparison with their results. I conducted two rounds of call back surveys while Whitcomb et al. (1996) conducted three. I also ran an occupancy analysis accounting for detection probability while Whitcomb et al. (1996) only used naïve occupancy with no formal occupancy modeling. With a p* value of 0.980, this implies that if I were to conduct a third survey, Spruce Grouse stand occupancy would remain at 4 out of 18 stands. Assuming that Whitcomb et al. (1996) had a similar detection probability to my study, there is a high likelihood that they observed all occupied stands (8) as well. This suggests that over the 25-year span since the Whitcomb et al. (1996) study, stand occupancy of Spruce Grouse on MDI has decreased from 8 stands to 4.

All small stands that were previously unoccupied remained unoccupied during my surveys, and large and medium sized patches such as Whalesback, Eagle Lake, China Hill, and Pretty Marsh became unoccupied. Stands that remained occupied by Spruce Grouse were, on average, larger than those not occupied. However, there is a level of uncertainty of an effect due to having confidence intervals that overlapped 0. This may mean that there are other habitat quality metrics besides stand size that effect occupancy which were not tested; such as shrub density, total basal area, canopy cover, conifer tree density, deciduous tree density, and sapling density as tested in Dunham 2016. Spruce

Grouse tend to have a home range of around 4ha and stands smaller than 20ha often do not support Spruce Grouse populations (Fritz 1979). Whitcomb et al. (1996) showed that stands < 20ha supported populations of Spruce Grouse on MDI in the 1990s. Of the four remaining occupied stands, only 1 stand was less than 20ha during my study. There was no statistical difference in micro-climatic parameters between occupied and unoccupied stands. Stand size appears to be a potential limiting factor in determining occupancy of Spruce Grouse.

The Spruce Grouse of MDI were deemed to resemble a spatially structured population by Whitcomb et al. (1996), which can be defined as sets of local populations that interact through individual dispersal (Revillaa & Wiegand. 2008). Patch occupancy may have decreased over the span of 25 years because of lack of stand recolonization following localized extinction. Small stands of suitable Spruce Grouse habitat would have low numbers of individuals, which could lead to poor reproductive productivity and localized extinction (Grant and Antonovics 1978; Guo et al. 2005). Prior research has found that when Adélie Penguin (*Pygoscelis adeliae*) colonies were isolated from one another by the grounding of immense icebergs, colony connectivity was disturbed and overall survival in small and medium sized patches was low (Dugger et al. 2010). When local populations in small- and medium-sized patches go extinct, a burden on populations in larger habitat patches to negate localized extinctions through greater local productivity and dispersal to newly vacant patches are necessary to maintain metapopulation stability. Should productivity in the larger stands decrease, the likelihood of neighboring patch recolonizations will decrease as well (Robles and Ciudad 2002). Research in New York and in Maine found that these spatially structured population characteristics can be

observed in Spruce Grouse populations at southern-range margins as a result of the mosaic between deciduous and coniferous forests, which leads to fragmented habitat (Ross et al. 2016, Whitcomb et al. 1996). Studies on the Bog Fritillary Butterfly, (*Boloria eunomia*) which exhibited spatially structured population characteristics, were found to be in a fragmented landscape at their southern range limit. This spatially structured population was able to persist in medium and large patches with individuals observed dispersing over longer distances compared to center range populations (Mennechez et al. 2003). Like center range populations, spatially structured populations found at range margins are more likely to persist in larger habitat patches, and stand size often affects whether a species occurs or not in a given area (Blomberg et al. 2012).

With stands occurring on both private and National Park lands, land management practices can also influence the maintenance of Spruce Grouse populations via suitable habitat. Private land is susceptible to land use practices which can lead to habitat loss. I observed portions of habitat within the privately-owned sections of the Pretty Marsh stand that showed signs of development leading to removal of forest cover and loss of potential habitat for Spruce Grouse. This site was previously occupied but I failed to detect Spruce Grouse there during my study. Of the 4 occupied stands, only 1 was located on private land; the Aunt Betsy Brook stand is one of the larger stands and is also comprised of predominately forested wetland, so there is little land suitable for development.

Habitat patches within Acadia National Park or conservation easements could also become unsuitable for Spruce Grouse through time as a result of small scale forest management practices and resulting forest succession. Research in northern Maine found

that Spruce Grouse abundance was highest in mid-successional, moderately dense, conifer-dominated stands that experienced intensive forestry practices to promote coniferous regeneration (Dunham 2016). Research in New York also found that forest maturation played a role in determining Spruce Grouse occupancy and apparent declines since the 1970s (Ross et al. 2016). Mid-successional forests are characterized by shorter and denser trees with a dense layer of ground vegetation. These forests are favorable for both shade intolerant species such as Tamarack and more shade tolerant species like Black Spruce, which are known components of Spruce Grouse habitat (Naylor and Bendell 1989; Bouta 1991). Ross et al. (2016) found that unoccupied stands were dominated by Balsam Fir, a very shade tolerant species. Tamarack and pines tend to replace themselves mainly on burned sites (Johnston 1990), while Balsam Fir is considered a later successional species, occurring 100+ years after fires (Bergeron et al. 2001). Fire is a natural disturbance regimen in central Canada and Michigan and Minnesota (Bergeron et al. 2001). Processes linked to natural forest disturbances in the eastern portion of the Spruce Grouse range are insects such as Spruce Budworm (*Choristoneura* sp.) (Ammann 1963), and major wind disturbances. A lack of active silvicultural management on Acadia National Park lands has led to a decrease in understory cover and mid-successional forests. Being a tourist destination in the eastern United States, insect outbreaks are typically suppressed and fires are uncommon. A major wildfire on MDI occurred in 1947 (National Park Service 2015). Three occupied stands and 2 previously occupied stands were affected by the fire of 1947. Other than the fire of 1947, there have been a minimal number of natural disturbances. If natural disturbance

regimes are suppressed without proper forest management, successional processes may lead to extirpation of Spruce Grouse on MDI.

Other causes for decline could be attributed to demographic stochasticity and an already low population size on the island. With small populations, demographic stochasticity has a substantial effect on population growth and extinction risk (Lande et al. 2003). Random mortality events can be crucial to a small population, as the death of one individual can have a disproportionate effect on the potential for population growth (Lee et al. 2011). I only observed 7 individual Spruce Grouse on MDI and only one of those individuals was a female. However, callback surveys are biased towards detecting males and not females, so I believe there are more females on MDI than one individual. With a small population, if a female were to die by random chance, the Spruce Grouse birth rate on MDI would decrease, due to losing a reproducing individual (Lee et al. 2011).

The persistence of small, relatively isolated populations may be dependent on immigration, because populations are often at higher risks of extinction when on islands isolated from the mainland (Diamond 1984). Spruce Grouse are found on Schoodic Peninsula, the closest mainland population, and the shore to shore distance from MDI to Schoodic Peninsula is approximately 9.2km, separated by Frenchman's Bay. Research on MDI found that maximum dispersal distance of juvenile Spruce Grouse was 7.2km (Whitcomb et al. 1996), while, other research has found individuals able to travel up to 11km (Schroeder 1985). Both studies had no instances of dispersal over water (Schroeder 1985, Whitcomb et al. 1996). The distance between the Schoodic Peninsula and MDI is within the maximum dispersal range, meaning there is potential for mainland

connectivity, but it is unknown if Spruce Grouse are capable of, or willing to disperse over bodies of water. It would be interesting to test for connectivity between MDI and Schoodic Peninsula given the potential barrier imposed by Frenchman's Bay.

Based on my research, the MDI population of Spruce Grouse has decreased since the 1990s. I recommend further monitoring to see if the population improves over the next few years or if it continues to decline. The decrease in occupancy I observed on MDI is similar to that observed in New York (Ross et al. 2016). There appears to be a southern-range effect on Spruce Grouse on MDI. Additionally, there may also be additive affects as a result of isolation on an island. It would also be interesting to see if the southern range populations on Schoodic Peninsula and the surrounding mainland also show characteristic declines observed in both Whitcomb et al. (1996) and Ross et al. (2016). Fortunately, Spruce Grouse found in Northern Maine appear to be performing well (Dunham 2016) and the species should be able to persist in the State. Climate change may affect these populations in the future, but more research is needed to determine how these populations will be affected.

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APPENDICES

APPENDIX A

Appendix Table A. Site coding, survey point coordinates, and occupancy survey history for Spruce Grouse on Mount Desert Island, Maine, summer 2017.

Site Name	Transect	Point	Code Name	X	Y	Survey 1	Survey 2
Jones Marsh	1	1	JM-1-1	550796	4918084	0	0
		2	JM-1-2	550946	4918084	0	0
		3	JM-1-3	551096	4918084	0	0
	2	1	JM-2-1	551546	4918384	0	0
		2	JM-2-2	551546	4918234	0	0
		3	JM-2-3	551546	4918084	0	0
	3	1	JM-3-1	551696	4917934	0	0
		2	JM-3-2	551846	4917934	0	0
		3	JM-3-3	551996	4917934	0	0
	4	1	JM-4-1	551846	4918384	0	0
		2	JM-4-2	551996	4918234	0	0
		3	JM-4-3	552146	4918084	0	0
Fresh Meadow	1	1	FM-1-1	553946	4918534	0	0
		2	FM-1-2	553946	4918384	0	0
		3	FM-1-3	553946	4918234	0	0
		4	FM-1-4	553946	4918084	0	0
	2	1	FM-2-1	554096	4918084	0	0
		2	FM-2-2	554096	4917934	0	0
		3	FM-2-3	554096	4917784	0	0
		4	FM-2-4	554096	4917634	0	0
Stony Brook	1	1	SB-1-1	557996	4918384	0	0
		2	SB-1-2	558146	4918534	0	0
	2	1	SB-2-1	557846	4918534	0	0
		2	SB-2-2	557996	4918684	0	0
		3	SB-2-3	558146	4918834	0	0
French Pond	1	1	FP-1-1	555446	4917034	0	0
		2	FP-1-2	555446	4916884	0	0
		3	FP-1-3	555446	4916734	0	0
		4	FP-1-4	555446	4916584	0	0
		5	FP-1-5	555446	4916434	0	0
		6	FP-1-6	555446	4916284	0	0
Aunt Betsy Brk.	1	1	ABB-1-1	554546	4916134	0	0
		2	ABB-1-2	554546	4915984	0	0
		3	ABB-1-3	554546	4915834	0	0
		4	ABB-1-4	554546	4915684	0	0
	2	1	ABB-2-1	554396	4915834	0	0
		2	ABB-2-2	554396	4915684	0	0

		3	ABB-2-3	554396	4915534	1	1
		4	ABB-2-4	554396	4915384	0	0
	3	1	ABB-3-1	554246	4915534	0	0
		2	ABB-3-2	554246	4915684	0	0
		3	ABB-3-2	554246	4915834	0	0
		4	ABB-3-4	554246	4915984	0	0
		5	ABB-3-5	554246	4916134	0	0
	4	1	ABB-4-1	554096	4915834	0	0
		2	ABB-4-2	554096	4915684	1	0
		3	ABB-4-3	554096	4915534	0	0
Southern Heath	1	1	SH-1-1	556196	4914184	0	0
		2	SH-1-2	556346	4914184	1	0
	2	1	SH-2-1	556346	4914334	0	0
		2	SH-2-2	556496	4914334	0	0
	3	1	SH-3-1	556496	4914484	0	0
		3	SH-3-3	556496	4914784	0	0
	4	1	SH-4-1	556046	4914784	0	0
		2	SH-4-2	556046	4914634	0	0
Whalesback	1	1	W-1-1	555146	4912834	0	0
		2	W-1-2	555146	4912984	0	0
		3	W-1-3	555146	4913134	0	0
		4	W-1-4	555146	4913284	0	0
	2	1	W-2-1	555296	4913284	0	0
		2	W-2-2	555296	4913434	0	0
		3	W-2-3	555296	4913584	0	0
		4	W-2-4	555296	4913734	0	0
	3	1	W-3-1	555446	4913734	0	0
		2	W-3-2	555446	4913584	0	0
		3	W-3-3	555446	4913434	0	0
		4	W-3-4	555446	4913284	0	0
		5	W-3-5	555446	4913134	0	0
		6	W-3-6	555446	4912984	0	0
		7	W-3-7	555446	4912834	0	0
	4	1	W-4-1	555596	4912834	0	0
		2	W-4-2	555596	4912984	0	0
		3	W-4-3	555596	4913134	0	0
		4	W-4-4	555596	4913284	0	0
		5	W-4-5	555596	4913434	0	0
	6	1	W-6-1	554396	4914034	0	0
		2	W-6-2	554546	4914034	0	0
		3	W-6-3	554696	4914034	0	0
		4	W-6-4	554846	4914034	0	0
	7	1	W-7-1	554846	4914184	0	0
		2	W-7-2	554846	4914334	0	0
		3	W-7-3	554846	4914484	0	0
		4	W-7-4	554846	4914634	0	0

		5	W-7-5	554846	4914784	0	0
		6	W-7-6	554846	4914934	0	0
		7	W-7-7	554846	4915084	0	0
	8	1	W-8-1	554996	4914784	0	0
		2	W-8-2	555146	4914634	0	0
		3	W-8-3	555296	4914484	0	0
		4	W-8-4	555446	4914334	0	0
		5	W-8-5	555596	4914184	0	0
	9	1	W-9-1	555446	4914184	0	0
		2	W-9-2	555446	4914034	0	0
		3	W-9-3	555446	4913884	0	0
Aunt Betty Pond	1	1	ABP-1-1	558146	4913284	0	0
		2	ABP-1-2	558146	4913434	0	0
		3	ABP-1-3	558146	4913584	0	1
		4	ABP-1-4	558146	4913734	0	0
	2	1	ABP-2-1	558296	4913734	0	0
		2	ABP-2-2	558296	4913584	0	0
		3	ABP-2-3	558296	4913434	0	0
		4	ABP-2-4	558296	4913284	0	0
		5	ABP-2-5	558296	4913134	0	0
	3	1	ABP-3-1	558446	4912984	0	0
		2	ABP-3-2	558446	4913134	0	0
		3	ABP-3-3	558446	4913284	0	0
		4	ABP-3-4	558446	4913434	0	0
		5	ABP-3-5	558446	4913584	0	0
	4	1	ABP-4-1	558596	4913434	0	0
		2	ABP-4-2	558596	4913284	0	0
		3	ABP-4-3	558596	4913134	0	0
		4	ABP-4-4	558596	4912984	0	0
Eagle Lake	1	1	EL-1-1	558596	4912384	0	0
		2	EL-1-2	558746	4912384	0	0
		3	EL-1-3	558896	4912384	0	0
		4	EL-1-4	559046	4912384	0	0
		5	EL-1-5	559196	4912384	0	0
	2	2	EL-2-2	559046	4912234	0	0
		3	EL-2-3	558896	4912234	0	0
		4	EL-2-4	558746	4912234	0	0
		5	EL-2-5	558596	4912234	0	0
	3	1	EL-3-1	558746	4912084	0	0
		2	EL-3-2	558896	4912084	0	0
		3	EL-3-3	559046	4912084	0	0
Sand Beach	1	1	SaB-1-1	565196	4909384	0	0
		2	SaB-1-2	565346	4909384	0	0
	2	1	SaB-2-1	565496	4909384	0	0
		2	SaB-2-2	565346	4909534	0	0
	3	1	SaB-3-1	565346	4909684	0	0

		2	SaB-3-2	565196	4909534	0	0
Pretty Marsh	1	1	PM-1-1	548846	4909834	0	0
		2	PM-1-2	548846	4909984	0	0
	2	2	PM-2-2	548996	4910134	0	0
		3	PM-2-3	548996	4909984	0	0
	3	1	PM-3-1	549146	4909834	0	0
		2	PM-3-2	549296	4909984	0	0
		3	PM-3-3	549446	4910134	0	0
St. Andrews	1	1	SA-1-1	547196	4905484	0	0
		2	SA-1-2	547196	4905634	0	0
		3	SA-1-3	547196	4905784	0	0
	2	1	SA-2-1	547346	4905634	0	0
		2	SA-2-2	547346	4905484	0	0
		3	SA-2-3	547346	4905334	0	0
W. Mt. West	1	1	WMW-1-1	549446	4904134	0	0
		2	WMW-1-2	549446	4903984	0	0
		3	WMW-1-3	549446	4903834	0	0
	2	1	WMW-2-1	549596	4903834	0	0
		2	WMW-2-2	549596	4903984	0	0
W. Mt. East	1	1	WME-1-1	550946	4903834	0	0
		2	WME-1-2	550946	4903684	0	0
		3	WME-1-3	550946	4903534	0	0
		4	WME-1-4	550946	4903384	0	0
	2	1	WME-2-1	551096	4903384	0	0
		2	WME-2-2	551096	4903534	0	0
		3	WME-2-3	551096	4903684	0	0
		4	WME2-4	551096	4903834	0	0
Dodge Point Rd.	1	1	DPR-1-1	547196	4901734	0	0
		2	DPR-1-2	547346	4901584	0	0
		3	DPR-1-3	547346	4901434	0	0
	2	1	DPR-2-1	547469	4901734	0	0
		2	DPR-2-2	547469	4901884	0	0
	3	1	DPR-3-1	547646	4901734	0	0
		2	DPR-3-2	547646	4901584	0	0
China Hill	1	1	CH-1-1	550196	4901134	0	0
		2	CH-1-2	550196	4901284	0	0
	2	1	CH-2-1	550346	4901284	0	0
		2	CH-2-2	550346	4901434	0	0
		3	CH-2-3	550346	4901584	0	0
		4	CH-2-4	550346	4901734	0	0
	3	1	CH-3-1	550496	4901734	0	0
		2	CH-3-2	550496	4901584	0	0
Bernard	1	1	B-1-1	550796	4900084	0	0
	2	1	B-2-1	551096	4899934	0	0
Hio Bridge	1	1	HB-1-1	553346	4900684	0	0
		2	HB-1-2	553496	4900543	0	0

	3	HB-1-3	553646	4900384	0	0
	4	HB-1-4	553796	4900234	0	0
	5	HB-1-5	553946	4900084	0	0
	6	HB-1-6	554096	4899934	0	0
2	1	HB-2-1	554096	4900084	0	0
	2	HB-2-2	553946	4900234	0	0
	3	HB-2-3	553796	4900384	0	0
	4	HB-2-4	553646	4900534	0	0
	5	HB-2-5	553496	4900684	0	0
3	1	HB-3-1	553646	4900684	0	0
	2	HB-3-2	553796	4900534	0	0
4	1	HB-4-1	553646	4899334	0	0
	2	HB-4-2	553646	4889184	0	0
	3	HB-4-3	553646	4899034	0	0
	4	HB-4-4	553646	4898884	0	0
	5	HB-4-5	553646	4898734	0	0
5	1	HB-5-1	553796	4898734	0	0
	2	HB-5-2	553796	4898884	0	0
	3	HB-5-3	553796	4899034	1	0
	4	HB-5-4	553796	4899184	0	0
	5	HB-5-5	553796	4899334	0	0
6	1	HB-6-1	553946	4899484	0	0
	2	HB-6-2	553946	4899334	0	0
	3	HB-6-3	553946	4899184	0	0
	4	HB-6-4	553946	4899034	0	0
	5	HB-6-5	553946	4898884	0	0
	6	HB-6-6	553946	4898734	0	0
	7	HB-6-7	553946	4898584	0	0
	8	HB-6-8	553946	4898434	0	0
	9	HB-6-9	553946	4898284	0	0
	10	HB-6-10	553946	4898134	0	0
7	1	HB-7-1	554246	4898134	0	0
	2	HB-7-2	554396	4898284	0	0
	3	HB-7-3	554546	4898434	0	0
8	1	HB-8-1	554396	4898584	0	0
	2	HB-8-2	554246	4898734	1	1
	3	HB-8-3	554096	4898884	0	0
9	1	HB-9-1	554096	4899034	0	0
	2	HB-9-2	554096	4899184	0	0
	3	HB-9-3	554096	4899334	0	0
10	1	HB-10-1	554246	4899334	0	0
	2	HB-10-2	554246	4899184	0	0
	3	HB-10-3	554246	4899034	0	0
	4	HB-10-4	554246	4898884	0	0
	5	HB-10-5	554246	4898734	0	0
11	1	HB-11-1	554396	4898884	0	0

	2	HB-11-2	554396	4899034	0	0
	3	HB-11-3	554396	4899184	0	0
	4	HB-11-4	554396	4899334	0	0
12	1	HB-12-1	554546	4899334	0	0
	2	HB-12-2	554546	4899184	0	0
	3	HB-12-3	554546	4899034	0	0

APPENDIX B

Appendix Table B. Stand occupancy with occupancy covariate values of stand area, average daily maximum temperature (°C), and average daily relative humidity (%), and their standard deviations (S.D.), on Mount Desert Island, Maine, summer 2017.

Site	Area (ha)	Occupied	Avg. Daily Max Temp	Temp S.D.	Avg. Daily Humidity	Humidity S.D.
HB	268.8	Yes	23.01	2.75	91.10	4.82
ABP	25.5	Yes	25.06	3.81	85.27	8.85
ABB	22.1	Yes	30.93	6.89	86.84	9.00
SH	14.8	Yes	25.97	3.84	84.85	7.87
W	77.0	No	27.19	4.54	82.94	8.68
PM	25.1	No	28.26	5.35	85.78	8.98
EL	19.5	No	29.65	5.42	83.92	8.83
JM	10.6	No	34.38	8.24	84.24	7.63
DPR	8.4	No	22.90	2.68	89.47	7.91
CH	8.1	No	25.66	3.89	89.11	8.19
WME	6.9	No	23.54	3.35	88.13	8.00
SB	6.7	No	26.48	4.12	88.78	6.12
FM	6.5	No	26.41	4.00	86.06	7.40
B	6.4	No	24.12	2.89	86.13	5.59
SA	5.8	No	23.10	3.51	88.36	6.33
SaB	5.8	No	23.76	4.63	94.49	7.94
FP	5.0	No	24.66	3.23	82.62	6.01
WMW	4.4	No	24.76	3.28	88.15	7.75

AUTHOR'S BIOGRAPHY

Christopher J. Gilbert was born on November 28, 1995 in Greenfield, Massachusetts. He grew up in Bernardston, Massachusetts and graduated from Pioneer Valley Regional High School in 2014. While at the University of Maine, Chris majored in Wildlife, Fisheries & Conservation Biology. Chris was a member of Sigma Phi Epsilon: Maine Alpha Chapter. An avid birdwatcher, Chris co-founded the Marsh Island Birding Club at the University of Maine. Chris has received the Robert I. Ashman Award during his time in the Wildlife, Fisheries & Conservation Biology Department.

Upon graduation, Chris will be working with seabirds off the coast of Maine and later on hopes to travel the United States working avian technician positions before returning to graduate school for his Master's degree and eventually his PhD.