



# Environmental conditions modulate compensatory effects of site dependence in a food-caching passerine

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**Abstract.** Although density regulates the abundance of most wild animal populations by influencing vital rates, such as fecundity and survival, the mechanisms responsible for generating negative density dependence are unclear for many species. Site dependence occurs when there is preferential filling of high-quality territories, which results in higher per capita vital rates at low densities because a larger proportion of occupied territories are of high quality. Using 41 yr of territory occupancy and demographic data, we investigated whether site dependence was a mechanism acting to influence fecundity and, by extension, regulate a population of Canada Jays in Algonquin Provincial Park, Ontario, Canada. As predicted by site dependence, the proportion of occupied territories that were of high quality was negatively correlated with population density and periods of vacancy were shorter for high-quality territories than for low-quality territories. We also found evidence that per capita fecundity was positively related to the proportion of occupied territories that were of high quality, but only when environmental conditions, which influence the entire population, were otherwise poor for breeding. Our results suggest that site dependence likely plays a role in regulating this population but that environmental conditions can modulate the strength of density dependence.

**Key words:** Canada Jays; density dependence; food hoarding; habitat heterogeneity; hoard-rot; *Perisoreus canadensis*; site-dependent fecundity; site-dependent regulation.

## INTRODUCTION

Density dependence, a common process regulating most wild animal populations (Lack 1966, Sinclair 1989, Ferrer and Donazar 1996, Rodenhouse et al. 1997), is characterized by a negative relationship between abundance and population growth, or individual vital rates, such as survival or fecundity (Sibly and Hone 2002). The strength of density dependence can vary between vital rates of a single population (Herrando-Pérez et al. 2012; Sutton et al., *in press*), between conspecific populations at different locations (Forchhammer et al. 1998, Johnson 2006, Thorson et al. 2015), and between species (Saitoh et al. 1999, Chen et al. 2019). It is, therefore, important to understand the mechanisms that promote density-dependent relationships and how additional variables, such as environmental conditions, may modulate the strength of density-dependent relationships (Coulson et al. 2001, Hansen et al. 2019).

One mechanism that can produce density dependence in wild populations is site-dependent regulation (Ferrer and Donazar 1996, Rodenhouse et al. 1997). Site-

dependent regulation occurs when organisms preferentially fill territories that vary in suitability, such that per capita fecundity and/or survival is negatively related to population density (because a lower proportion of individuals occupy high-quality territories; Rodenhouse et al. 1997). Thus, for site-dependent regulation to act on a population there must be habitat heterogeneity and individuals must be territorial (Brown 1969, Pulliam and Danielson 1991). Site-dependent regulation predicts that high-quality territories will be occupied at a faster rate than low-quality territories, per capita fecundity will be negatively correlated with density, but that fecundity within a territory class should not decline with increasing density (i.e., fecundity will remain high in high-quality territories even as density increases; Brown 1969, Ferrer and Donazar 1996, Ferrer et al. 2006, 2008, Grünkorn et al. 2014). Density-dependent relationships resulting from site-dependent regulation are, therefore, not produced by a crowding mechanism, but through the preferential use of sites that differ in suitability (Rodenhouse et al. 1997).

Despite the fact that territoriality and variation in habitat quality are common features of natural systems, there is only limited evidence for site-dependent regulation acting on wild populations, with most work

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focusing on birds (Rodenhouse et al. 1997, Penteriani et al. 2003, Kokko et al. 2004, Nevoux et al. 2011, Ferrer et al. 2014), in particular birds of prey (Sergio and Newton 2003). Many studies investigating site-dependent regulation have reported preferential occupation of high-quality sites (Kokko et al. 2004, Ferrer et al. 2014, Flesch et al. 2015, Zuberogoitia et al. 2019) and that site dependence regulates fecundity (Krüger and Lindström 2001, Kokko et al. 2004, Nevoux et al. 2011, Zuberogoitia et al. 2019). Additionally, when site-dependent regulation is acting on a population, high-quality territories can contribute a disproportionate amount of the overall number of young produced in a given year (Ferrer and Donazar 1996, Zuberogoitia et al. 2019). A relatively small number of studies have investigated how extrinsic conditions, such as weather, can interact with territory quality and modulate the effects of density on fecundity, and results are equivocal, with some studies suggesting that high-quality territories may buffer individuals from severe weather events (Franklin et al. 2000, Ferrer et al. 2014, Zuberogoitia et al. 2019), while others suggest that weather events may influence all territories equally (Reynolds et al. 2017).

The Canada Jay (*Perisoreus canadensis*) is a year-round territorial passerine whose range includes all of North America's boreal forest north to the tree line and subalpine forests of the Rocky Mountains as far south as Arizona (Strickland and Ouellet 2020). During the summer and fall, Canada Jays cache a variety of perishable food items, including mushrooms, berries,

arthropods, and vertebrate flesh, in the bark and branches of trees (Strickland and Ouellet 2020), and later depend on those caches for their over-winter survival and late-winter reproduction (Sechley et al. 2014, Derbyshire et al. 2018). Given this critical dependence on perishable cached food items, two factors have been proposed as being especially important for Canada Jay survival and reproductive success. The first is a consistent, below-freezing winter temperature regime, which is supported by evidence indicating that Canada Jay reproductive performance is *greater* following falls and winters of *lower* than normal temperatures and/or numbers of fall freeze-thaw events (Waite and Strickland 2006, Sutton et al. 2019, *in press*). The second is the availability and quality of storage sites that preserve cached food over time. Algonquin Provincial Park, lying in a transition zone between southern, mainly broadleaf forests and northern, mainly coniferous forests has a highly heterogeneous patchwork of differing environments (Fig. 1C, D; Strickland 2015). Using simulated caches, Strickland et al. (2011) provided evidence that, compared to deciduous trees, conifers were better able to preserve perishable food items and they speculated that this was because of the antimicrobial properties of conifer resins. A higher proportion of conifers on Canada Jay territories in Algonquin Provincial Park, Ontario, Canada is also associated with higher rates of occupancy (Strickland et al. 2011), a greater likelihood of successfully fledging young (Strickland et al. 2011, Whelan et al. 2016), and a higher probability of both adults and

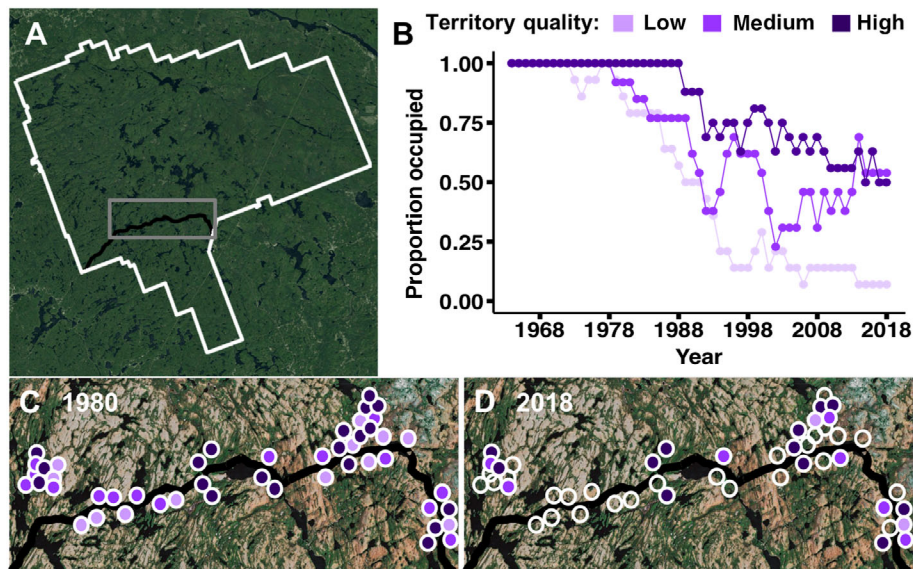


FIG. 1. Study area, distribution of occupied territories, and decline in territory occupancy over time of Canada Jays in Algonquin Provincial Park, Ontario, Canada. (A) Study area (gray box) within Algonquin Provincial Park. (B) Decline in territory occupancy in relation to territory quality (as defined by Strickland et al. 2011) indicated by the shades of purple, with darker shades representing higher quality territories. Circles in panels C and D represent the distribution of occupied territories in a high (1980) and a low density (2018) year, respectively. Territory quality is again indicated by shades of purple. Empty circles represent territories that were not occupied during that year.

juveniles dispersing onto these territories (Norris et al. 2013).

We examined whether site-dependent regulation of fecundity was acting on a population of Canada Jays in Algonquin Provincial Park. To do this, we used 41 yr of occupancy and demographic data to examine the effect of density and territory quality on territory occupancy, the effect of territory quality on the time that a territory remained vacant, and the effect of density and the proportion of occupied territories that were of high quality on per capita fecundity, estimated by brood size. We focused on fecundity rather than survival because fecundity is the major vital rate driving population growth rate and is also negatively density dependent (Sutton et al., *in press*). The regulation of fecundity is, therefore, likely to contribute strongly to population regulation of Canada Jays in Algonquin Provincial Park. We predicted that site-dependent regulation would result in an interaction between density and territory occupancy, such that density would have the strongest effect on the occupancy of low-quality territories. The slope of the relationship between density and territory occupancy would be steepest for low-quality territories and shallowest for high-quality territories. We also predicted that high-quality territories would remain vacant for shorter periods of time compared to lower-quality territories. Finally, we predicted that the proportion of occupied territories that were of high quality would influence per capita fecundity and also be a better predictor than overall density of the population.

Due to the strong influence of environmental conditions on reproductive performance (Waite and Strickland 2006, Sutton et al. 2019, *in press*), we also investigated two competing hypotheses of how weather could influence the strength of site-dependent regulation of fecundity. The first hypothesis was that high-quality territories would buffer breeders from the negative effects of freeze-thaw events by limiting degradation of cached food. Because breeding pairs on high-quality territories would have more cached food supplies, due to superior ability of conifers to preserve cached food over time that could be used to support reproduction, we predicted that there would be an interaction between the proportion of occupied territories that are of high quality and the number of freeze-thaw events on per capita fecundity. In years with a higher than average number of fall freeze-thaw events (poor breeding conditions), we expected a positive relationship between the proportion of occupied territories that were of high quality and per capita fecundity. However, in years with a low number of freeze-thaw events (good breeding conditions), we expected the proportion of occupied territories that were of high quality to have no effect on per capita fecundity because environmental conditions would not have pronounced effects on cached food quality (i.e., caches are being preserved by environmental conditions) and all territories would perform equally well. Alternatively, a competing hypothesis could be that fall freeze-thaw

events cause a decline in reproductive success equally across all levels of territory quality. Following this, we predicted that per capita fecundity would be negatively correlated with the number of fall freeze-thaw events and that this effect would be consistent across years, regardless of the proportion of occupied territories that were of high quality. This means that the negative effect of freeze-thaw events will decrease the magnitude, but not the direction, of the slope of the relationship between the proportion of occupied territories that were of high quality and per capita fecundity.

## METHODS

### *Study system and field methods*

We used demographic and territory occupancy data collected between 1977 and 2018 from an individually marked population of Canada Jays in Algonquin Provincial Park, Ontario, Canada (45°35' N, 78°30' W). The study area, situated along the highway 60 corridor in the park (Fig. 1A), is located within the transition zone of the Great Lakes–St. Lawrence hardwood forest and the boreal forest along the southern edge of the Canada Jay's range (Strickland et al. 2011).

From mid-February until 1 March, a population count was conducted to estimate the number of individuals in the study area. During the population count, we visited each territory multiple times to identify breeding adults and non-breeding juveniles by resighting their unique color band combinations. The number of individuals present during this period was used as an estimate of density for the study area. If no individuals were detected on a given visit to a territory, a suet bait would be left in the territory and checked multiple times every day for at least the next 5 d. Canada Jays are attracted to suet baits and typically take no more than 1–2 d to discover a suet bait placed within their territory. Therefore, if a suet bait remained untouched, or no Canada Jays were observed going to the suet bait, the territory was considered vacant. In addition to this monitoring, we also used observations by visitors to the park to help identify individuals and determine if a territory was vacant. Together, our monitoring and public observations give us a high degree of confidence that if no individuals were observed on a territory that territory was vacant. Throughout the study period, additional territories have been added to allow for the continuous monitoring of 20–25 breeding pairs each year, with 40 territories monitored in 1988, 48 in 1998, 49 in 2009, and 61 territories in 2018. Despite additional territories being added over time, count methods have not changed over time providing a consistent method to estimate density in the study area.

Occupancy was determined for all territories each year and a territory was considered occupied if at least one Canada Jay was present. Continuous monitoring of all territories, regardless of whether or not they were

occupied, also allowed us to determine when a territory first became vacant and when it was reoccupied in order to determine the number of years it remained vacant. In many cases, territories were vacated and reoccupied multiple times and we treated each of these reoccupation events separately. For example, if a territory was occupied from 1980–1983, 1990–1996, and 2000–2018, we considered this as two separate periods of vacancy (7 and 4 yr, respectively). If a territory was vacant at the end of the study period (2018), we considered the number of years it remained unoccupied to be from the point it last became vacant until 2018.

As stated above, we also monitored 20–25 breeding pairs and this occurred throughout the late-winter breeding season, which began in mid-February and ended in May. During this time, all nests within the study area were found and monitored until young were approximately 11–14 d old, at which point nestlings were marked with a unique combination of three color leg bands and one aluminum USFWS/CWS leg band (Sutton et al. 2019). Due to logistical constraints, we were unable to access all nests to record clutch size, so brood size, determined when nests were accessed to band nestlings, was used as an estimate of fecundity (Sutton et al., *in press*).

Overall the study population has experienced a *in press* decline in territory occupancy and abundance since the 1980s of approximately 50% (Sutton et al., *in press*; Waite and Strickland 2006). This decline occurred over the course of 27 yr from 1977 until 2003 and the population has remained relatively stable since 2003 (Sutton et al., *in press*).

### *Territory quality*

We used estimates of territory quality calculated by Strickland et al. (2011). Briefly, territory quality was estimated as the proportion of conifers within a 450 m radius buffer around the mean nesting location based on all known nesting attempts on a territory (Strickland et al. 2011). Territories were subsequently placed in one of three categories based on the proportion of conifers present (low, 0–40%; medium, 40–58%; and high 58–100%) using Jenks' optimization method (Strickland et al. 2011).

### *Statistical models for testing predictions of site-dependent regulation*

To test the effect of density on territory occupancy, we constructed a series of generalized linear mixed-effect models (GLMM) with a binomial distribution and logit link function that included all possible combinations of density, territory quality (high, medium, low), and the interaction between the two. We also included territory identity (ID) as a random effect because territories were monitored each year. We used an information-theoretic approach to compare and rank model sets that were

developed based on our a priori hypotheses. Models were compared using Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) to identify the top model(s) (all models with  $\Delta AIC_c \leq 2$ ) and  $AIC_c$  weights were used to further distinguish between top models. These models were then compared to an intercept only model to assess the effect of density on territory occupancy.

To investigate the effect of territory quality on time that a territory remained vacant after abandonment, we constructed a GLMM with a Poisson distribution and a log link function that included territory quality as a fixed effect and territory ID as a random effect. We used occupancy data collected over the course of our entire study period from the point that a territory was monitored until the end of data collection in 2018.

We constructed a simple linear regression to determine the effect of density on the proportion of occupied territories that were of high quality (for a given season, calculated as the number of occupied high-quality territories divided by the total number of occupied territories) and the average number of young produced by each territory class. One prediction generated by site-dependent regulation is a negative correlation between density and the proportion of occupied territories that were of high quality. Furthermore, the average number of young produced by a given territory class should be constant regardless of population density.

The effect of site-dependent regulation on per capita fecundity was assessed using a series of GLMMs with a Poisson distribution and a log link function that included all possible combinations of the proportion of occupied territories that were of high quality, number of fall freeze-thaw events (due to the effect of freeze-thaw events on cached food quality and subsequent reproductive performance; Sutton et al. 2016, 2019) and an interaction between these fixed effects. We used the proportion of occupied territories that were of high quality in this set of models because it represents a more explicit test of site-dependent regulation than using density because site-dependent regulation predicts that per capita fecundity should be lower when fewer of the occupied territories in a given area are of high quality. To determine if this was a better predictor of per capita fecundity than density, we also constructed a second set of models that included density instead of the proportion of occupied territories that were of high quality. In both sets of models, male and female ID were included as random effects to account for individuals breeding in multiple years. We used an information-theoretic approach to compare and rank model sets that were developed based on our a priori hypotheses. Models were compared using Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) to identify the top model(s) (all models with  $\Delta AIC_c \leq 2$ ) and  $AIC_c$  weights to further distinguish between top models. These models were then compared to an intercept only model to assess the effect of density, the proportion of occupied

territories that were of high quality, and fall freeze-thaw events on per capita fecundity.

For all models predicting per capita fecundity, we separated the time series into two distinct periods: (1) when the population was declining (1977–2003) and (2) when the population remained stable (2004–2018; Sutton et al., *in press*). Site-dependent regulation has been proposed to only act on increasing or stable populations (Ferrer et al. 2006), so we fit models predicting per capita fecundity using demographic data from the period of time the population was stable and the entire time series (1977–2018) to examine if patterns of regulation were consistent over time.

All statistical analyses were conducted in R version 3.6.0 using the lme4 package (Bates et al. 2015). Visreg (Breheny and Burchett 2017) and ggplot (Wickham 2009) were used to visualize the output of the models and create our figures.

## RESULTS

### *Territory occupancy and length of territory vacancy*

The top model predicting territory occupancy included density, territory quality, and the interaction between these two effects ( $AIC_c$  weight = 1; Table 1). As predicted by site-dependence regulation, the slope of the relationship between density and territory occupancy was steepest for low-quality territories and shallowest for high-quality territories (Fig 2A; Appendix S1: Table S3).

The time that a territory remained vacant after being abandoned varied widely from 1 to 44 yr (mean  $\pm$  SD;  $10 \pm 10$ ). As predicted by site-dependence regulation, territory quality was a good predictor of the length of time for which a territory remained vacant ( $-0.53 \pm 0.15$ ), with high-quality territories remaining vacant for a shorter period of time than low-quality territories (Fig. 2B).

The proportion of occupied territories that were of high quality was negatively correlated with density ( $-0.004 \pm 0.0006$ ,  $R^2 = 0.52$ ), suggesting that, at high densities, a lower proportion of occupied territories were of high quality.

TABLE 1.  $AIC_c$  table for models predicting territory occupancy in Canada Jays.

Models predicting territory occupancy	$K$	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight
Territory quality $\times$ Density	5	1589.9	0	1
Territory quality + Density	4	1622.0	32.1	0
Density	3	1852.1	262.2	0
Territory quality	3	1895.3	305.4	0

Notes: Fixed effects included in each model are listed in addition to the number of parameters ( $K$ ), Akaike information criterion corrected for sample size ( $AIC_c$ ) value,  $\Delta AIC_c$  value, and  $AIC_c$  weight. Top models included all models with  $\Delta AIC_c \leq 2$ .

### *Per capita fecundity*

Brood size ranged from 0 (for failed nests) to (very rarely) 5 nestlings (mean  $\pm$  SD;  $1.7 \pm 0.4$ ; Appendix S1: Table S1). When the population was stable (2004–2018), the top model predicting brood size included the proportion of occupied territories that were of high quality, the number of fall freeze-thaw events, and the interaction between these two effects (Table 2). The interaction between the proportion of occupied territories that were of high quality and the number of freeze-thaw events in the fall suggested that, when breeding conditions were poor (i.e., a higher than average number of fall freeze-thaw events), brood size increased with the proportion of occupied territories that were of high quality (Fig. 3; Appendix S1: Table S4). In contrast to the proportion of occupied territories that were of high quality, density was a poor predictor of brood size when the population was stable ( $\Delta AIC_c > 4$ ; Table 2).

Over the course of the entire time series (1977–2018), there was weaker evidence for the effect of the proportion of occupied territories that were of high quality on per capita fecundity. Similar to when the population was stable, the top model predicting brood size, included the proportion of occupied territories that were of high quality, the number of fall freeze-thaw events, and the interaction between these two effects (Appendix S1: Table S2, Fig. S1). However, there was support for two additional models: one included only the number of fall freeze-thaw events ( $\Delta AIC_c = 1.2$ ) and the other included the additive effects of the proportion of occupied territories that were of high quality and the number of fall freeze-thaw events ( $\Delta AIC_c = 1.9$ ; Appendix S1: Table S2). The average number of nestlings produced in each territory quality class did not vary with density over the course of the entire study (low,  $-0.16 \pm 0.17$ ; medium,  $-0.056 \pm 0.10$ ; high,  $0.097 \pm 0.086$ ), meaning that changes in density did not cause declines in individual performance regardless of territory quality.

## DISCUSSION

By testing all the predictions of site-dependent regulation (Rodenhous et al. 1997) using demographic data from a single population, we provide compelling evidence that Canada Jay abundance in Algonquin Provincial Park is regulated, in part, by site dependence. We found strong evidence that density and territory quality influenced territory occupancy and that high-quality territories remained vacant for shorter periods of time. This preferential filling of high-quality territories also resulted in an increase in per capita fecundity, but only when there was a higher than average number of freeze-thaw events in the fall preceding breeding. Under this scenario, individuals reproducing on high-quality territories were buffered from weather conditions that negatively influenced cached food quality (Sutton et al. 2019), thereby supporting the hypothesis that

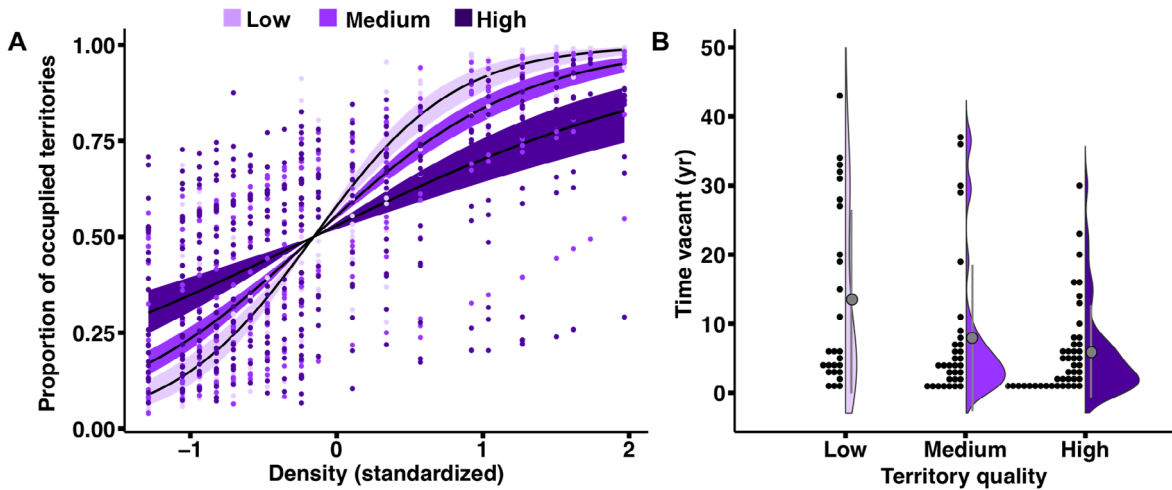


FIG. 2. (A) The effect of population density on territory occupancy depended on territory quality. Points represent partial residuals and the lines represent the predicted slopes from the generalized linear mixed-effect model. (B) Territory quality was a good predictor of time that a territory remained vacant. The large gray dot represents the mean with the gray line representing standard error. Raw data are represented by small black dots on the left side of each violin.

TABLE 2. AIC<sub>c</sub> table for models predicting Canada Jay brood size while population was stable (2004–2018).

Models predicting brood size	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight
Fall freeze-thaw × Proportion high	6	1026.2	0	0.59
Fall freeze-thaw	4	1029.5	3.3	0.11
Proportion high	4	1029.6	3.4	0.11
Density	4	1030.6	4.4	0.07
Fall freeze-thaw + Proportion high	5	1031.1	4.9	0.05
Fall freeze-thaw + Density	5	1031.5	5.3	0.04
Fall freeze-thaw × Density	6	1032.5	6.3	0.03

Notes: Fixed effects included in each model are listed in addition to the number of parameters (K), AIC<sub>c</sub> value, ΔAIC<sub>c</sub> value, and AIC<sub>c</sub> weight. Top models included all models with ΔAIC<sub>c</sub> ≤ 2 and AIC<sub>c</sub> weights were used to further differentiate between models within ΔAIC<sub>c</sub> ≤ 2. Fall freeze-thaw is the frequency of fall freeze-thaw events, Proportion high is the proportion of territories occupied that were of high quality.

environmental conditions modulate density dependence. Furthermore, we provide evidence that high-quality territories remain vacant for shorter periods of time than lower-quality territories. Re-occupation of vacant territories is an important component of site-dependent regulation that can have consequences on population dynamics, but evidence for preferential reoccupation of high-quality territories remains limited.

Given that weather could have a pronounced influence on density dependence, long-term changes in climate may modulate the magnitude of an effect of density on population vital rates (Franklin et al. 2000, Coulson et al. 2001, Jacobson et al. 2004, Previtali et al. 2009, Flesch et al. 2015). If climate change causes an increase in the fluctuations of either resources or predator

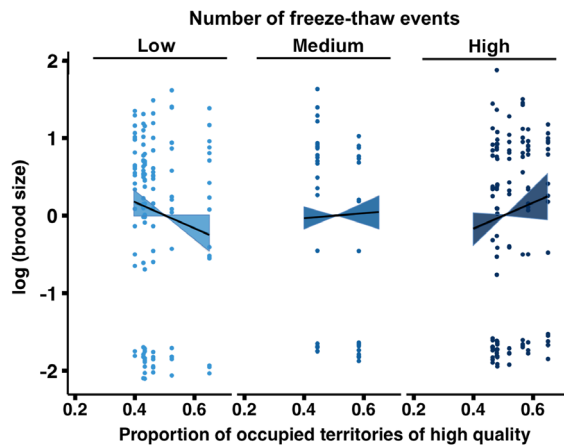


FIG. 3. The effect of the proportion of occupied territories that were of high quality on brood size depended on the quality of environmental conditions for breeding, represented by the number of fall freeze-thaw events while the population was stable (2004–2018). Points represent partial residuals and the lines represent the predicted slopes from the top generalized linear mixed-effect model, as determined by comparing AIC<sub>c</sub> scores.

abundance (Coulson et al. 2001, Lima et al. 2002a, b, Jacobson et al. 2004, Previtali et al. 2009), this could result in shifts in territory quality (i.e., territories becoming higher or lower quality). It could also exacerbate differences between territories, resulting in more pronounced density-dependent relationships over time. For example, in high rainfall years, only the best protected nest sites of Griffon Vultures (*Gyps fulvus*) produced young (Zuberogoitia et al. 2019). Our results suggest that a similar process is likely taking place with Canada Jays in Algonquin Park because, in years with

an increased number of freeze-thaw events, we saw a positive effect of the proportion of occupied territories that were of high quality on fecundity. As temperatures continue to increase in the park and more freeze-thaw events are likely to occur, density-dependent regulation of fecundity could become stronger.

Despite site-dependent regulation acting on the Canada Jays of Algonquin Provincial Park, the population has not increased over time and instead has remained stable at low abundance. While the number of fall freeze-thaw events may increase the strength of density dependence, it also influences overall fecundity of the population (Sutton et al. 2019). When a higher than average number of freeze-thaw events occur in the fall, the fewest young are produced (Sutton et al. 2019) and, likely also the fewest recruits. This means that despite a greater proportion of the population inhabiting high-quality territories, per capita fecundity remains low when environmental conditions are not favorable for reproduction and could, in part, explain why the population has not increased over time. Additionally, biased juvenile dispersal into high-quality territories outside the study area could mean that fewer individuals will recruit into the population and further limit an increase in abundance.

In addition to the site-dependent regulation of fecundity, it is likely that intraspecific competition also plays a role in regulating Canada Jays in Algonquin Provincial Park by acting on vital rates other than fecundity. Results from a detailed population model constructed using demographic data from our study population (Sutton et al., *in press*) provides evidence that density influenced not only fecundity, but also juvenile apparent survival and female immigration. In contrast to fecundity, adult and juvenile apparent survival does not vary with territory quality (Norris et al. 2013). It is, therefore, likely that site dependence is not acting on Canada Jay survival and instead, intraspecific competition for territories or food resources may be the underlying cause of the relationship between density and apparent survival. While fecundity seems to be the primary vital rate driving variation in population growth in this population (Sutton et al., *in press*), if the relative contribution of apparent survival increased, the underlying mechanism producing density-dependent regulation of this population could also shift. It is, therefore, important to consider how multiple mechanisms may promote relationships between density and vital rates within a single population and the contribution of a given vital rate to population growth in order to understand important factors regulating wild populations (Nevoux et al. 2011, Grünkorn et al. 2014).

One of the challenges of describing how populations are regulated is being able to distinguish between site dependence and interference competition (Ferrer et al. 2006, Beja and Palma 2008). To distinguish between these mechanisms, previous studies have examined how the coefficient of variance in fecundity (Ferrer and

Donazar 1996), skewness of fecundity (Ferrer et al. 2006), and territory-quality-specific estimates of fecundity (Kokko et al. 2004, Zuberogoitia et al. 2019) vary with density. However, simulation studies suggest that these metrics are not able to distinguish between site-dependent regulation and interference competition (Beja and Palma 2008, but see Ferrer et al. 2008). An alternative approach is to more explicitly identify predictor variables that differentiate between the two hypotheses. Our use of the proportion of occupied territories that are of high quality directly tests the relationship proposed by site-dependent regulation and allows for the two hypotheses to be differentiated. If site-dependent regulation is occurring, we would expect a positive relationship between the proportion of occupied territories that are of high quality and fecundity, and a negative relationship if interference competition is acting. Despite the benefits of using the proportion of occupied territories that are of high quality, it requires detailed knowledge of how territories are distributed across the landscape and the aspects of habitat that promote variation in territory quality. If territory quality can be estimated and remains relatively constant over time, using the proportion of occupied territories that are of high quality is likely a better way to differentiate between site dependence and interference competition promoting density dependence.

While our previous work has linked variation in percent conifers to multiple metrics related to reproductive performance and survival (Strickland et al. 2011, Norris et al. 2013, Whelan et al. 2016), our estimate of territory quality is arguably still quite coarse and may account for some unexplained variation in our models predicting both territory occupancy and per capita fecundity. Territory quality was derived from the proportion of coniferous cover in a 450 m diameter circle centered on the mean nest location but may not accurately represent the true area being used by a breeding pair if, for example, nests tended to be located near the edge of the areas the jays actually used. Further, our estimate of territory quality is assumed to be linked to preservation of cached food, which is essential for Canada Jays to survive and reproduce during the winter (Strickland et al. 2011), but may not capture other landscape features that contribute to variation in territory quality. Resources and predators may be unequally distributed across the landscape and could increase variation in quality between and within a quality class. Better estimates of territory quality may therefore be derived by measuring resource availability (Barnes et al. 1995, Rodenhouse et al. 2003), predator abundance (Rodenhouse et al. 2003), or measuring patterns of space use at a finer scale in order to accurately assess the habitat an individual or breeding pair uses. Using higher resolution estimates of territory quality could in turn increase the amount of variation explained by models assessing site-dependent regulation of wild populations. Furthermore, examining patterns of dispersal and prospecting behavior could help to identify

specific cues used to assess territory quality. For example, Spanish Imperial Eagles (*Aquila adalberti*) that did not hold established territories (i.e., “floaters”) were more likely to enter territories with higher productivity (Ferrer et al. 2015).

The degree of habitat heterogeneity can often vary across a species’ range and this will likely play an important role in driving variation in how populations are regulated. In Algonquin Provincial Park, a high degree of heterogeneity with respect to forest composition exists at the scale of territories, which is critical for site-dependent regulation to be acting on a population (Dhondt et al. 1992). However, throughout much of the Canada Jay boreal forest range, habitat is more uniformly composed of conifers, especially spruce (*Picea*) species (Strickland and Ouellet 2020). This suggests that the underlying cause of variation in territory quality in Algonquin may not apply to other Canada Jay populations. Studies elsewhere throughout the range could help to determine whether density-dependent regulation occurs in other populations, and if the mechanisms promoting density dependence vary between populations. In more uniform habitat, competition for resources or predation risk could be more important regulators of population vital rates (Krüger and Lindström 2001, Nevoux et al. 2011). Few studies have investigated how density-dependent relationships vary between populations of the same species, but this could be a fruitful avenue of research and shed light on how climate and density interact to influence population growth across broad spatial scales.

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