2021

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Original Publication Citation
Winter, R. E., & Shields, W. M. (2021). Effects of weather on foraging success and hunting frequency in winter-irruptive snowy owls (*Bubo scandiacus*) in Upstate New York. *Journal of Raptor Research*, 55(4), 584-593. https://doi.org/10.3356/jrr-19-89

J. Raptor Res. 55(4):584–593

EFFECTS OF WEATHER ON FORAGING SUCCESS AND HUNTING FREQUENCY IN WINTER-IRRUPTIVE SNOWY OWLS (*BUBO SCANDIACUS*) IN UPSTATE NEW YORK

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Abstract.—The effects of weather on an individual can often alter the population dynamics of a species. Knowledge of how weather influences individual behavior is therefore essential in understanding its full impact in the context of population ecology. Snowy Owls (*Bubo scandiacus*) exhibit expensive long-distance migrations in winters following population irruptions. During irruptive movements, many owls migrate past the southernmost extent of their traditional wintering grounds, the mechanism for which is still debated. We propose and test the "milder climate" hypothesis; Snowy Owls wintering in lower latitudes are better able to meet their metabolic demands due to higher temperatures and lower snow cover. During the Snowy Owl irruption of 2014–2015, we examined this hypothesis by assessing the influence of local weather variables on foraging success, frequency of prey capture attempts, and overall activity budgets in a sample of wintering Snowy Owls in New York, USA. We used eBird, an online citizen science resource, to help locate Snowy Owls, which we observed from an automobile. We found that none of the weather variables tested affected foraging success. However, the lack of effect of snow depth on foraging success may suggest that hearing is more important for hunting in Snowy Owls than previously thought. Hunting frequency decreased with increasing temperatures, suggesting Snowy Owls were better able to meet their metabolic demands in higher temperatures. We thus offer support for the milder climate hypothesis; Snowy Owls wintering in lower latitudes may be able to offset the energetic expenses of long-distance movements.

Key Words: *Snowy Owl*; Bubo scandiacus; *irruptive migration*; *weather-dependent foraging*; *milder climate hypothesis.*

EFECTOS DE LA METEOROLOGÍA EN EL ÉXITO DE FORRAJEO Y LA FRECUENCIA DE CAZA EN INDIVIDUOS DE *BUBO SCANDIACUS* QUE IRRUMPEN EN INVIERNO EN ÁREAS SEPTENTRIONALES DEL ESTADO DE NUEVA YORK, ESTADOS UNIDOS

Resumen.—Los efectos de la meteorología sobre los individuos pueden alterar las dinámicas poblacionales de una especie con frecuencia. El conocimiento de cómo el tiempo influye el comportamiento individual es por ende esencial para entender su impacto completo en el contexto de la ecología de poblaciones. *Bubo scandiacus* realiza costosas migraciones de larga distancia en los inviernos que siguen a las irrupciones poblacionales. Durante los movimientos de irrupción, muchos búhos migran más allá del límite meridional de sus zonas de invernada tradicionales; y el mecanismo por el cual realizan esto aún es objeto de debate. Proponemos y evaluamos la hipótesis del "clima moderado", la cual indica que los individuos de *B. scandiacus* que invernan a latitudes más bajas son capaces de satisfacer sus demandas metabólicas debido a las temperaturas más altas y a la menor cobertura de nieve. Durante la irrupción de individuos de *B. scandiacus* del periodo 2014–2015, examinamos esta hipótesis evaluando la influencia de variables meteorológicas locales en el éxito de búsqueda de alimento, en la frecuencia de intentos de captura de presas y en los tiempos de actividad general en una muestra de individuos de *B. scandiacus* en el norte de Nueva York, EEUU. Usamos eBird, un recurso de ciencia ciudadana en línea, para ayudar a localizar a los individuos de *B. scandiacus*, que observamos desde un automóvil. Encontramos que ninguna de las variables meteorológicas evaluadas afectó el éxito de búsqueda de alimento. Sin embargo, la ausencia de un efecto causado por la

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profundidad de la nieve sobre el éxito de búsqueda de alimento de *B. scandiacus* sugeriría que la audición es más importante para cazar de lo que se pensaba hasta ahora. La frecuencia de caza disminuyó con el aumento de las temperaturas, sugiriendo que *B. scandiacus* fue capaz de satisfacer sus demandas metabólicas en zonas con temperaturas elevadas. Nuestros resultados apoyan la hipótesis del clima moderado; los individuos de *B. scandiacus* que invernan en latitudes más bajas podrían ser capaces de compensar el coste energético de los movimientos de larga distancia.

[Traducción del equipo editorial]

Introduction

The effects of weather on animals can be observed at several different orders of magnitude, from physiology and individual behavior (Bronikowski and Altmann 1996, Romero et al. 2000) to reproductive success, dispersal, and population dynamics (Grassel et al. 2016, Kuusaari et al. 2016, Albon et al. 2017). Weather can affect animals directly by causing changes in metabolic requirements (Gardner et al. 2017) or indirectly by causing changes in food abundance (Grant et al. 2000). Moreover, the effects of weather on the individual can often lead to alterations in population dynamics of species (e.g., Sergio 2003). In-depth knowledge of the effects of weather on individual behavior is therefore essential in understanding the effects of such variables in the context of population ecology. However, such information is severely lacking for most species. Additionally, even though the effects of weather on individual behavior have long been established, relatively few studies have examined weather-dependent foraging success explicitly (e.g., Dunn 1973, Grubb 1977, Avery and Krebs 1984, Sergio 2003, Sarasola and Negro 2005). Moreover, the effects of weather on foraging behavior and performance are likely most pronounced in animals inhabiting ecosystems that experience drastic variation in weather conditions, such as the Arctic tundra, as these animals have developed several adaptations to cope with extreme climatic variability (Martin and Wiebe 2004). Studies on weather-dependent foraging in such taxa are thus highly important.

The Snowy Owl (*Bubo scandiacus*) is one of the primary avian predators of the Arctic tundra, a region that is widely known for its high climatic variability and high-amplitude, multi-annual cyclic fluctuations in population densities of small mammals such as lemmings (*Lemmus* and *Dicrostonyx* sp.; Ims and Fuglei 2005, Krebs 2011). Snowy Owls are commonly known to specialize on lemmings during the breeding season and exhibit strong positive numerical responses to changes in lemming population densities (Therrien et al. 2014a, 2014b). During the winter following a highly productive breeding season, Snowy Owls can exhibit irruptive migration, a form of facultative migration characterized by irregular movements of large numbers of individuals to lower latitudes (Newton 2006, Robillard et al. 2016). The irruptive movements of Snowy Owls have been well documented, mostly in eastern North America, since the 1830s with numerous reports on numbers of owls, food habits, and unusual locality records (Gross 1947, Boxall and Lein 1982). In recent years, several studies have examined the mechanisms behind these irruptions (e.g., Therrien et al. 2014a, 2014b, 2015, 2017, Robillard et al. 2016, Curk et al. 2018, Santonja et al. 2019). While the "breeding output" hypothesis (plentiful food resources during the breeding season allow for the production of large numbers of offspring that then disperse southward in winter; Curk et al. 2018) can explain the massive numbers of owls migrating southward during irruption years, it does not explain why many individuals migrate past the southernmost extent of their traditional wintering range during irruption years. Milder weather conditions, higher prey abundance, and competition avoidance have been cited as mechanisms to explain why juvenile Snowy Owls migrate further south in winter than do adults, a phenomenon known as differential migration (Kerlinger and Lein 1986, Robillard et al. 2016, Santonja et al. 2019), but these mechanisms have not been tested explicitly. Additionally, while the majority of adult Snowy Owls remain in the Arctic during winter (Fuller et al. 2003, Therrien et al. 2011), there are still considerable numbers of adults that migrate to temperate latitudes during irruption years (Holt et al. 2015, Curk et al. 2018), the mechanisms for which remain unknown. We propose that the milder climatic conditions of lower temperate latitudes may be a contributing factor for this phenomenon (the milder climate hypothesis). Under this hypothesis, individuals that migrate farther south during irruption years would theoretically be able to offset the large energy expenditure required to perform such longer migratory movements if thermoregulatory demands were lower for Snowy Owls wintering in temperate latitudes than those wintering in higher latitudes.

Here, we test this hypothesis by investigating the effects of weather variables on the frequency and success of prey capture attempts, and by examining overall activity budgets in Snowy Owls wintering in upstate New York, USA, during the 2014–2015 irruption. Our aim was to assess whether climatic conditions at temperate latitudes were favorable for wintering Snowy Owls relative to foraging success and metabolic demands. Snow cover is known to protect small mammals from generalist predators (Korpimäki 1986, Aitchison 2001, Korslund and Steen 2006), thus reducing food availability for Snowy Owls during winter (Chang and Wiebe 2018b). Under our hypothesis, we therefore expected snow depth to have a negative effect on foraging success in Snowy Owls. Additionally, Snowy Owls wintering in high latitudes have high metabolic demands for thermoregulation in cold temperatures (Gessaman 1972) and would thus have to capture prey at higher rates as temperatures decreased to meet increased thermoregulatory demands. We therefore expected Snowy Owl hunting frequency to decrease with increasing ambient temperature. The foraging success, feeding ecology, and hunting behaviors of Snowy Owls have been studied in their breeding grounds (Watson 1957) and in locations where they are regular winter residents (Boxall and Lein 1982, 1989, Chang and Wiebe 2018a). There are, however, no such observational studies on Snowy Owls during irruption years. Thus, our study represents the first to analyze the effects of environmental variables on foraging success in Snowy Owls in such years.

METHODS

Study Area and Site Selection. We observed Snowy Owls between 25 January and 19 March 2015 at various locations within 166 km of Syracuse, New York, USA (Fig. 1). At these sites, we observed owls in several types of farmlands and open areas. The primary habitat types in which we observed Snowy Owls included unmanaged grasslands (characterized by the presence of tall native grasses and sparsely distributed shrubs), agricultural land (including stubble fields, fallow fields, etc.), and industrial areas (including airport fields, residential yards, athletic fields, and parking lots). We selected study sites based on previous sightings of Snowy Owls reported on eBird, a citizen science program run by the Cornell Lab of Ornithology that engages volunteer observers to report bird observations using standardized protocols (Sullivan et al. 2009). To increase the likelihood of successfully locating a Snowy Owl, we only selected sites where Snowy Owls had been reported at least once every 2–4 d during the data collection period.

Observational Methods. We located and observed Snowy Owls from an automobile using either a pair of 10–22 × 50 binoculars or a 20–60 × 80 spotting scope. Observations typically lasted from 2 to 12 hr. We identified, aged (adult or juvenile), and sexed individuals based on plumage characteristics (Boxall and Lein 1982). After locating an owl, we recorded snow depth (cm) using a meter stick, temperature (°C) using a Kestrel Weather Meter (Kestrel Instruments, Boothwyn, PA), habitat type, and estimated % cloud cover.

Activity budget. We recorded continuous behavioral observations during daylight hours (0600–1800 H), and timed the durations of all activities using a stopwatch. Owl activities consisted of loafing/idling, perch-change flights, walking/running, search flights, hunting, foraging, and other. With the exception of foraging, the loafing/idling behavioral category consisted of all stationary activities, including preening, resting, scanning in an alert posture, and head-bobbing. Perch-change flights consisted of unidirectional flights from one specific location to another (e.g., a flight from a telephone pole to a fence post) in which the owl did not perform a hunting attempt. We distinguished prey capture attempts from perch-change flights to the ground based on the manner in which the owl landed on the ground. During prey capture attempts, owls struck the ground with their talons, landed abruptly, and almost tumbled forward rather than landing lightly and deliberately as they did in a perch-change flight to the ground. Owls conducting search flights meandered about their chosen hunting grounds with no intended destination while scanning for prey. Occasionally, we observed owls either walking or running around on the ground in what we presumed was an attempt to search for prey. We characterized other owl activities as those that did not correspond with any of the other behavioral categories, and occurred on fewer than five occasions. We recorded temperature, % cloud cover, and snow depth each hour of the observation period.

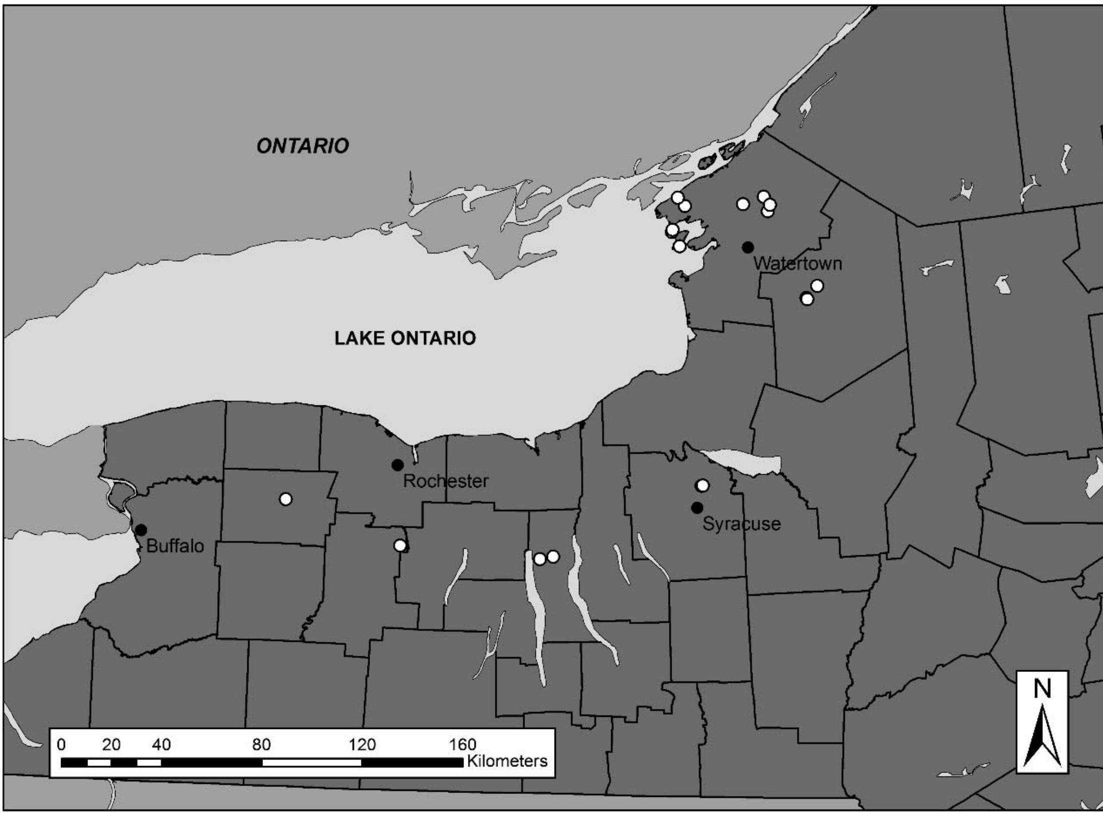

Figure 1. White circles indicate locations where Snowy Owls were observed in upstate New York, USA from 25 January to 19 March 2015.

Foraging success. For each prey capture attempt, we estimated distance (m) from the owl's perch to its intended prey, total elapsed time (sec) from when the owl left its perch to the end of the hunting attempt (i.e., the moment at which a given owl ceased movement after executing a hunting strike), whether or not the hunting attempt was successful, and prey type (if either the attempt was successful or the intended prey item was clearly visible). We also recorded all weather variables (i.e., temperature, % cloud cover, and snow depth) after each prey capture attempt.

Statistical Analysis. We performed all statistical analyses in R 3.5.2 (R Core Team 2018) and all averages are expressed with ±SE. We examined the effects of environmental factors on hunting success through a generalized linear model (GLM) framework. We built a candidate set of logistic regression GLMs *a priori* by fitting age, sex, habitat type, and weather variables (mean temperature, mean % cloud cover, and snow depth) as explanatory variables, and used the outcome of the prey capture attempt (successful or not) as a binomial response variable. We constructed a candidate set of linear mixed-effects (LMER) models *a priori* by using the lme4 package (Bates et al. 2015) to examine factors influencing hunting frequency (hunts/hr). We built LMER models by using mean temperature, mean % cloud cover, snow depth, age, sex, and habitat type as fixed effects, while individual was included as a random factor.

We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) for model selection. We considered models to be well supported by the data if $\Delta AIC_c < 2$. If no single model had a model weight (w_i) > 0.90, we performed model averaging using the MuMIn package (Bartón 2018) to reduce prediction error and thereby obtain more reliable predictions. We considered variables to be biologically relevant if

Table 1. Mean and range of temperature (°C), % cloud cover, and snow depth (cm) during behavioral observations of Snowy Owls wintering in upstate New York, USA from 25 January to 19 March 2015.

WEATHER VARIABLE	MEAN	SE	MIN.	MAX.
Temperature (°C)	−5.039	1.712	−20.556	7.778
Snow depth (cm)	32.536	4.292	5.080	63.500
% Cloud cover	51.263	9.345	0	100

their coefficients had 95% confidence intervals that did not overlap zero.

RESULTS

Hunting Rates and Success. We observed 16 individual Snowy Owls (three adult females, six adult males, six juvenile females, one juvenile male) perform a total of 50 prey capture attempts throughout the study period. Temperatures ranged from –20.6°C to 7.8°C, snow depths ranged from 5.1 cm to 63.5 cm, and cloud cover ranged from 0 to 100% (Table 1). Owls directed nearly all of their capture attempts toward small mammals (49 of 50 capture attempts). Snowy Owls executed 60% of prey capture attempts in agricultural areas, 34% in industrial areas, and 6% in unmanaged grasslands. Snowy Owls performed capture attempts at a mean rate of 0.36 hunts/hr ± 0.09 and were successful in capturing prey items in 23 of 50 capture attempts for a mean hunting success rate of 38.8% ± 9.7.

Snowy Owl hunting success was best explained by age (w_i = 0.349) and snow depth (w_i = 0.221); however, GLM model averaging revealed that none of the variables tested were biologically relevant with regard to foraging success in our sample of Snowy Owls (Table 2).

Model averaging with LMER models revealed hunting frequency was best explained by sex (w_i = 0.322) and mean temperature (w_i = 0.292; Table 3). Mean temperature was the only biologically relevant weather variable with regard to hunting frequency; hunting frequency decreased as temperature increased (β = –0.022, SE = 0.01, CI = –0.044, –0.001; Fig. 2A). There was no apparent relationship between the two other weather variables (snow depth and mean % cloud cover) and hunting frequency (Fig. 2B, 2C).

Diurnal Activity Budgets. Owls spent 99.2% ± 0.139 of daylight hours loafing/idling on average, and all other activities composed <1% of their diurnal activity budget. For these activities, perch change flights accounted for 0.5% ± 0.069 of diurnal activities, search flights accounted for 0.06% ± 0.049, hunting accounted for 0.09% ± 0.027, walking/running accounted for 0.057% ± 0.038, foraging accounted for 0.014% ± 0.004, and other accounted for 0.055% ± 0.041. Behaviors categorized as "other" included instances where Snowy Owls exhibited aggression toward intruding Common Ravens (*Corvus corax*) or Rough-legged Hawks (*Buteo lagopus*), as well as one instance where an owl was observed walking on the ground, picking at the snow and vegetation with its talons and beak, most likely to expose tunnels made by small mammals.

DISCUSSION

Effects of Weather Variables. We found no apparent relationship between any of the weather variables and foraging success. Perhaps the most surprising result is the lack of effect that snow depth had on foraging success. The Snowy Owls observed almost exclusively (49 of 50 prey capture attempts) hunted small mammals, namely mice (*Peromyscus*

Table 2. Model selection and model averaging results for generalized linear models with a binomial distribution, examining the effects of weather variables (temperature [°C], % cloud cover, and snow depth [cm]), age, sex, and habitat type on foraging success of Snowy Owls wintering in upstate New York, USA from 25 January to 19 March 2015.

MODEL / PARAMETER	df	logLik	AIC_c	ΔAIC_c	w_i	β	SE	z	95% CI
Age	2	−32.349	68.953	0.000	0.349	−1.148	0.596	1.877	−2.347 – 0.051
Snow depth	2	−32.803	69.862	0.908	0.221	0.023	0.014	1.613	−0.005 – 0.050
Intercept	1	−34.296	70.676	1.723	0.147	−0.229	0.640	0.354	−1.497 – 1.039
Cloud cover	2	−33.524	71.303	2.350	0.108	0.008	0.006	1.186	−0.005 – 0.021
Temperature	2	−34.036	72.328	3.374	0.065	−0.028	0.040	0.693	−0.108 – 0.051
Habitat type	3	−33.003	72.527	3.574	0.058	−0.857	0.675	1.237	−2.214 – 0.501
Sex	2	−34.280	72.815	3.862	0.051	0.109	0.670	0.159	−1.239 – 1.457
Global model	8	−30.458	80.428	11.475	0.001	NA	NA	NA	NA

Table 3. Model selection and model averaging results for linear mixed-effects regression models examining the effects of weather variables (mean temperature [°C], mean % cloud cover, and snow depth [cm]), age, sex, and habitat type on hunting frequency of Snowy Owls wintering in upstate New York, USA, from 25 January to 19 March 2015.

MODEL / PARAMETER	df	logLik	AIC_c	ΔAIC_c	w_i	β	SE	z	95% CI
Sex	4	−10.568	31.358	0.000	0.322	−0.356	0.172	1.933	−0.716 – 0.005
Mean temperature	4	−10.666	31.554	0.196	0.292	−0.022	0.010	2.009	−0.044 – −0.001
Intercept	3	−12.485	32.234	0.876	0.208	0.373	0.163	2.216	0.043 – 0.704
Mean cloud cover	4	−12.254	34.731	3.373	0.060	−0.002	0.002	0.657	−0.006 – 0.003
Age	4	−12.363	34.948	3.590	0.053	0.092	0.184	0.470	−0.292 – 0.476
Snow depth	4	−12.485	35.192	3.834	0.047	0.000	0.005	0.032	−0.010 – 0.010
Habitat type	5	−11.770	37.070	5.712	0.019	0.277	0.234	1.104	−0.214 – 0.768
Global model	10	−8.325	54.984	23.626	<0.001	NA	NA	NA	NA

spp.) and voles (*Microtus* spp.). These small mammals often occupy subnivean habitats during winter months and snow cover is known to protect them from generalist predators (Korpimäki 1986, Aitchison 2001, Korslund and Steen 2006). Indeed, previous studies have shown snow depth to have a negative effect on foraging success not only in mammalian predators such as coyotes (*Canis latrans*; Gese et al. 1996) and foxes (*Vulpes* spp.; Lindström and Hörnfeldt 1994, Bilodeau et al. 2013), but in Boreal Owls (*Aegolius funereus*; Korpimäki 1985) as well. Thus, we expected to find a similar relationship between snow depth and foraging success in Snowy Owls, but we observed no such effect.

While sight and movement are undoubtedly the primary tools used for prey location in Snowy Owls (Holt et al. 2015), our findings indicate that hearing may be more important for hunting than previously thought. In all instances where Snowy Owls hunted in snow depths > 20 cm, they plunged into the snow to capture animals residing below the snow's surface, and therefore must have used hearing to discern the location of prey items in these instances. An alternative hypothesis is that individual Snowy Owls located subnivean prey by visually detecting the displacement of snow by small mammals moving beneath the surface. Such a technique is likely used when small mammals move through snow relatively close to the surface, where the snow's density and structural integrity are lowest and where the displacement of snow by small mammals would therefore be most visible. Small mammals moving through snow at lower depths, however, where snow density and structural integrity are greater, likely

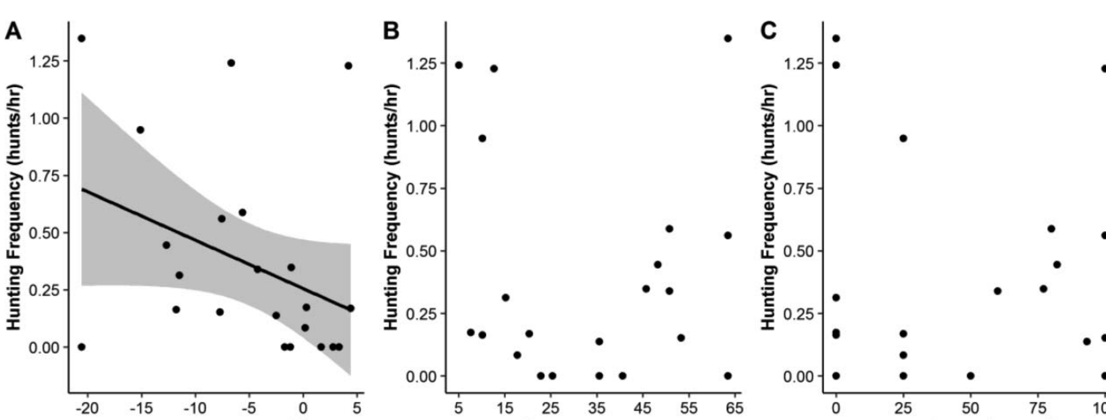

Figure 2. Linear mixed-effects models depicting changes in hunting frequency of Snowy Owls in upstate New York, USA, from 25 January to 19 March 2015 with respect to (A) mean temperature, (B) snow depth, and (C) mean % cloud cover. The gray area in A represents the 95% confidence interval around the parameter estimate. The confidence intervals for B and C were not significant and are not shown (Table 3).

compress the snow surrounding them and may be able to move through the snow without causing disturbance visible from the surface (Sanecki et al. 2006). Thus, in instances where Snowy Owls plunged deep into the snow to capture subnivean prey items, we speculate that it is more likely that owls used hearing to locate prey than by visual means. Smith (1997) reported observations similar to ours, in which owls hovered, apparently using hearing before dropping through 20 cm of snow to catch voles. Moreover, given that snow depth did not affect foraging success in our observations, it is thus likely that either (a) Snowy Owls can detect subnivean prey at all (or nearly all) depths below the snow's surface and only perform capture attempts when prey items are within grasping range (i.e., the range at which Snowy Owls are able to extend their talons below the snow's surface) or (b) Snowy Owls can only detect subnivean prey that are within grasping range. However, given the relatively limited range of snow depths observed in our study (Table 1), further study is needed to confirm our speculative suggestions.

Although ambient temperature did not appear to affect foraging success in Snowy Owls, temperature was among the best predictors of hunting frequency (Table 3). Given our LMER model averaging results, it appears temperature is indeed biologically relevant, at least in our study sample, in its effect on Snowy Owl hunting frequency, which decreased with increasing ambient temperatures (Fig. 2A). Previous studies have shown that Snowy Owl metabolic requirements increase with decreasing ambient temperatures (Gessaman 1972, Boxall and Lein 1989). Thus, to meet their metabolic requirements, owls must consume more prey, and therefore perform more prey capture attempts as ambient temperatures decrease. Furthermore, the thermoneutral zone (i.e., the range of ambient temperatures in which neither physical nor chemical mechanisms used for thermoregulation need be employed) for Snowy Owls extends from 2.5°C to 18.5°C (Gessaman 1972), which could explain why Snowy Owl hunting frequency was lowest when ambient temperatures rose above 2.5°C (Fig. 2A). Snowy Owls wintering in lower latitudes are more likely to experience ambient temperatures within their thermoneutral zone than those wintering in higher latitudes. Therefore, Snowy Owls migrating past the southernmost extent of their traditional wintering range during irruption years may mitigate the energetic expenses of performing a longer migratory flight if the higher air temperatures at lower latitudes reduce thermoregulatory demands during winter months. Northern Gannet (*Morus bassanus*) individuals that migrate from the North Sea and winter in western Africa are able to mitigate the increased energetic expenses of performing a longer migration because they experience lower thermostatic demands (higher sea surface temperatures during winter) than those that remain in the North Sea (Garthe et al. 2012). The same principle may be true for Snowy Owls as well, and could therefore serve as a potential incentive for some individuals to migrate farther south during irruption years if food availability at lower latitudes is equal to, or perhaps even slightly less than, that of higher latitudes.

Activity Budgets. When compared to previous studies, our findings regarding the diurnal activity budgets of winter irruptive Snowy Owls appear similar to those of Snowy Owls wintering within their traditional range. Indeed, Boxall and Lein (1989) found that Snowy Owls wintering in southern Alberta, Canada spent 98% of daylight hours perched, which is similar to our finding of winter irruptive Snowy Owls spending a mean of 99.2% of daylight hours loafing/idling. Boxall and Lein (1989) also found that Snowy Owls spent 1.3% of daylight hours in flight, whereas the Snowy Owls observed in our study spent a mean of 0.6% of daylight hours in flight. Similarly, we found Snowy Owls performed prey capture attempts at a mean rate of 0.36 hunts/hr, which is the same mean rate of 0.36 hunts/hr (mean based on 5 mo) reported in Boxall and Lein's (1989) study. The similarities in these findings may have arisen from similarities in climatic conditions observed in both studies, though temperatures in Boxall and Lein's (1989) study appeared to be slightly lower than those in our study. However, more study on Snowy Owl behavior in winter during both irruption years and typical years are needed to make a more robust comparison.

Habitat Use. When selecting habitat, Snowy Owls have been assumed to avoid residential and industrial areas because of human disturbance (Lein and Webber 1979, Boxall and Lein 1982). However, more recent studies on Snowy Owl habitat use during winter have documented owls using industrial/residential areas more frequently than previously thought (Smith et al. 2012, Therrien et al. 2017). Although the majority of our observations of Snowy Owls took place in agricultural habitats, we often observed owls hunting in areas that are subject to more anthropogenic effects such as airports, athletic fields, residential yards, and even parking lots. Despite their preferences for certain hunting grounds, neither hunting frequency nor foraging success differed among habitats. Several previous studies on raptor foraging have demonstrated that habitat characteristics can greatly influence hunting success (Collopy and Bildstein 1987, Buchanan 1996). However, it appears as though this principle does not apply to the Snowy Owls observed in this study. Our observations thus offer further support for the notion that Snowy Owls are highly adaptable generalist predators capable of using a diverse array of habitat types during winter months.

Conclusion

In our sample of wintering Snowy Owls, foraging success was not influenced by weather variables. Indeed, milder climatic conditions characteristic of lower latitudes did not appear to be more beneficial for wintering Snowy Owls than those of higher latitudes based on our findings that neither snow depth nor temperature influenced foraging success. The observed decrease in hunting frequency, however, in response to increasing temperatures did offer some support for the milder climate hypothesis. Such large-scale, long-distance movements, whereby some individuals migrate past the southernmost extent of traditional wintering grounds during irruption years, require large energy expenditures and may also entail "costs such as uncertainty, hazards, or the risk of 'moving for nothing'" (Therrien et al. 2014b). If Snowy Owls wintering in lower latitudes experience reduced thermoregulatory expenses and are able to meet metabolic requirements more easily than those wintering in higher latitudes, individuals wintering in lower latitudes may be able to offset the large energy expenditure required for long-distance migration. However, given the limited sample size ($n = 16$), duration (7.5 wk, one winter), and geographical extent of our study, our conclusions relative to the importance of weather variables is somewhat limited. We thus encourage further studies comparing foraging success, foraging frequency, and energy expenditures of Snowy Owls wintering in higher latitudes relative to those wintering in lower latitudes, in both typical and irruptive years. In addition to climate characteristics, other researchers have cited competition avoidance and increased prey availability as potential explanations for the extent to which some individuals migrate during irruption years (e.g., Robillard et al. 2016, Santonja et al. 2019). While there has been some support for competition avoidance (resulting from differences in social dominance) in previous research examining differences in winter distributions attributed to age and sex (Kerlinger and Lein 1986), studies investigating agonistic interactions between conspecifics, as well as the effects of winter population density on foraging success, energy expenditure, and prey capture rates during both typical and irruptive years are needed to confirm this.

Acknowledgments

We thank the Honors Program at State University of New York College of Environmental Science and Forestry for providing financial support for the fieldwork, and Eric Walters for providing feedback on the manuscript. We thank the eBird staff at the Cornell Lab of Ornithology and the many observers in upstate New York who reported their Snowy Owl sightings to eBird during the data collection period, without whom, this study would have scarcely been possible. We also thank the police departments of Cape Vincent, Fayetteville, and Batavia, New York for allowing R. E. Winter to continue his observations of Snowy Owls despite a few citizens voicing concerns regarding him sitting in a parked car on the side of the road for several hours while periodically using multiple pieces of optic equipment. We verify that the reported research did not require permits or institutional review as the study was purely observational.

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Received 24 October 2019; accepted 13 October 2020
Associate Editor: Christopher J. Farmer