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ABSTRACT

The snowy owl (*Bubo scandiacus*) is a charismatic raptor that exhibits irruptive movements to exploit unpredictable resources in the Arctic tundra. During irruption years, many owls migrate past the southernmost extent of their traditional wintering grounds and must adjust to entirely unfamiliar habitats. The conditions associated with these new habitats may impact aspects of snowy owl behavior, and may influence snowy owls' abilities to adapt to their wintering grounds during irruption years. I analyzed the hunting success, hunting behaviors, and diurnal activities of winter irruptive snowy owls in New York, USA, from January-March, 2015, and assessed how environmental factors (temperature, time period, cloud cover, snow depth, habitat type, etc.) influence snowy owl hunting success and behavior. I used an online citizen science resource, eBird, to locate snowy owls and I observed them from an automobile. Snowy owls were successful in 45.1% of 51 prey capture attempts. Adult owls were 30% more successful in capturing prey than were juveniles. Snowy owls used variants of the sit-and-wait technique to capture mammalian prey. Owls executed hunting attempts more frequently at low temperatures than at high temperatures. Snowy owl hunting activity peaked during the morning and late afternoon. Snowy owls were more successful in capturing prey at 50-100% cloud cover than at 0-50% cloud cover. All other environmental factors had no detectable influence on snowy owl hunting success. When compared to previous studies, winter irruptive snowy owls were equally adapted to their wintering grounds as were wintering snowy owls during non-irruption years.

KEY WORDS behavior, *Bubo scandiacus*, hunting success, irruptive migration, New York, snowy owl, wintering range

INTRODUCTION

The incredibly harsh and desolate landscape that is the Arctic tundra is widely known for its high seasonality and high-amplitude, multi-annual cyclic fluctuations in the population densities of small mammals such as lemmings (*Lemmus* and *Dicrostonyx* sp.) (Therrien et al. 2014). These sudden spikes in the population densities of lemmings are highly unpredictable on a yearly basis, and can affect the breeding densities and reproductive success of several avian and mammalian predators (Therrien et al. 2014).

The snowy owl (*Bubo scandiacus*) is a unique and charismatic raptor, and is one of the main avian predators of the Arctic tundra (Gross 1947, Boxall and Lein 1982, Therrien et al. 2014). Snowy owls are commonly known to specialize on lemmings during the breeding season (Watson 1957, Boxall and Lein 1982, Therrien et al. 2014). Snowy owls have been able to exploit this pulsed resource via irruptive migrations, which allow them, as well as several other species, to inhabit and breed in environments with highly unpredictable resources despite the inherent uncertainties and associated costs of such movements (Therrien et al. 2014, Robillard et al. 2016). Snowy owls can exhibit large variations in breeding numbers in relation to the local lemming abundance (Therrien et al. 2014). When lemmings are abundant, snowy owls can raise large clutch sizes of up to 14 eggs, and snowy owl populations spike tremendously as a result (Robillard et al. 2016). During the winter following a productive breeding season, large numbers of snowy owls irrupt and migrate into southern Canada and northern United States (Robillard et al. 2016). The irruptive movements of snowy owls have been well documented since the 1830's with numerous reports on numbers of owls, food habits, and unusual locality records (Gross 1947, Boxall and Lein 1982). Despite the extensive documentation of snowy owl irruptions, the mechanisms behind these irruptions are still debated, and there are still some questions that have yet to be answered. In light of the snowy owl irruption during the winter of 2013-2014, the desire to study and investigate the ecology and life histories of snowy owls has grown immensely.

The hunting success, feeding ecology, and hunting behaviors of snowy owls have been studied frequently in their breeding grounds (Watson 1957) and in locations where they are regular winter residents (Boxall and Lein 1982, 1989). There are, however, no such behavioral studies on snowy owls during irruption years. In addition, behavioral studies on snowy owls in the United States are severely lacking. There is but one such study in which a researcher observed a single wintering snowy owl in Michigan, USA, and reported on its hunting success, hunting behaviors, and diurnal activity budget (Chamberlin 1980). The lack of behavioral studies on winter irruptive snowy owls in the USA is likely due to the highly unpredictable nature of irruptive individuals. Studies on hunting success and activity budgets require many hours of observation time, and it is thus exceedingly difficult to obtain an adequate amount of data when the species in question exhibits highly unpredictable movements. However, with the advent of modern technology and the online birding resource known as eBird, researchers are now able to reliably locate and track down birds that were previously too unpredictable to study. Therefore, with these technological advances, behavioral studies on unpredictable bird species, such as winter irruptive snowy owls, are now far more feasible.

In this paper, I investigated the hunting behaviors, hunting success, and diurnal activities of winter irruptive snowy owls in New York, USA. I analyzed changes in snowy owl hunting behavior in relation to several environmental factors. I examined the influence of several biotic and abiotic factors on snowy owl hunting success. I assessed and compared the effectiveness of different snowy owl hunting methods. I compared my findings to those of previous studies on wintering snowy owls during non-irruption years to assess the degree to which winter irruptive snowy owls are able to adapt to their new wintering grounds.

METHODS

Study Area and Site Selection

I observed snowy owls from January 25th to March 19th, 2015 at various locations throughout New York, USA. Most sites were located in Jefferson and Lewis counties. I also observed snowy owls at the Syracuse Hancock International Airport, in farmlands in the towns of Fayette and Geneva, and at the Genesee County Airport in Batavia.

At these sites, I observed owls in several types of farmlands and open areas. The primary habitat types where I observed snowy owls included: ungrazed grasslands, fields containing mainly tall grasses, sparsely distributed shrubs, and small trees; stubble fields, farmlands that contained remnants of harvested crops such as old corn stalks; fallow fields, farmlands that were plowed but not cultivated for one or more growing seasons (characterized by tall grasses and herbaceous plants); airport fields, grassy areas contained within an airport; manicured fields/yards, grassy areas that were regularly mowed; and parking lots.

I selected potential study sites based on previous sightings of snowy owls that had been reported on eBird; a citizen science website run by the Cornell Lab of Ornithology where birdwatchers submit checklists of their bird sightings. Site selection depended on the frequency and regularity of snowy owl reports (at least once every 2-4 days) as well as the number of owls reported in a given area (usually $\geq$2 owls in a given area). Following such criteria increased the likelihood of locating an owl after driving to a particular site.

Observational Methods

I located owls from an automobile using either a pair of 10-22×50 binoculars or a 20-60×80 spotting scope and observed them for periods lasting 2-12 hours. For each individual owl I observed, I determined its age (adult or juvenile) and gender based on plumage characteristics (Fig. 1a, 1b, 1c, 1d), and I made note of any unique plumage characteristics that could be used for the identification of individuals in the future. After locating an owl at a given site, I recorded the date, location, time of day, snow depth (in cm) using a meter stick, starting temperature (in °C) using a Kestrel Weather Meter, type of precipitation (if any), estimated percent cloud cover, habitat type, perch type, and estimated perch height (in m), which I divided into three categories (0 m, 1-5 m, and >5 m).

Diurnal activities.— I collected and recorded continuous behavioral observations during daylight hours (6:30-20:30). I timed the durations of all activities using a stopwatch, and recorded specific notes on behavior by hand. I divided all owl activities into several distinct behavioral categories, which included 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. I did not record these activities as separate behavioral categories because for this study, I chose to focus on behaviors that were closely associated with hunting and hunting success. I characterized perch change flights as unidirectional flights from one specific location to another (e.g. a flight from a telephone pole to a fence post) where the owl did not perform a hunting attempt. I distinguished perch-change flights to the ground from hunting flights based the manner in which the owl would land on the ground. When performing a perch-change flight, an owl would, moments before landing, slow down, increase the angle of attack of its wings, hover briefly, and then land lightly on the ground. When performing a hunting flight, however, the owl would slow down very little, if at all, before landing, and it would visibly strike the ground with its talons. If the owl chose to land on the ground rather than continue flying, it would land abruptly and almost tumble forward rather than land lightly and deliberately as it would in a perch-change flight to the ground. Owls conducting search flights would meander about their chosen hunting grounds with no intended destination while scanning for prey. Occasionally, I observed owls either walking or running around on the ground in what I presumed to be an attempt to search for prey. The "other" behavioral category consisted of owl activities that did not correspond with any of the other behavioral categories, such as pellet regurgitation and intra- and interspecific interactions (excluding predation). When owls exhibited changes in behavior, I recorded the time of day, temperature, percent cloud cover, precipitation type (if any), habitat type (e.g. if the individual flew into a different type of farm field), and perch type and height (for stationary activities only).

Hunting observations.— If a given owl performed a hunting attempt, I recorded the hunting method that the owl used, estimated distance (in m) from the owl's perch to its intended prey, total elapsed time 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). I also reported any behaviors that owls exhibited before and after executing each hunting attempt.

Statistical Analysis

Following data collection, I entered the data using two different computer software programs. I entered and analyzed all diurnal activity data using Microsoft Excel. I calculated the total amount of time that owls spent performing each activity and the percentages of time that owls devoted to each behavioral category. In order to display and interpret the data more effectively, I analyzed the non-loafing activities separately and calculated the relative percentages of time that owls devoted to each non-loafing activity.

I entered and analyzed all hunting observations using Minitab 17. I first entered the data in such a way that it was organized by each hunting attempt. I pooled all continuous variables into equal intervals for analytical purposes. I then determined the frequencies at which snowy owls performed hunting attempts in relation to all discrete measured variables. I performed several analyses of variance (ANOVA) and Chi-square tests to determine the influence of each variable on snowy owl hunting success. I constructed a separate dataset where I organized the data by observation period. I then performed several linear regression analyses to determine the influence of different continuous variables (e.g. ambient temperature, percent cloud cover, and snow depth) on the frequency at which snowy owls perform hunting attempts.

RESULTS

Diurnal Activities of Snowy Owls

Over the 1.5-month-long survey period, I collected 144 h of continuous observational data. Owls spent 98.98% of daylight hours loafing/idling (Fig. 1A).All other activities comprised 1.02% of daylight hours (Fig. 1A). Of the behavioral categories other than loafing/idling, perch-change flights accounted for ~50%, and hunting accounted for ~28% (Fig. 1B). The remaining 22% of activities consisted of search flights, walking/running, foraging, and other (Fig. 1B).

Hunting Behaviors and General Observations

I observed snowy owls execute a total of 51 hunting attempts. Owls used several techniques for capturing prey. Of these techniques, owls most commonly used the "still hunting" or sit-and-wait technique (46 of 51 hunting attempts). When using the sit-and-wait technique, hunting owls typically perched on tall objects (≥5 m in height), such as tree tops, utility poles, and buildings, and scan the surrounding area for several minutes. If an owl was unable to locate a prey item, it would either continue loafing on its perch, or fly to a different perch located >100 m away and continue searching for prey. If an owl located a prey item, it would usually assume an alert, upright posture while staring intently at the presumed location of the prey item. Owls sometimes exhibited several head-bobs, which are thought to facilitate the determination of distance to prey (Boxall and Lein 1982). After determining the exact location of the prey item, owls would then perform a low, direct flight toward the prey item, and execute a hunting strike (the event in which an owl strikes the surface of the ground with its talons to capture its intended prey item).

Even though owls used the sit-and-wait technique in the vast majority of their capture attempts, owls often exhibited different behaviors before, during, and after executing a hunting strike. I chose to recognize these behavioral differences as variants of the sit-and-wait technique. I observed four different variants of the sit-and-wait technique, the "swoop" method, the "pounce" method, the "land-and-pounce" method, and aerial pursuit. An owl using the "swoop" method would typically perform a low, direct flight towards the prey, strike the surface of the ground with its talons while remaining airborne, and then continue flying. Owls used the "swoop" method in 16 of 51 capture attempts (Table 1). An owl using the "pounce" method would approach its prey similarly, but instead of executing the hunting strike while remaining airborne, it would abruptly land on the ground in such a reckless fashion that the owl would almost tumble forward. Owls used the “pounce” method more often than other hunting methods (23 of 51 hunting attempts) (Table 1). An owl using the “land-and-pounce” method would first perform a non-hunting flight to the ground without executing a hunting strike, then scan the surrounding area in an alert posture for a period of time lasting anywhere from a few seconds to several minutes. Once the owl located its prey, it would then perform an additional flight followed by a subsequent hunting strike. Afterward, regardless of the success of the hunting attempt, the owl would then return to its initial commanding perch and continue loafing and/or searching for prey. Owls used the “land-and-pounce” method on 6 capture attempts (Table 1). Occasionally, I would witness an owl perform the first step of the “land-and-pounce” method, where it would perform a non-hunting flight to the ground, and scan the surrounding area for up to several minutes. However, instead of performing an additional hunting flight afterward, the owl would return to its initial perch and continue scanning for prey. I characterized such behaviors as perch-change flights rather than hunting attempts because in these instances, owls did not execute a hunting strike and, therefore, did not attempt to capture a prey item. In one instance, I witnessed an owl attempt to capture a prey item via aerial pursuit. In this instance, a juvenile female owl decided to chase a long-tailed duck (*Clangula hyemalis*) and attempted to capture it while airborne. The attempt was not successful. This was the only instance where an owl performed a capture attempt on a non-mammalian prey item. I once observed a juvenile female owl use the ground hunting technique to capture prey. The owl walked around on the ground and repeatedly pecked at the ground with its beak in an attempt to capture small mammals. The owl struck the ground with its beak 5 times within a 5-minute period. None of these capture attempts were successful.

Hunting Activity and Success

The overall hunting success rate for winter irruptive snowy owls in New York, USA was 45.10% (23 of 51 capture attempts). Juvenile owls seemed to use a greater variety of hunting methods than adult owls. Adult owls used the "swoop" method, the "pounce" method, and the "land-and-pounce" method (Fig. 2). Adults showed equal preference for the "swoop" and "pounce" methods (Fig. 2). Juveniles, however, used every observed hunting method at least once and showed a strong preference for the "pounce" method (Fig. 2). Adult owls were 30% more successful in capturing prey (15 of 25 capture attempts) than were juvenile owls (8 of 26 capture attempts) (Pearson Chi-Square, $\chi_1^2 = 4.398$, $P = 0.036$). The hunting success rate of female owls did not differ from that of male owls (ANOVA, $P = 0.679$). Hunting success rates did not seem to differ when owls used different hunting methods (ANOVA, $P = 0.242$) (Table 1).

Owls directed most of their capture attempts toward small mammals (49 of 51 capture attempts). Although, in one observation, an owl was able to successfully capture a medium-sized mammal. I was unable to identify the captured mammal as it was hidden behind a small pile of snow. However, I was able to estimate the size of the prey item because, rather than consuming the prey whole within seconds after killing it, the owl dissected it with its beak for approximately 2 minutes before returning to its perch. Since the owl was unable to consume its prey whole, I concluded that the prey item was a medium-sized mammal such as a squirrel or a rabbit.

I observed owls hunting in several different habitat types, which were, in order of decreasing number of hunting attempts, stubble fields, fallow fields, airport fields, parking lots, ungrazed grasslands, and manicured fields/lawns (Fig. 3). Owl hunting success remained consistent across all habitat types (ANOVA, $P = 0.213$). Owls performed 31 of 51 (60.78%) hunting attempts from tall perches (≥5 m in height) such as tree tops, utility poles, and buildings

(Fig. 4A, 4B). Owls initiated 7 of 51 (13.73%) hunting attempts from short perches (1-5 m in height) such as fence posts, snowbanks, and scrap piles (Fig. 4A, 4B). Owls performed the remaining 13 hunting attempts (25.49%) from the ground (Fig. 4A, 4B); 5 of which involved the ground hunting method, and 8 of which involved hunting flights. Snowy owl hunting success was consistent across all perch types (ANOVA, $P = 0.509$). Perch height did not seem to have any effect on snowy owl hunting success either (ANOVA, $P = 0.480$).

Snowy owl hunting attempts ranged from 0.30 m to 400.00 m away from their hunting perches; most of which (68.63%) occurred within 100 m of their hunting perches (Fig. 5). Owls sought after prey items that were located, on average, 71.73 m ± 9.81 SE away from hunting perches. The average distance from perch to prey varied when owls used different hunting methods (Table 1). When owls used the "land-and-pounce" method, the mean distance from perch to prey, 198.30 m ± 41.00 SE (Table 1), was greater than when owls used other hunting methods (except for the aerial pursuit method because I only once witnessed an owl use this method) (ANOVA, $P \leq 0.001$). The mean distances between prey items and hunting perches remained consistent when owls used other hunting methods (including the swoop, pounce, aerial pursuit, and ground hunting methods) (ANOVA, $P > 0.05$). Distance between prey items and hunting perches did not seem to influence snowy owl hunting success (ANOVA, $P = 0.280$).

Snowy owl hunting activity varied between different time periods. There was a pronounced peak in owl hunting activity in the late afternoon (16:30–18:30), during which owls performed nearly half of their hunting attempts (25 of 51) (Fig. 6). Periods of moderate hunting activity occurred in the mid-morning (8:30–10:30) and late morning (10:30–12:30) (Fig. 6). Periods of low hunting activity occurred in the early morning (6:30–8:30), early afternoon

(12:30–14:30), mid-afternoon (14:30–16:30), and early evening (18:30–20:30) (Fig. 6). Owl hunting success remained consistent across all time periods (ANOVA, $P = 0.713$).

Owls exhibited variation in hunting activity in response to changes in ambient temperature (Fig. 7). During the survey period, ambient temperatures ranged from −20.56° C to 7.78° C. Owls performed more hunting attempts when ambient temperatures were between −12° C and −7° C than at other temperatures (Fig. 7). When I grouped the data by observation period, I found a weak, negative, linear correlation between daily maximum ambient temperature and number of hunting attempts per observation period (Linear Regression, $P = 0.071$) (Fig. 8A). However, I discovered that the dataset contained an observation with an unusually large residual of 6.36. Consequently, I deemed this observation to be an outlier. In this particular observation, an adult male owl executed 8 hunting attempts in one observation period, during which the maximum ambient temperature was 4.44° C. After I removed the outlier from the dataset, the correlation between daily maximum ambient temperature and number of hunting attempts became much stronger (Linear Regression, $P = 0.006$) (Fig. 8B). However, ambient temperature had no such effect on snowy owl hunting success (ANOVA, $P = 0.336$).

During the survey period, snow depth ranged from 0 cm to 64 cm. Owls performed 53% (27 of 51) of their hunting attempts at snow depths of 0-16 cm, and 33% (17 of 51) of their hunting attempts at snow depths of 48-64 cm (Fig. 9). Owls performed the remaining 14% of their hunting attempts at snow depth levels of 16-48 cm (Fig. 9). When I grouped the data by observation period, there was no correlation between daily snow depth and number of hunting attempts for each observation period (Linear Regression, $P = 0.535$). Snow depth did not seem to have any effect on owl hunting success (ANOVA, $P = 0.551$). Owls performed the majority (37 of 51) of their hunting attempts when no precipitation was present. Owls executed 9 hunting attempts during snowfall and 5 hunting attempts during rainfall. Owl hunting success remained consistent regardless of the presence or type of precipitation (ANOVA, $P = 0.634$).

Percent cloud cover did not seem to have any effect on the frequency of snowy owl hunting attempts. Owls performed 27 and 24 hunting attempts at percent cloud cover levels of 0-50% and 50-100%, respectively. When I grouped the data by observation period, I found no correlation between daily maximum percent cloud cover and the number of hunting attempts for each observation period (Linear Regression, $P = 0.671$). Owls were 25% more successful in capturing prey (14 of 24 hunts) at levels of 50-100% cloud cover than at levels of 0-50% cloud cover (9 of 27 hunts) (ANOVA, $P = 0.077$). This difference was significant at $\alpha = 0.1$, but this was not the case at a significance level of $\alpha = 0.05$.

DISCUSSION

Diurnal Activities and Behavioral Patterns

Activity budgets.— The diurnal activity budgets of winter irruptive snowy owls were similar to those of snowy owls wintering within their traditional range. Boxall and Lein (1989) found that snowy owls spent 98% of daylight hours perched, which is almost alarmingly similar to my findings regarding the percentage of daylight hours that owls spent loafing/idling (Fig. 1A).

Diurnal hunting patterns.— Winter irruptive snowy owls exhibited higher levels of hunting activity in the late afternoon/early evening (16:30-18:30) and mid/late morning (8:30-12:30) than during other times of day (Fig. 6). Several previous studies report similar patterns in the diurnal activities of wintering snowy owls (Shields 1969, Chamberlin 1980, Boxall and Lein 1989). These studies reported that snowy owls exhibited pronounced peaks in activity during the early morning and late afternoon/early evening (Shields 1969, Chamberlin 1980, Boxall and Lein 1989). The diurnal activity patterns of snowy owls often correlate with those of their prey, such as mice (*Peromyscus* spp.) and voles (*Microtus* spp.) (Shields 1969, Boxall and Lein 1989). Even though snowy owl hunting activity varied throughout the day, snowy owl hunting success was consistent at all times of day.

Hunting Activity and Foraging Success

Hunting grounds.— When selecting a habitat in which to hunt, snowy owls preferred stubble fields and fallow fields to other habitat types (Fig. 3). It is therefore likely that stubble fields and fallow fields are more productive than other habitat types because of the relatively high prey availability within such areas (Lein and Webber 1979, Boxall and Lein 1982). It has been presumed that snowy owls tend to avoid residential and industrial areas when selecting a habitat due to human disturbance (Lein and Webber 1979, Boxall and Lein 1982). However, I often observed owls hunting in industrial areas such as airports, athletic fields, and even manicured lawns (Fig. 3). Thus, human disturbance might not be as influential on the habitat selection and hunting activity of wintering snowy owls as previously thought. Despite their preferences for certain hunting grounds, snowy owl hunting success remained consistent across all habitat types. On numerous occasions, researchers have found that habitat characteristics can greatly influence the hunting success of raptors (Collopy and Bildstein 1987, Buchanon 1996). However, based on my observations, this principle does not seem to apply to winter irruptive snowy owls. Although, since owls showed clear preferences for certain habitat types, I did not observe owls hunting in all habitat types equally, making it difficult to test the influence of habitat structure on snowy owl hunting success.

Owls initiated considerably more hunting attempts from tall perches (≥5 m in height) than from short perches (1-5 m in height) (Fig. 4B). Previous studies on wintering snowy owls report similar findings (Chamberlin 1980, Boxall and Lein 1982). Owls also initiated more hunting attempts from the ground than from short perches (Fig. 4A, 4B). Although snowy owls preferred to hunt from tall perches rather than from short perches, snowy owl hunting success seemed to remain constant regardless of the perch type or perch height. Since taller perches tend to provide better vantage points for locating prey (Boxall and Lein 1982), I expected that snowy owls would be more successful in capturing prey when hunting from taller perches than when hunting from shorter perches. However, based on my observations, it would seem as though the increased ability for snowy owls to locate prey when hunting from taller perches does not necessarily translate into an increased ability to capture prey.

Abiotic factors, hunting activity, and foraging success.— Ambient temperature had a significant influence on snowy owl hunting activity. The strong, negative, linear correlation between daily maximum ambient temperature and number of hunting attempts per observation period suggests that snowy owls tend to hunt more frequently when ambient temperatures are relatively low (−22°C to −7°C) than when ambient temperatures are relatively high (−2°C to 8°C) (Fig. 8A, 8B). This is likely due to the fact that snowy owls have higher metabolic requirements at relatively low ambient temperatures than at relatively high ambient temperatures (Gessaman 1972, Boxall and Lein 1989). Thus, in order to meet their metabolic requirements, owls must consume more prey, and therefore must perform more hunting attempts at low ambient temperatures than at high ambient temperatures.

Small mammals such as voles and mice are undoubtedly the most important prey for winter irruptive snowy owls in New York, USA. Since these small mammals often occupy and depend upon subnivean habitats during winter months and use snow cover to avoid predators (Gese et al. 1996, Aitchison 2001), one could expect that snowy owls would be more successful in capturing prey in low snow cover than in deeper snow. However, in my observations, snow depth had no influence on snowy owl hunting success. Much like other members of the family Strigidae, snowy owls use their highly developed sense of hearing to locate prey (Johnsgard 1988). Therefore, a plausible explanation for my observations, with regard to the influence of snow depth on hunting success (or lack thereof), would be that snowy owls are constantly aware of the exact locations of prey items in relation to the snow surface. Snowy owls are also likely aware of the maximum distance at which they are able to extend their talons below the snow surface. Thus, it is likely that snowy owls do not pursue prey items that are beyond their grasping range. If snowy owls pursued all prey items that they were able to detect, then snow depth would certainly influence their foraging success because a large proportion of their hunting attempts would be in pursuit of prey items that are beyond their grasping range.

Cloud cover seemed to have a greater influence on snowy owl hunting success than any of the other environmental factors that I tested. Snowy owls were 25% more successful in capturing prey at levels of 50-100% cloud cover than at levels of 0-50% cloud cover. Reduced visibility during periods of low cloud cover might be a plausible explanation for this relationship. When cloud cover is low, and the sun is not occluded, the high levels of incident sunlight that reflect off of the snow surface may disrupt snowy owls' vision, thus reducing their ability to locate and capture prey. When cloud cover is high, and the sun is occluded, snowy owls are likely unaffected by the resulting low levels of light because of their crepuscular tendencies. Although the relationship between cloud cover and snowy owl hunting success was not statistically significant when $\alpha = 0.05$, this relationship was significant when $\alpha = 0.1$. Therefore, it is evident that the relationship between cloud cover and snowy owl hunting success is sufficiently substantial to merit further research.

Hunting methods.— Although snowy owls used the sit-and-wait technique almost exclusively when hunting, owls used several iterations of this technique; each of which differed in the behaviors that owls exhibited before, during, and after executing a hunting strike. Previous reports on the hunting behaviors of snowy owls do not recognize the various forms of the sit-and-wait technique that I previously described (Chamberlin 1980, Boxall and Lein 1982). This is presumably the case because researchers likely thought these small differences in snowy owl hunting behavior to be insignificant. However, the mere existence of these behavioral differences suggests that each variant of the sit-and-wait technique serves a particular function. It is likely that snowy owls utilize each of these variants under different circumstances. For instance, the utilization of a particular hunting method may depend on the location of a prey item in relation to the surface of the snow.

If a prey item is located at or near the snow surface, the "swoop" method would be a more efficient method of capture than the "pounce" method. When owls use the "swoop" method, rather than landing abruptly in the snow and flying back to their perch afterwards, as they do when using the "pounce" method, they are able to remain airborne both during and after the hunting strike. Thus, when using the "swoop" method, instead of expending relatively large amounts of energy in taking off from the ground after landing, as they do when using the "pounce" method, owls are able to make efficient use of their momentum during the hunting attempt. However, in instances where prey are located relatively far below the snow surface, owls must extend their talons far below the snow surface to capture prey, making it difficult for owls to remain airborne after performing a hunting strike if they were to use the "swoop" method. Thus, in these instances, owls must use the "pounce" method to capture prey because the "swoop" method would be highly impractical.

The mean distance from perch to prey when snowy owls used the "land-and-pounce" method was greater than when owls used other hunting methods (Table 1). In fact, in each hunting attempt where owls used the "land-and-pounce" method, the prey items that owls pursued were more than 100 m away from their hunting perches. Based on this observation, it is therefore probable that snowy owls used the land-and-pounce method as a means of searching for and capturing distant prey items that were difficult to locate from hunting perches. It is likely that owls would perform the first flight of the land-and-pounce method to hone in on prey when owls were unable to pinpoint the exact locations of prey items from their initial hunting perches. After performing the first flight to the ground, owls were then able to further examine the area in which their prey was located. Once they discovered the exact location of prey, owls were then able to pounce on the prey from a much shorter distance. From these inferences, one could further suggest that snowy owls are more likely to use the land-and-pounce method when prey is relatively scarce in a particular area. Snowy owls might use the land-and-pounce method in situations where the only prey present in a particular area are located relatively far (>100 m) away from snowy owl hunting perches, but are not far enough away to merit a change of perch.

In spite of the apparent differences between these hunting methods and the contexts in which snowy owls used them, hunting success did not differ when owls used different hunting methods. Thus, all observed hunting methods seemed to be equally effective for capturing prey. However, owls used some hunting methods far more often than others, which made it rather difficult to perform a valid statistical analysis to compare the effectiveness of different hunting methods. Although, one could assume that snowy owls would use effective methods of prey capture more often than ineffective hunting methods. Perhaps determining the frequencies at which snowy owls use different hunting methods might be a more useful approach for assessing their effectiveness rather than measuring the difference in hunting success when snowy owls use different methods.

Age and hunting success.— The hunting behaviors and habits of juvenile snowy owls differed from those of adults. Juvenile snowy owls used a greater variety of hunting methods than did adults. Juveniles used all observed hunting methods at least once whereas adults only used the “swoop”, “pounce”, and “land-and-pounce” methods (Fig. 3). The observed juvenile snowy owls, being inexperienced hunters, were likely experimenting with different hunting methods to discover which methods were most effective and efficient for capturing prey. Adult snowy owls were also 30% more successful in capturing prey than were juveniles. My observations suggest that juvenile snowy owls are not as efficient in capturing prey as are adults. My findings regarding this matter are in accordance with those of previous studies (Boxall and Lein 1982). In such studies, researchers found that juvenile snowy owls appeared to be inept at handling prey, and thus had more difficulty in subduing prey than did adults (Boxall and Lein 1982). The researchers listed several occasions where prey escaped from juveniles after capture as well as instances where juveniles dropped their prey (though, I did not witness any such occurrences in my observations) (Boxall and Lein 1982). It is therefore presumed that the manipulation of prey after capture is a skill that juvenile owls acquire with age and experience (Boxall and Lein 1982).

The evident ineptitude of juvenile snowy owls with respect to hunting indicates that they are also relatively incapable of meeting their energy requirements, and thus may undergo higher mortality rates than adults (Boxall and Lein 1982). The consideration of this notion is essential, especially in the context of winter irruptions, when investigating the fluctuations in snowy owl population structure because of the many additional costs that are associated with irruptive migration. Such large-scale, long-distance movements require large energy expenditure and may entail other costs such as uncertainty, hazards, and the risk of 'moving for nothing' (Therrien et al. 2014). Additionally, by performing these extensive movements from year to year, individuals lose detailed knowledge and familiarity within a given area, which is often a prime advantage of breeding site fidelity in many species (Therrien et al. 2014). Thus, when these costs are combined with the inexperience and ineptitude of juvenile owls at capturing prey, it is all the more likely that juveniles are to experience much greater mortality rates during irruption years than adults. Therefore, knowledge of the sex and age structure of wintering snowy owls during irruption years would be valuable because age-dependent mortality is presumably one of the main underlying causes for snowy owl population fluctuations following irruption years.

Overall Hunting Success and Final Conclusions

The overall hunting success rate for winter irruptive snowy owls in New York, USA was 45.10%. After performing a comparative analysis, I discovered that my findings regarding the hunting success of snowy owls were exceedingly similar to those of previous studies (ANOVA, $P = 0.945$) (Chamberlin 1980, Boxall and Lein 1982). Based on this notion, it seems as though winter irruptive snowy owls are not any more or less successful in capturing prey than snowy owls wintering within their traditional range. Since habitat structure can influence hunting success of raptors (Collopy and Bildstein 1987, Buchanon 1996), one can therefore assume that hunting success can be used to indicate whether or not individuals are well-adapted to a particular habitat. The conditions that irruptive snowy owls face during the winter in New York, USA do not seem to inhibit their ability to capture prey. Therefore, winter irruptive snowy owls in New York, USA seem to be equally adapted to their chosen wintering grounds as are owls that winter within their traditional range during non-irruptive years.

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Table 1. Number of hunting attempts, hunting successes, percent success rate, and average distance from perch to prey (m) for each hunting method used by winter irruptive snowy owls in New York, USA, January–March, 2015.

Hunting method	Mean ($\bar{x}$) distance from perch to prey (m)	No. of hunting attempts	No. of successes	Success rate
Swoop	49.69 ± 25.11 SE	16	8	50.00%
Pounce	68.39 ± 20.94 SE	23	12	52.17%
Land-and-pounce	198.30 ± 41.00 SE	6	3	50.00%
Ground hunting	0.00 ± 44.92 SE	5	0	0.00%
Aerial pursuit	100.00 ± 100.40 SE	1	0	0.00%

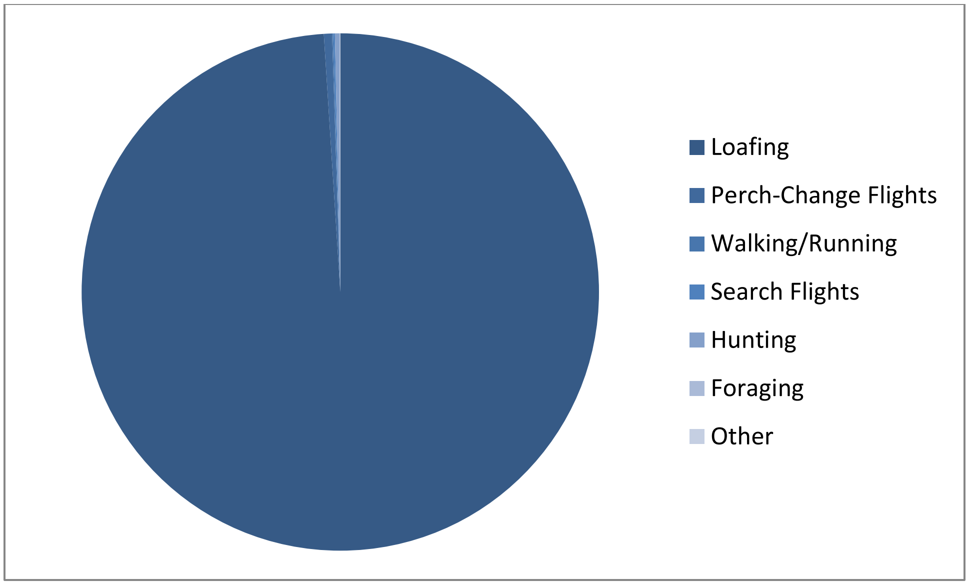

Fig 1A.

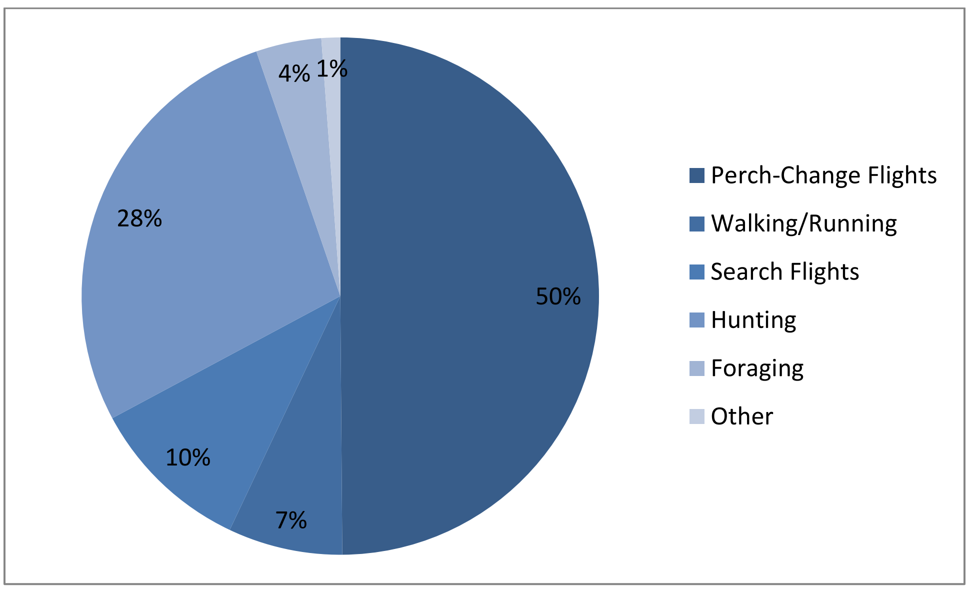

Fig 1B.

Figure 1. Diurnal activity budgets of winter irruptive snowy owls in New York, USA, January–March, 2015, showing (A) the overall amount of time that snowy owls devoted to each behavioral category and (B) the relative percentages of time that snowy owls spent performing different activities when loafing/idling was excluded.

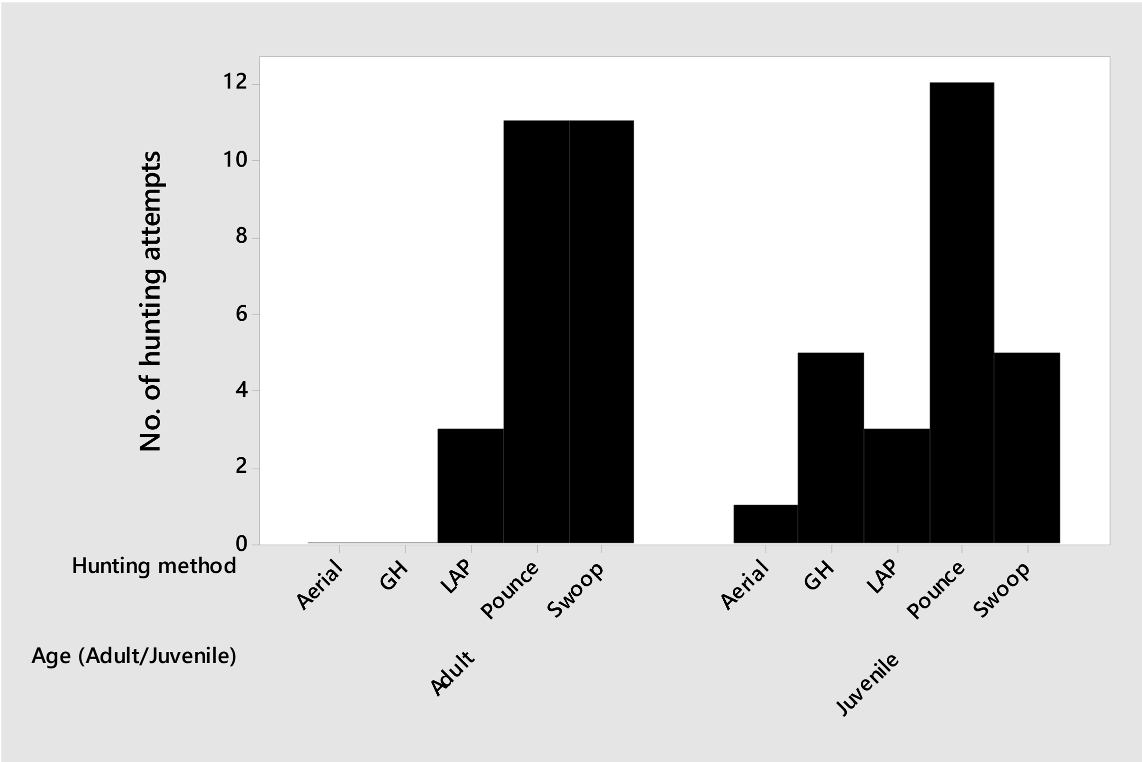

Figure 2. A comparison of the frequencies at which adult and juvenile snowy owls in New York, USA, January–March, 2015, used different hunting methods when pursuing prey items.

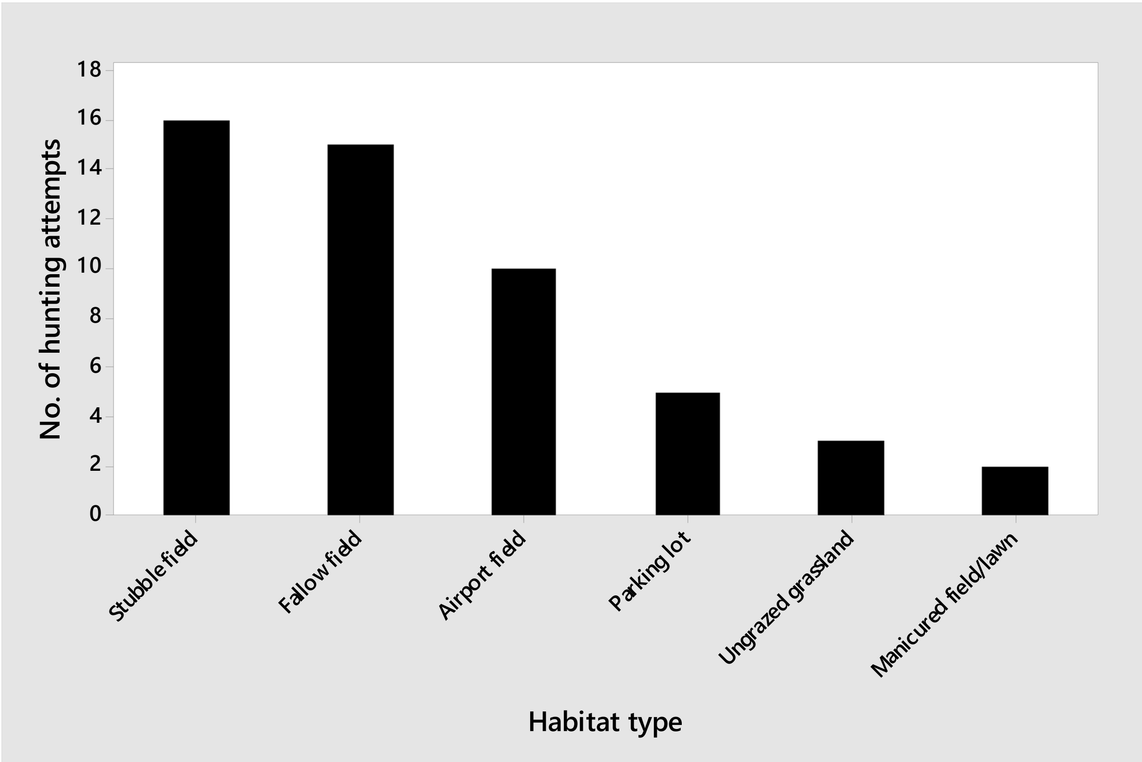

Figure 3. Partitioning of winter irruptive snowy owl hunting attempts among different habitat types in New York, USA, January–March, 2015.

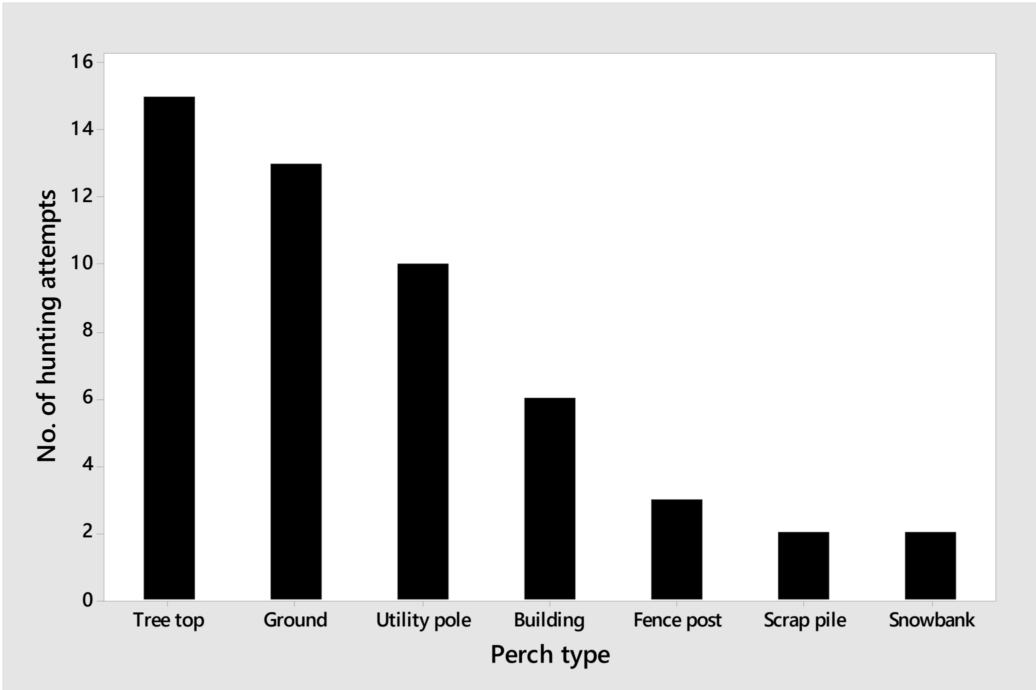

Fig 4A

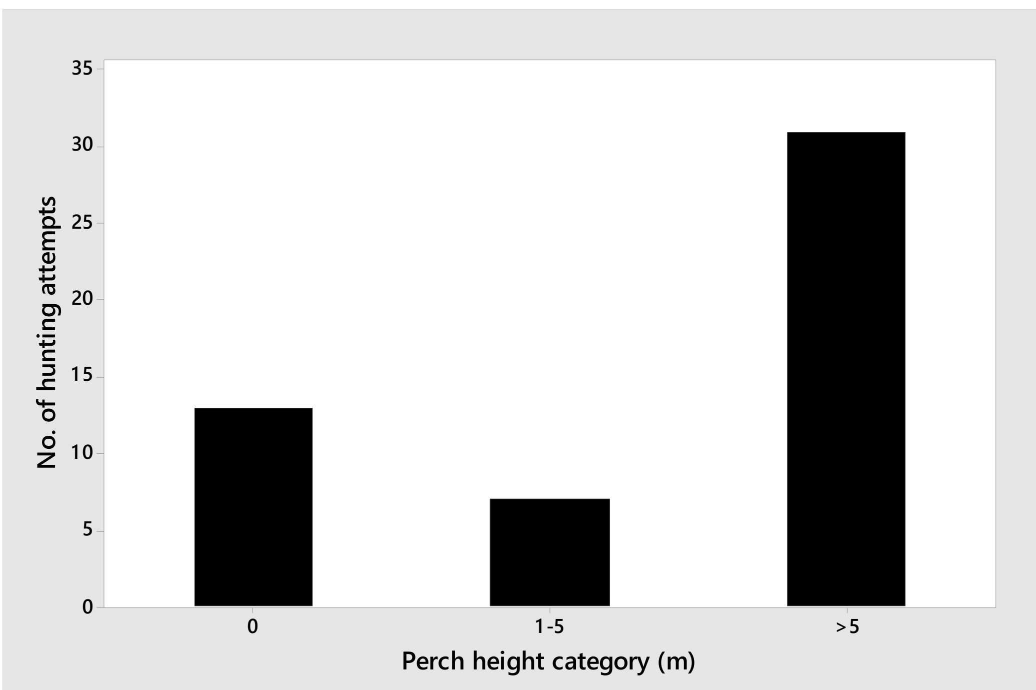

Fig 4B

Figure 4. Influence of different perch characteristics on the hunting behaviors of winter irruptive snowy owls in New York, USA, January–March, 2015. (A) Number of hunting attempts initiated from different perch types and (B) number of hunting attempts in relation to perch height.

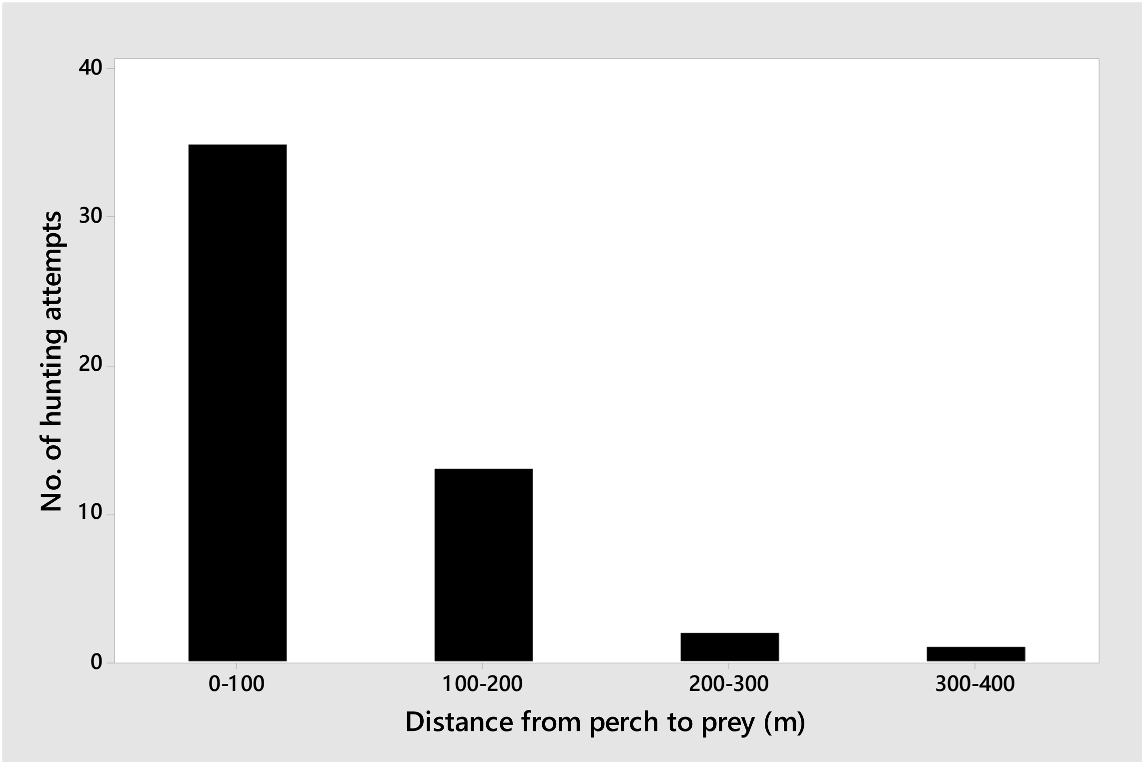

Figure 5. Distribution of hunting attempts in relation to the distances of prey items from hunting perches of winter irruptive snowy owls in New York, USA, January–March, 2015.

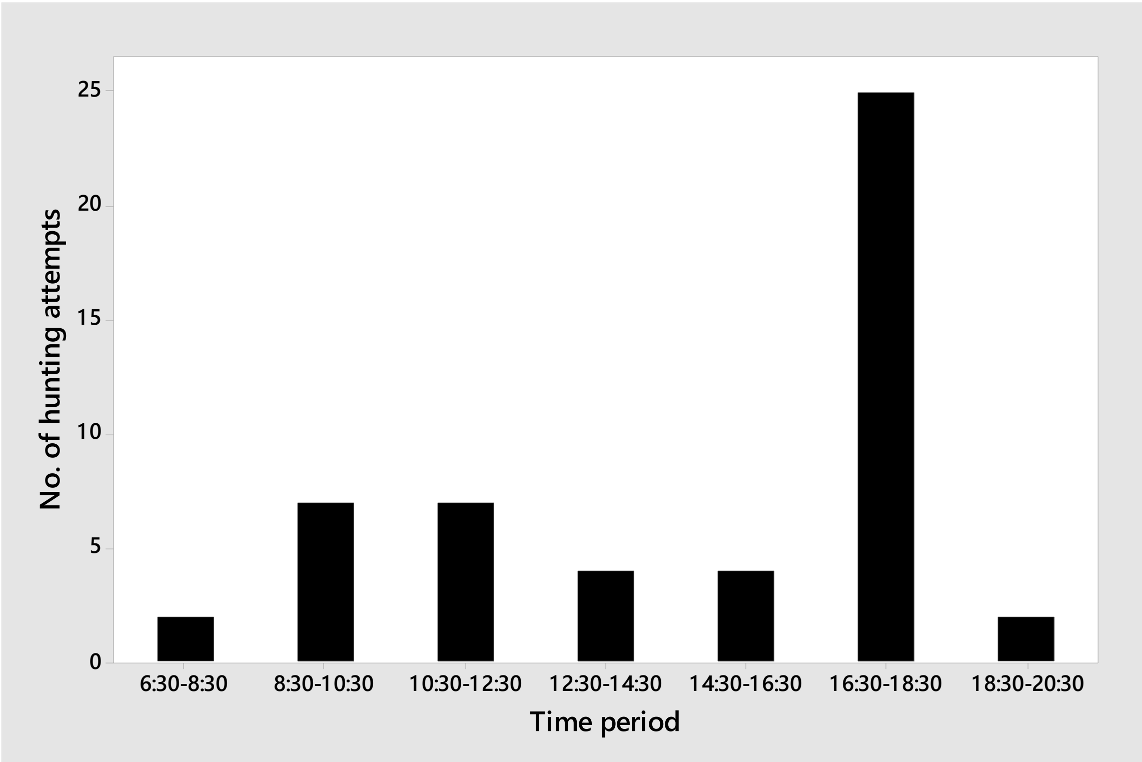

Figure 6. Relationship between time of day and number of hunting attempts executed by winter irruptive snowy owls in New York, USA, January–March, 2015.

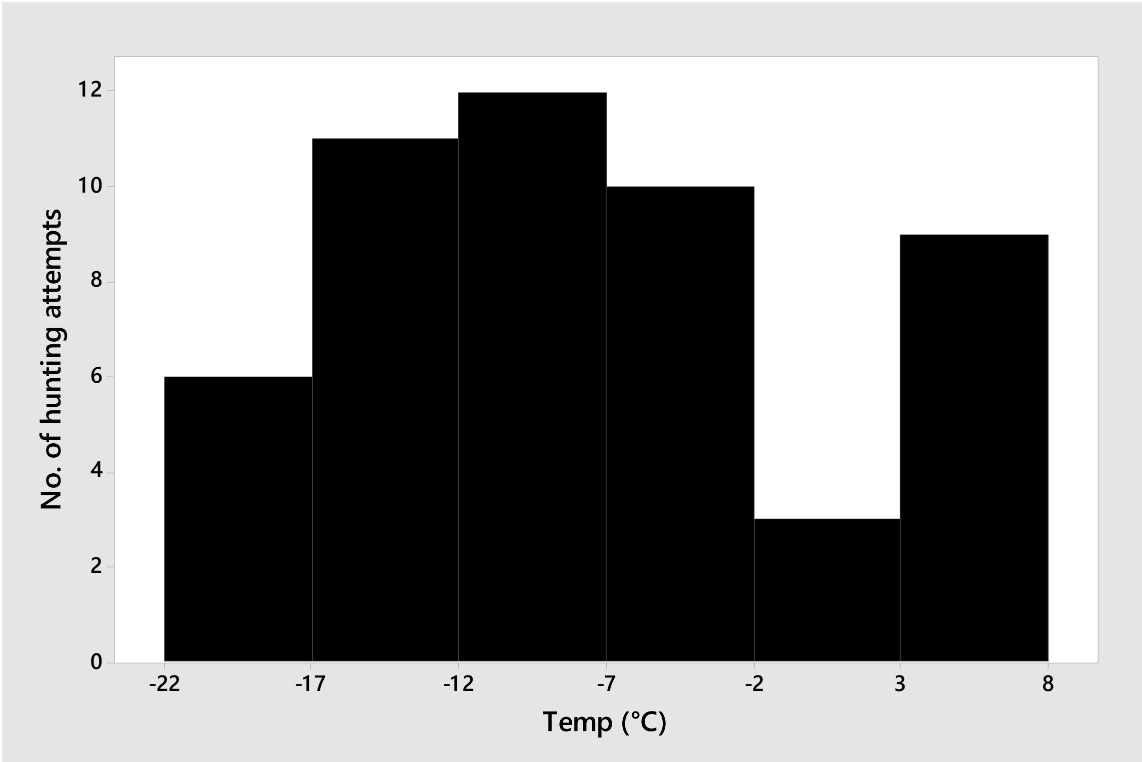

Figure 7. Distribution of hunting attempts by winter irruptive snowy owls in New York, USA, January–March, 2015 at different ambient temperatures (°C).

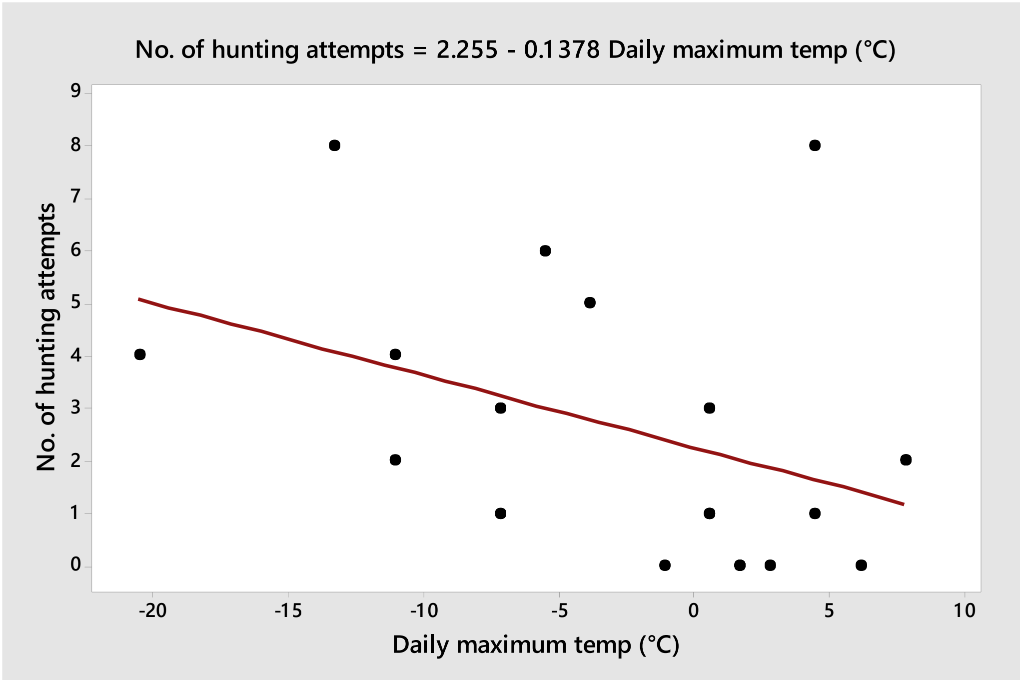

Fig 8A.

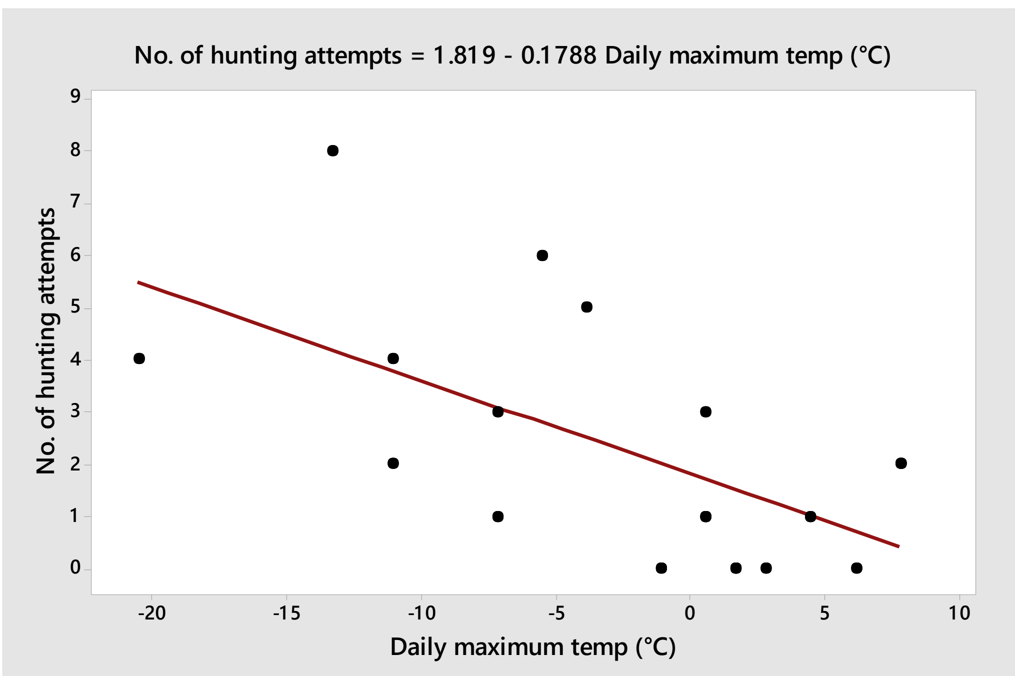

Fig 8B.

Figure 8. Linear regression analyses depicting the relationship between daily maximum temp (°C) and capture attempts by winter irruptive snowy owls in New York, USA, January–March, 2015. Displayed here is (A) a regression analysis containing an outlier in the dataset and (B) a regression analysis in which the outlier was removed from the dataset. The data are grouped by observation period. The linear regression equations are displayed at the top of each figure part.

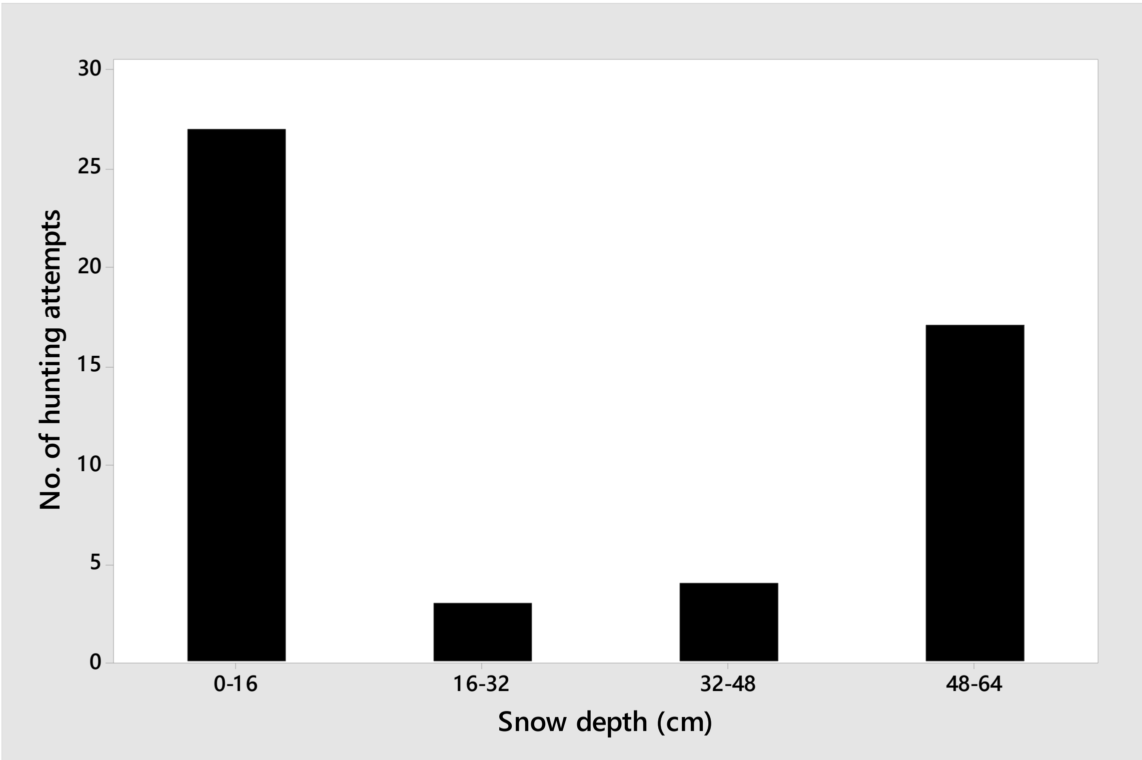

Figure 9. Relationship between snow depth (cm) and number of hunting attempts that winter irruptive snowy owls in New York, USA performed from January-March, 2015.