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ORIGINAL ARTICLE

Timing of attacks by a predator at a prey hotspot

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Abstract Predators and responsive prey might be engaged in a behavioral game in which predators manage responsiveness or fear level in their prey, but the supporting evidence is limited. I investigate a potential case between a predator, the peregrine falcon, and a prey species, the semipalmated sandpiper, during fall staging by sandpipers. For the falcons, attacking vulnerable sandpipers roosting on the shore too early would discourage roosting, but waiting too long might be problematic as well since the roost could disband. Sandpipers are expected to be responsive against potential attacks, but being responsive too long comes at the cost of curtailing rest. The evolutionary stable solution in this game suggests that falcons should attack at all possible times, but concentrate their attacks in the early phases of roosting. Responsiveness by sandpipers, which I measured using the rate of false alarms during roosting, should decrease with time spent roosting. I provide evidence in support of these two predictions, suggesting that falcons and sandpipers are engaged in a war of attrition.

Keywords Behavioral game · False alarm · Peregrine falcon · Semipalmated sandpiper

Introduction

The simple expectation that predators should congregate in areas of high prey density has proven to be just that, a simple but unrealistic prediction in many predator–prey systems (Lima 2002). For mobile predators and stationary prey, for instance, interference between predators foraging in the same prey patch forces predators to disperse spatially (Fretwell and Lucas 1969). As a consequence, given a sufficient number of predators, even the poorest prey patches can become attractive to predators aiming to maximize their foraging success (Sutherland 1983; Yates et al. 2000; van Gils et al. 2006).

The situation becomes even more complicated for prey species that can adopt flexible anti-predator tactics to reduce predation risk. For instance, prey individuals can hide following attacks (Hugie 2003) or move to alternative locations to make it more difficult for a predator to learn their whereabouts (Mitchell and Lima 2002). In addition, susceptible prey individuals can become more vigilant against predators, which might reduce the attack success of predators (Mitchell 2009). Such interactions between predators and responsive prey can be seen as instances of a behavioral game in which the success of a tactic adopted by the predator or the prey depends on what the other actor in the process can do in response (Sih 1984; Brown et al. 1999; Kotler et al. 2002). Evolutionary stable solutions in predator–prey behavioral games can include random prey movement across the habitat, high vigilance, unpredictability in prey hiding time, and

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Significance statement Predators can manage fear level in their prey through their attack strategy. Empirical evidence for such manipulation is scant. I investigated a potential behavioral game between a predator, the peregrine falcon, and one prey, the semipalmated sandpiper, during fall migratory stopover by the sandpipers in the upper Bay of Fundy, Canada. I show that falcons typically waited to launch their attacks on roosts of sandpipers despite very high predictability in the timing and location of roosts from day to day. Combined with a wide range of attack times, this strategy probably instilled uncertainty in the minds of vulnerable sandpipers. Sandpipers responded by adopting a high vigilance strategy during the early phases of roosting. In addition to direct threats, predators can thus also manipulate fear level in their prey to increase their success.

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unpredictability in predator waiting time or return time to a prey patch.

There have been few empirical attempts to examine management of prey responsiveness or fear level by predators. One study documented unpredictable returns by an avian predator at bird feeders, presumably to instill uncertainty in the minds of the prey birds about attack time, but the responsiveness of the prey birds was not documented (Roth and Lima 2007). Laboratory studies showed that an avian predator can space its visits to the same prey patches to avoid returning while the prey are still expected to hide (Katz et al. 2010, 2013). but randomness in prey hiding time and predator return time was not investigated. One field study documented randomness in prey hiding time following an attack and randomness in predator waiting time (Hugie 2004). Another field study showed that a predator can make repeated attacks on a group of prey to weed out the more responsive individuals (Quinn and Cresswell 2012).

Another type of game involves a prey species that has just arrived at a foraging patch where a predator might be lying in ambush (Beauchamp and Ruxton 2012a). The hidden predator must choose how quickly to attack the prey individuals and the prey individuals must adapt their responsiveness to predation threats as a function of time spent in the patch. The evolutionary stable solution identified in this game involves unpredictability in predator attack time and a gradual decrease in responsiveness for the prey. This type of game provides another opportunity to examine predator management of prey responsiveness, but it has not yet been investigated empirically. In the following, I present a study system that involves an observant predator and responsive prey individuals. I describe how the game outlined above was adapted for this specific system and generate testable predictions.

Study system

I investigated interactions between a predator, the peregrine falcon (*Falco peregrinus*), and a prey species, the semipalmated sandpiper (*Calidris pusilla*), during fall staging by sandpipers. The semipalmated sandpiper is a small shorebird that roosts in large numbers on the shore when rising tide water covers the mudflats where it feeds (Hicklin and Gratto-Trevor 2010). Up to a quarter million birds can gather at one roost on any given day during fall staging. Roosts are located close to the tree cover that borders mudflats. Roosting sandpipers are especially vulnerable to falcons that use tree cover to hide their swift approach (Beauchamp 2008; Sprague et al. 2008; Dekker et al. 2011).

I examined the timing of attacks by falcons on sandpiper roosts in Chignecto Bay, one arm of the upper Bay of Fundy, New Brunswick, Canada (Fig. 1). In this area, sandpipers roost in large numbers at four sites located within 13 km of one another and all within visual range (Fig. 1). Roosts in this area can thus be considered prey hotspots for falcons: they form at a very predictable time each day (at high tide) and at very predictable spatial locations.

Although peregrine falcons have a broad diet (White et al. 2002). I surmise that such a large number of sandpipers located close to shore must represent a sizable opportunity. About two or three active falcon nests can be found in the study area. During fall staging by the sandpipers, juvenile falcons have left the nest and hunt by themselves, but are sometimes seen with their parents. I estimate that between 4 and 12 falcons were active in the study area during fall staging depending on the year. Some of the falcons probably return to the area year after year.

War of attrition between falcons and sandpipers

Sandpipers meander in large flying flocks during the rising tide before approaching the shore to roost. These large flocks, which can contain tens of thousands of birds, can easily be seen kilometers away. Given that the flocks can be detected from afar, local falcons probably have little trouble locating promising hunting sites each day and can wait for the sandpipers to start roosting. The few large roost sites in the study area are also located at predictable locations each day. Sit-and-wait is a common hunting tactic for peregrine falcons (Dekker 1980; Dekker and Bogaert 1997; Dekker and Ydenberg 2004). Their problem is rather to choose when to attack birds at the roosting sites.

A recent model investigated a game between an observant predator and responsive prey individuals at a foraging patch (Beauchamp and Ruxton 2012a). The model considered a solitary predator species and a prey species foraging in groups. The group foragers settle in a patch to feed and face the possibility that the predator lies in ambush. Only one predator can be present at a patch at any one time. The predator is not always present at the foraging patch, but when present this predator can be detected with prey vigilance. The predator must choose when to launch an attack after the group foragers settle in the patch. Individual prey must choose how to allocate their limited time between anti-predator vigilance and feeding. Allocating more time to vigilance can help to detect the predator but this is at the expense of valuable feeding time.

The hiding predator faces the following problem. Attacking after a fixed delay following prey settlement in the patch is predictable: the prey individuals would be selected to be extra vigilant up to that time and be more difficult to surprise. Waiting too long, however, can increase the chances that the foragers detect the hiding predator or that the foragers leave the patch prematurely.

The group foragers face the following problem. Maintaining extra vigilance up to a fixed delay after settlement is predictable: the hiding predator would simply wait to launch its attack after that time. Maintaining high vigilance for too

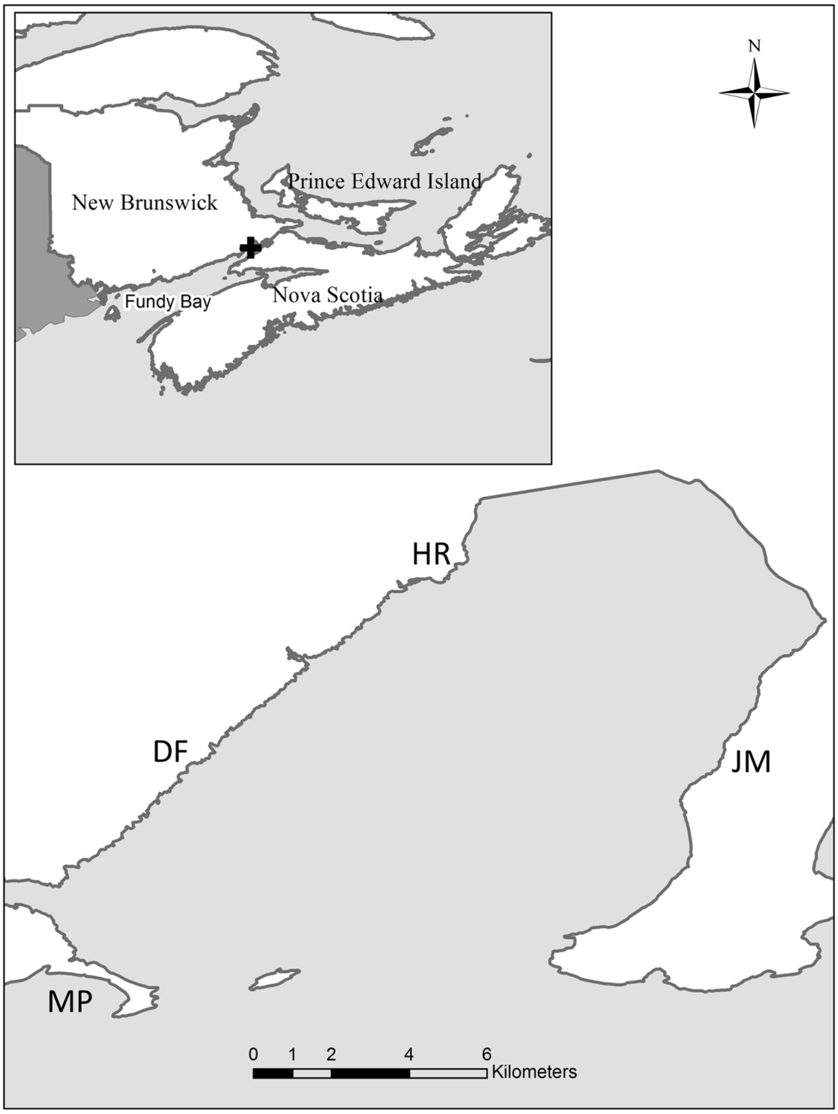

Fig. 1 Spatial distribution of the four major semipalmated sandpiper roosting sites in the Chignecto Bay, an inlet of the upper Bay of Fundy in eastern Canada (*DF* Daniel's flat, *MP* Mary's Point, *HR* Hopewell Rocks, *JM* Johnson's Mills)

long, however, is costly as it detracts from accumulating valuable resources.

Analysis of this attrition game showed that a stable solution takes the following form: the hiding predator should show variability in attack time to reduce predictability. Nevertheless, the hiding predator should show a preference for early attacks to avoid detection and early prey departure. The group foragers should show a gradual decrease in vigilance over time, which is beneficial to detect potential attacks early in the patch and to reduce wasteful vigilance should the predator be absent.

Predictions

For falcons, the model predicts a tendency to avoid attacking shortly after roost settlement (too predictable). Attack times should show considerable variability but should be concentrated in the early phases of roosting. For the prey species, the model specified how vigilance should change as a function of time spent in the patch. Individual vigilance, however, proved quite difficult to measure in large roosting flocks of sandpipers. Instead of measuring vigilance directly, I chose an indirect measure to test the model.

Vigilance is often viewed as a tactic to allay fear, with high vigilance betraying more fear (Brown et al. 1999; Waser et al. 2014; Putman and Clark 2015). A decrease in vigilance would thus indicate lower fear levels or a general decrease in prey responsiveness to potential threats. I surmise that less vigilant animals are less likely to react to potential signs of danger, real or imagined. In the absence of attacking falcons, a decrease in vigilance would translate into fewer false alarms made in response to innocuous signals or imagined threats. False alarms are common in roosting flocks of sandpipers (Beauchamp 2010) and in many other species of birds and mammals as well (Lindström 1989; Cresswell et al. 2000; Blumstein et al. 2004). As a result of decreased responsiveness to threats, I predicted a decrease in the rate of false alarms with time spent roosting. Practically, this means that time spent on shore by roosting sandpipers between two false alarms should increase with time spent roosting.

Many variables can influence false alarm rate. In sandpipers, false alarms increased with roost size and became less prevalent as fall staging progressed (Beauchamp 2010). To isolate the effect of time spent roosting, it is therefore important to control statistically for roost size and migration phenology. It might also be the case that adjustments in responsiveness are less likely in situations where fear levels are high (Lea and Blumstein 2011). This could be the case in smaller flocks that are more vulnerable to attacks (Quinn and Cresswell 2004) or earlier in fall staging when false alarms are more common. If this is the case, I predicted an interaction between the rate of false alarms and roost size and/or migration phenology.

Methods

Study area

The study was conducted from late July to mid-August over five field seasons (2008, 2009, 2013–2015) during the peak of adult fall migration at Daniel's flat (45.73° N, 64.65° W), one of the four roost sites in the Chignecto Bay (Fig. 1). Tides there average 11.5 m in height and expose mudflats twice daily.

Data collection

The monitored roosting site was located on a large pebbly beach bordered by a salt marsh. Thick wooded cover extended about 50 to 100 m away beyond the salt marsh. Depending on tide height and when sandpipers first arrived at the site, the roost could be located at different distances from this cover. I monitored the roosting site from 1 h before high tide to 2 h after high tide.

When the birds first landed at the roosting site, I counted the number of birds present if the roost was small. For larger roosts, I used local landmarks to determine the approximate area of the roost and then multiplied this area by 100 birds/m^2 (Mawhinney et al. 1993). A focal observation with a roost is referred to as a roosting event. A roosting event ended if roost size changed due to the arrival or departure of birds, if the birds relocated elsewhere in the roosting site, if the birds abandoned the roosting site altogether, or when the birds started to feed. Most days included only one roosting event, but occasionally two or more events took place.

During a roosting event, birds frequently flew in alarm only to return some time later at the same location. Therefore, each roosting event included periods during which birds rested on the shore or flew around. Each period spent on the shore before an alarm flight is referred to as a roosting episode. I recorded the timing and duration of each roosting episode and each subsequent alarm flight before the return to the shore. For each alarm flight, I assessed whether it was caused by the attack of a peregrine falcon.

To determine the latency to attack by a peregrine falcon during a roosting event, I only focused on the first roosting event of each day since changes in roost size and location during subsequent events could potentially influence the choice to attack. I also only used the first attack by a falcon during a roosting event. Repeated attacks by falcons occurred occasionally during the same roosting event; such attacks were conservatively considered non-independent given that it was probably the same falcon attacking repeatedly. The latency of attack was censored if no attack took place during a roosting event.

Blinding

It was not possible to record data blind because my study involved focal animals in the field.

Statistical analysis

I used the Kaplan–Meier survival analysis to determine the median latency to attack by a peregrine falcon during a roosting event. The lower bound for the 95 % confidence interval could be calculated for the median latency. If the value of 0 is included in the confidence interval, this means that falcons did not delay their attacks after roost settlement. The model included year as a strata to determine whether the latency to attack varied from year to year.

I aimed to determine whether roosting sandpipers became less responsive during a roosting event. For these calculations, I only included data from roosting events during which no attacks occurred or data prior to an attack. I also considered all roosting events on a given day. Roosting events lasting less than 600 s were discarded as they tended to include too few roosting episodes. I predicted that the duration of a roosting episode during a roosting event would increase with cumulative time spent roosting in that event, which is equivalent to testing for a gradual decrease in false alarm rate. I used a mixed linear model with flock id as a random factor and a series of co-factors including year, roost size and migration phenology (the number of days from the beginning of the field season: day 1 = 28 July). Flock id controls for factors unique to a particular flock such as time of day or temperature, which might influence roosting dynamics. In addition, the random factor controls for the non-independence of sequential roosting episodes in the same roosting event by the same flock. Year was included as a fixed factor to determine whether the patterns tended to be stable from year to year.

I also considered interactions between cumulative time spent roosting and the above three co-factors. Non-significant interaction terms were removed for the final model. For this analysis, roost size, the duration of a roosting episode, and cumulative time spent roosting were $\log_{10}$ transformed to normalize distributions. For ease of interpretation, roost size was classified into two categories: small (<1000) or large based on median roost size across years. Least-square means (SEM) are provided below for categorical variables.

Results

Peregrine falcons attacked roosting sandpipers frequently, but not always before the end of the first roosting event (Table 1). Falcons used stealth attacks on all occasions. Flying low over the salt marsh, the falcons approached the roost location swiftly and tried to capture fleeing sandpipers. Falcons typically launched from 1 to 3 attacks/h sandpipers spent on the shore (Table 1).

Latency of attacks during the first roosting event ranged between 45 and 6765 s, and 75 % of the attacks took place during the first 25 min of a roosting event. The survival analysis revealed a statistically significant heterogeneity among years ($p=0.04$; Fig. 2), with attacks occurring sooner during a roosting event in 2008 and 2009 than in the later years. The lower bound of the confidence interval about the median latency to attack estimated from the survival analysis excluded the value of 0 each year (Table 1).

Depending on tide height, sandpipers typically started roosting around high tide and left the roost to feed 1 to 2 h later when undisturbed. Sandpipers roosted on the shore almost every monitored day during fall staging. Roosts ranged in size from 25 to 100,000 (Table 1), with typically several thousand present each day. A roosting event without an attack typically lasted about 21 min (max=140 min) (Table 1).

The mean duration of a roosting episode varied statistically significantly among years ($F_{4,\,57}=5.1, p=0.001$; Table 1) and increased with roost size ($F_{1,\,57}=4.2$, $p=0.04$; small, 1.69 (0.081); large, 1.72 (0.068), log units). Mean duration of a roosting episode also increased in the later stages of the migration phenology ($F_{1,\,57}=17.1$, $p=0.0001$; early, 1.50 (0.074); late, 1.91 (0.069), log units).

I now turn to the prediction that the mean duration of a roosting episode varies with time spent roosting. There was an overall increase in the mean duration of a roosting episode with cumulative time spent roosting ($F_{1,\,467}=5.7, p=0.02$) and significant interactions between cumulative time spent roosting and other variables in the model. In particular, there was a statistically significant interaction between cumulative time spent roosting and year ($F_{4,\,467}=4.0, p=0.003$) and roost size ($F_{1,\,467}=8.0, p=0.005$), but not with migration phenology. With respect to year, the mean duration of a roosting episode was not related to cumulative time spent roosting in 2008 (β(SEM)=−0.16 (0.14), $p=0.25$), in 2009 (β(SEM)=0.16 (0.13), $p=0.22$), and in 2013 (β(SEM)=−0.036 (0.14), $p=0.79$) but increased with time spent roosting in 2014 (β(SEM)=0.43 (0.12), $p=0.0002$) and 2015 (β(SEM)=0.30 (0.11), $p=0.008$). With respect to roost size, the mean duration of a roosting episode was not related to cumulative time spent roosting in small roosts (β(SEM)=−0.050 (0.10), $p=0.62$) but increased with time spent roosting in large roosts (β(SEM)=0.33 (0.072), $p<0.0001$; Fig. 3).

Discussion

Despite high temporal and spatial predictability in roost location, peregrine falcons avoided attacking the birds at the onset

Table 1 Comparative statistics of semipalmated sandpiper roosts and peregrine falcon attacks over five field seasons

Variable	Study year				
	2008	2009	2013	2014	2015
Sandpiper roosts					
Median roost size (min, max)	1750 (34, 15,000)	300 (25, 10,000)	1000 (50, 100,000)	3000 (100, 30,000)	1000 (50, 22,000)
Median duration (s) of an undisturbed roosting event (min, max)	665 (205, 1444)	1310 (630, 2295)	1678 (390, 6460)	2057 (190, 8388)	940 (437, 8260)
Peregrine falcon attacks					
Median latency of attack (s) (lower bound of the 95% confidence interval)	1400 (395–)	1425 (495–)	5295 (2835–)	5295 (425–)	6765 (609–)
Proportion of first roosting events with an attack (*n*)	0.46 (13)	0.60 (15)	0.36 (14)	0.47 (15)	0.33 (12)
Number of attacks per h spent by sandpipers on shore (number of attacks)	0.97 (10)	2.68 (13)	2.67 (14)	1.24 (12)	1.14 (8)

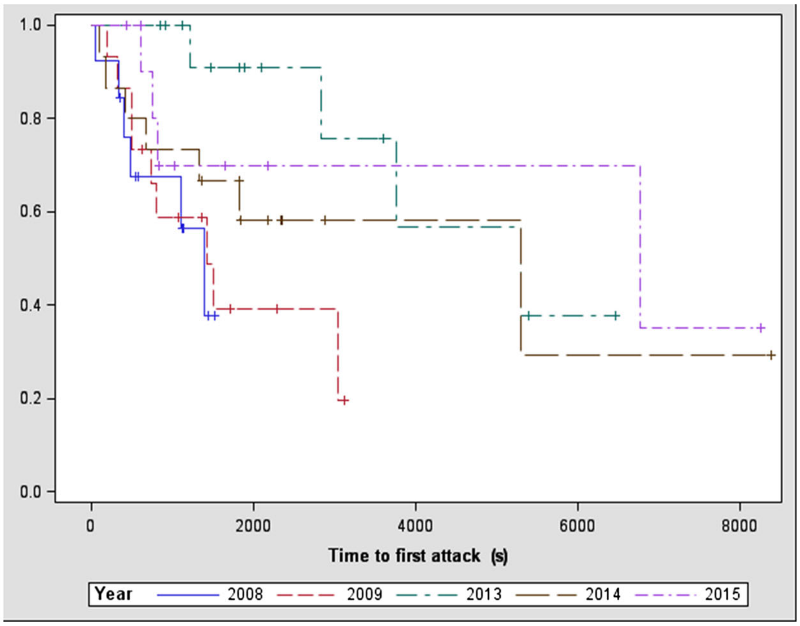

Fig. 2 Probability that peregrine falcons launched an attack on roosting sandpipers as a function of time spent roosting (s) in five different years. *Crosses* show censored data points (no attack took place during a roosting event). Probabilities were obtained from the Kaplan–Meier survival analysis.

of roosting. Generally, attacks occurred in the early phases of roosting, but could take place in the later stages as well. In addition to this inherent variability in attack time within a given year, the pattern of attack varied among years with earlier attack times in some years than others.

The timing of attacks by peregrine falcons support the prediction that observant predators faced with responsive prey at hotspots should typically delay their attacks. A wide range of attack times would instill uncertainty in the minds of roosting sandpipers. Lack of predictability in attack times was reported

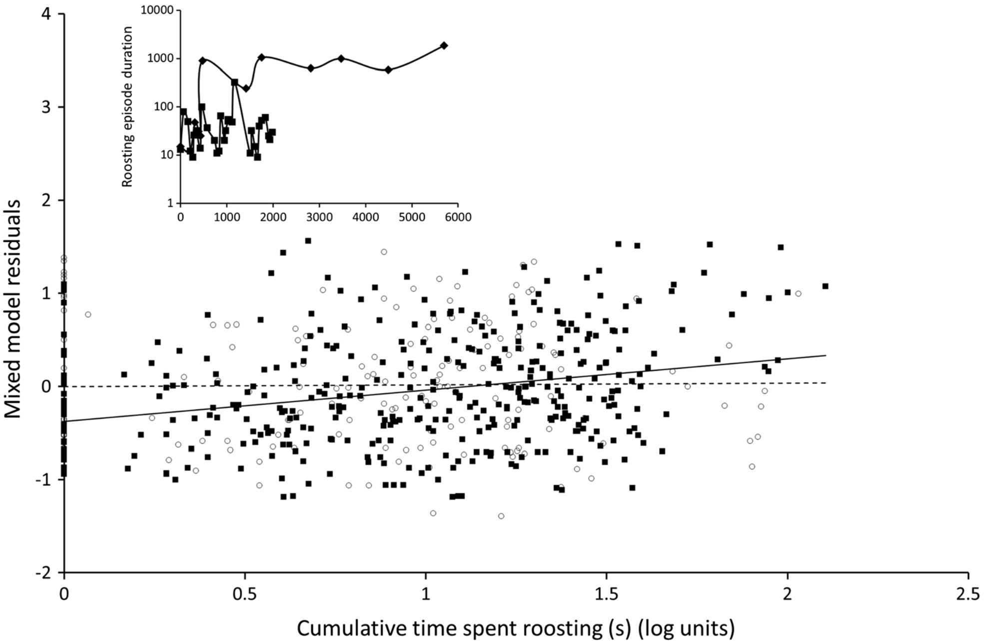

Fig. 3 The mean duration of sequential roosting episodes increases with cumulative time spent roosting (s; log units) in large roosting flocks of semipalmated sandpipers (*filled squares*) but not in small flocks (*open circles*). Residuals of a regression model of the mean duration of roosting episodes with year, roost size, and migration phenology as fixed factors and flock id as a random factor, but excluding cumulative time spent roosting, are plotted against cumulative time spent roosting. Linear trend lines are shown for large (*thick line*) and small roosts (*dashed line*).The *inset* illustrates two particular examples, one of which shows an increase in roosting episode duration (log scale) as time spent roosting (s) increased

for sharp-shinned hawks (*Accipiter striatus*) visiting bird feeders (Roth and Lima 2007) although this could simply mean that the hawks did not really perceive feeders as hotspots. In that study, hawks had access to more than a dozen feeders and it is not clear whether prey birds were available there at all times. By contrast, falcons here faced extremely high temporal and spatial predictability in prey availability. In addition to delayed first attacks, repeat attacks by a predator over a short time period might also represent a form of prey management to weed out more responsive prey birds (Quinn and Cresswell 2012). Peregrine falcons often attacked sandpipers several times during the same roosting event, but I could not establish whether the remaining sandpipers were more vulnerable to subsequent attacks.

As judged from the interval between alarm flights, sandpipers often showed the same responsiveness over the entire roosting period. However, in two of the study years, sandpipers decreased their responsiveness as roosting progressed, suggesting variability in the response of sandpipers to falcon attacks among years. Reduced responsiveness from the beginning of a foraging or a resting bout has been documented in other species (Desportes et al. 1991; Trouilloud et al. 2004; Welp et al. 2004; Beauchamp and Ruxton 2012b; Wheeler and Hik 2014). but it is not clear whether these species faced observant predators.

Low attack rate in 2014 and 2015, compared with previous years, might explain why sandpipers only decreased their responsiveness with time spent roosting in those 2 years. In addition, a decrease in responsiveness with time might also make more sense if the falcons that are present are less threatening. When less-skilled juvenile falcons attacked, sandpipers often reformed the roost minutes later rather than abandon the site altogether. The lower perception of risk might explain decreased responsiveness over time. Unfortunately, it was not possible to assess age of the falcons for most attacks. I also note that too predictable a decrease in responsiveness with time spent roosting might provide clues as to when to attack for falcons. The idea that the temporal pattern in responsiveness is sensitive to perceived risk might also explain why the decrease in responsiveness with time was only apparent in the larger roosts. Reduced responsiveness might be too risky in smaller roosts with fewer alert individuals. Higher vigilance is well known in small foraging groups (Beauchamp 2015).

Short attack delays by falcons are certainly compatible with the idea that falcons waited in ambush before launching an attack on the roosting birds. Longer delays are also predicted by the model, but such delays could also be explained by other factors. For instance, the falcons might arrive at a roosting site after a delay rather than wait there as the model implies. A delay could arise if falcons chased other types of prey earlier or failed to notice the location of roosting sandpipers. I argued that the occurrence of roosting sandpipers in such large numbers so close to cover constitutes a very good foraging opportunity for falcons. High spatial and temporal predictability in their occurrence also make roosting sandpipers hard to ignore. Their large meandering flocks near a roosting site and frequent false alarms at the roosting site also make them highly conspicuous, suggesting that lack of interest or lack of information are not very likely to explain attack delays. Nevertheless, studies with marked falcons would allow a more direct assessment of their hunting tactics.

A tactic of restraint by predators, such as the one identified here, could be invaded by competitors attacking sandpipers very early after roost formation. Losing the element of surprise would probably greatly reduce the success of waiting falcons (Cresswell 1996). However, this solution would probably backfire as sandpipers would become more reluctant to roost close to shore, leading to a decline in predation success for all. Future studies with marked falcons could shed light on the development of hunting tactics in this system where learning probably plays an important role.

The possibility that predators manage fear level in their prey to increase hunting success warrants more research in vertebrate as well as in invertebrate predator–prey systems in which predators and prey interact closely.

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Ethical standards This observational study complies with the current laws in Canada. This study received no external funding. I declare that I have no conflict of interest.

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