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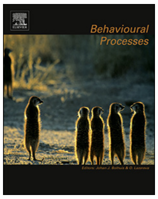

Can scalar timing explain variability in scanning patterns?

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ABSTRACT

Why are scanning patterns so variable? Theory predicts that for prey species facing non-stalking predators scans to monitor predators should occur at fixed rather than unpredictable times. Yet, empirical distributions of inter-scan intervals (ISIs) are very variable. One hypothesis to explain variability is that animals initiate several of their scans in response to external disturbances that occur at random times. I propose, instead, that animals actually aim to initiate scans at fixed times, which are adjusted to perceived predation risk, but well-established cognitive processes on interval timing induce variability in ISIs. Signatures associated with scalar timing, a leading theory of interval timing in animals, include a linear increase in the standard deviation of ISIs as a function of mean ISI duration. The increase is expected to be proportional to mean ISI duration, which implies that the CV (SD*100/Mean) of ISIs is unrelated to mean ISI duration. Finally, the distribution of ISIs should be gamma-like with right skew. I tested these predictions in groups of domestic fowls (*Gallus gallus domesticus*) under controlled conditions and in groups of American flamingos (*Phoenicopterus ruber*) in the field. I found support for most but not all predictions in these two species. In particular, CV of ISIs increased with the mean, a deviation that I attribute to non-independent vigilance amongst group members. Cognitive processes associated with scanning patterns warrant further empirical testing.

1. Introduction

Foraging exposes prey species to predation threats. To detect threats, individuals sporadically interrupt foraging to scan their surroundings (Beauchamp, 2015). Scanning detracts from the accumulation of resources, but gives foragers a better chance to detect threats before it is too late to escape (Bednekoff and Lima, 1998).

Stalking predators like cats break cover to attack prey after a surreptitious approach. Such predators could take advantage of any regularity in prey scanning to advance closer. Therefore, theory predicts that prey facing stalking predators should initiate scans at unpredictable times (Bednekoff and Lima, 2002; Scannell et al., 2001), thus inducing considerable variability in the duration of intervals between successive scans (inter-scan intervals or ISIs). When facing non-stalking predators, such as raptors that rely on surprise attacks, theory predicts that prey should initiate scans at fixed rather than unpredictable times. The distribution of ISIs induced by such regular scanning should be much less variable and centered about the fixed time appropriate for the level of predation risk (Bednekoff and Lima, 2002).

A conundrum in vigilance research is why empirical distributions of ISIs are so variable when prey face non-stalking predators. Indeed, ISI distributions often span a large range of values rather than being tightly clustered (Elcavage and Caraco, 1983; Beauchamp, 2006; Sullivan, 1985; Carro and Fernandez, 2009; Pays et al., 2010). Deviation from the expected ISI duration is not ideal: initiating a new scan too early likely provides little additional information and waiting too long might slow reaction time to a fast approaching predator. Some researchers proposed that external disturbances cause this large, unexpected variability by interrupting foraging at random times (Ruxton and Roberts, 1999).

Here, I want to draw attention to an additional explanation based on an internal rather than an external source of randomness. I propose that in line with theory, prey aim to initiate scans at regular intervals, but that well-established cognitive processes associated with interval timing induce considerable variability in ISIs.

Interval timing is ubiquitous in the animal world. For instance, animals use their internal clock to estimate when to leave a patch or when to expect the next food delivery (Kacelnik et al., 1990; Oprisan and Buhusi, 2014). In influential models of interval timing, keeping time with an internal clock is noisy because tick intervals are not constant (Gibbon et al., 1984). In addition, when timing a fixed interval, animals compare the current, already noisy value on their clock with a value retrieved randomly from memory of past timing events associated with this particular fixed interval. However, encoding in the memory of these earlier timing events introduced an additional source

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of noise. Consequently, animals draw different values from memory on different instances of timing the same fixed interval. When the particular retrieved value from memory and the current time on the clock are close enough, animals stop the clock and initiate a response (here it would be a scan for vigilance). With such processes, the duration of an ISI should vary substantially from one interval to the other.

Interval timing under this model leaves empirical signatures. In particular, the noise (or error) around the expected fixed interval should increase linearly with mean interval duration. Consequently, a plot of the standard deviation of ISIs should show a strong, linear positive relationship with the mean duration of these intervals. This noise is also expected to be proportional to the mean interval duration, which implies that the coefficient of variation (CV: SD*100/Mean) of these ISIs should be constant regardless of mean interval duration. These expectations arise from the scalar property of interval timing based on the above model (Gibbon et al., 1984). Finally, scalar timing should lead to a right skew in the distribution of ISIs rather than a normal distribution (Gibbon, 1992).

I examined these predictions in two species of birds, one foraging under controlled conditions in the laboratory and the other in the field. I observed birds in groups of different sizes to induce variation in the expected duration of ISIs. Due to greater safety in larger groups (Beauchamp, 2014), expected mean duration of ISIs should increase at the expanse of vigilance as group size increases.

In the laboratory, I studied domestic fowls (*Gallus gallus domesticus*). Ancestral fowls probably faced a wide range of terrestrial and aerial predators (Nicol, 2015). Domesticated fowls still show antipredator vigilance (Schütz et al., 2001) and this vigilance decreases with group size (Beauchamp, 2017a). In the field, I studied the American flamingo (*Phoenicopterus ruber*). This large species faces few natural predators (Allen, 1956), but reacts strongly to the presence of people (Baldassarre and Arengo, 2000). Vigilance also decreases with group size in this species (Beauchamp and McNeil, 2003). I expected scans to be initiated at fixed rather than unpredictable times (subject to the above processes) because neither species is closely associated with a stalking predator.

2. Methods

2.1. Laboratory

Thirteen female domestic fowls of a layer breed served as experimental subjects. Birds had access to a 3 × 3 x 3 m indoor pen under a 13L:11D photoperiod regime and to a similar sized covered outdoor pen exposed to natural light. The wire mesh in the outdoor pen allowed visual and auditory contact with local threats including foxes, dogs, cats, and hawks. Perches, patches for dust bathing, water, and a commercial layer feed were available at all times except during trials. This laboratory study was approved by the Animal Care Committee of the Faculty of Veterinary Medicine, University of Montréal.

Trials took place in the outdoor pen. I tested all birds in randomly formed groups of four different sizes: 1, 2, 4, and 6. Birds were food deprived for 3 h prior to a trial to increase feeding motivation. Birds in a given group were given 3 min to settle down in the outdoor pen after which a food patch with a large amount of the layer feed was uncovered to signal the start of a trial. Each trial lasted 3 min and was videotaped.

When feeding, birds alternated between bouts with the head down to handle food and bouts with the head up to scan the surroundings. I played videos one frame at a time (1 frame = 33 ms) to measure the duration of all ISIs during a trial. An ISI started when a bird pecked at food and ended when the bird lifted the head and maintained the bill at the horizontal level.

2.2. Field

I observed American flamingos at the Chacopata lagoon complex (10°40′ N, 63°46′ W) on the north side of the Araya Peninsula, Sucre State, in northeastern Venezuela from 20 December 2001 to 6 January 2002. I watched feeding flamingos at two lagoons using binoculars during the day and a binocular light intensification module (ITT Night Quest 250) affixed with a 12X camera lens at night. For each group, I observed one focal subject located in the middle of the aggregation. As flamingos were not marked, some birds might have been sampled more than once, but this appears unlikely given the large number of flamingos foraging in the area (> 200 at that time). Focal observations lasted 10 min or until the focal subject stopped foraging, was lost from sight or if group size changed. Feeding flamingos alternated between bouts with the head below water to filter food and bouts with the head up to scan the surroundings. With a watch, I timed the duration of all ISIs for each subject starting when the head of the flamingo disappeared underwater and ending when the head rose above water and the bill was held horizontally.

2.3. Statistical analysis

For each species, I used a linear mixed model to assess the relationship between SD of all ISIs during a trial or a focal observation and their mean. For domestic fowls, I added id as a random factor to take into account multiple measurements for each individual. I transformed the data with the logarithm base 10 to normalize the distributions. Under the assumption of constant CV, the slope of the relationship between log SD and log mean should be equal to 1. Using a one-tailed, one-sample runs test for randomness, I tested the linearity assumption of the above models (Siegel and Castellan, 1988). A nonlinear relationship would have longer runs of positive or negative residual values in a row than predicted under the null hypothesis of randomness.

With untransformed data, I tested whether the observed skewness in the distribution of ISIs differed from that predicted under the normal distribution using published statistical tables providing the probability of observing skewness values larger than expected for a given sample size (Pearson and Hartley, 1970). For domestic fowls, I tested skewness using all ISIs for each group size separately. For flamingos, I tested skewness using all ISIs in the following three group size classes: 1, 2 to 5, and 6 and larger.

3. Results

In domestic fowls, SD of ISIs increased with the mean ($F_{1,35} = 404.1$, $p < 0.0001$; Fig. 1 top panel). The slope (SEM) was significantly larger than 1 (1.13 [0.056], $t_{35} = 2.4$, $p = 0.024$) indicating that CV increased with the mean. The runs test revealed no significant departure from a linear relationship ($z = 1.2$, $p = 0.88$).

In flamingos, SD of ISIs also increased with the mean ($F_{1,60} = 222.0$, $p < 0.0001$; Fig. 1 lower panel). The slope (SEM) was also significantly larger than 1 (1.18 [0.079], $t_{60} = 2.4$, $p = 0.029$), and there was no significant departure from a linear relationship according to the runs test ($z = 0.16$, $p = 0.56$).

The distribution of ISIs was significantly right-skewed at all group sizes for domestic fowls ($p < 0.05$, Fig. 2) and for all group size classes in flamingos ($p < 0.05$, Fig. 3).

4. Discussion

When facing unpredictable predator attacks, prey species should become vigilant at regular intervals adjusted to predation risk. This was clearly not the case in domestic fowls and in flamingos: in both species, the range of ISIs was large for a given group size and SD of ISIs actually increased in a linear fashion as group size increased. In both species, CV of ISIs also increased in the larger groups. The distribution of ISIs for a given group size was skewed to the right. These results lend some but not full support to the hypothesis that birds in this study timed the onset of their scans using a noisy internal clock.

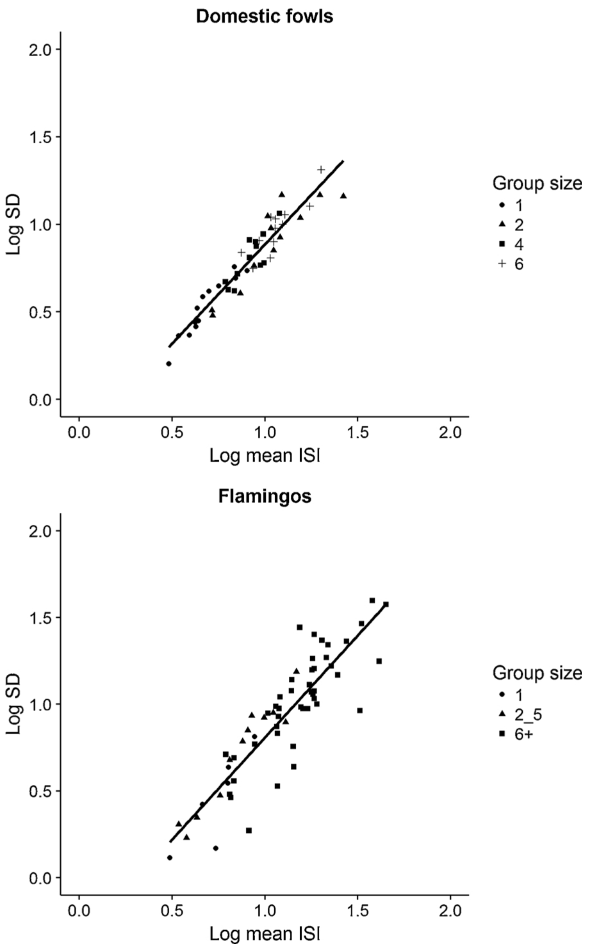

Fig. 1. Variability of inter-scan intervals.
Relationship in log scale between the standard deviation of inter-scan intervals (ISIs) and the mean of these intervals in domestic fowls (n = 13) tested at four different group sizes in the laboratory (top panel) and in American flamingos in three ranges of group sizes observed in the field (lower panel). Thick lines show a simple regression line across the data to illustrate the fit of the model.

Scalar timing of vigilance bouts predicts all of the above features except for the increase in the CV of ISIs with longer ISI duration. Increases in CV with longer interval duration have been reported in the psychological literature on timing (Lejeune and Wearden 2006), and are often related to external factors affecting the internal timing mechanism. One possibility here for the two social species is that other group members influenced the timing of vigilance bouts. Vigilance in many species is not independent amongst group members (Beauchamp, 2009; Pays et al., 2007; McDougall and Ruckstuhl, 2018). An individual in a group might thus postpone vigilance if nearby companions are still feeding or become vigilant sooner than expected if the others are vigilant. These external influences would increase variability in ISI duration especially in the larger groups where social influences are probably stronger. Future studies are needed to determine whether the fit to scalar timing predictions is stronger when vigilance copying is not involved.

Can mechanisms other than scalar timing explain some features of the data? External disturbances, rather than internal noise arising from scalar timing, could explain some of the variability in the distribution of ISIs (Ruxton and Roberts, 1999), but such noise appears unlikely to act alone here if at all. Random external disturbances are more likely to curtail the duration of longer ISIs. This should create more errors for the longer ISIs as observed here in each species. This observation, therefore, is not unique to scalar timing. However, the skew in the distribution of ISIs should be to the left rather than to the right (as was the case here) because random external disturbances can only influence the duration of an ISI if they occur before a scan was set to occur. In any case, external disturbances are not an issue in flamingos because they feed with their heads under water. Visual disturbances are also not very relevant in domestic fowls because they close their eyes much of the time when they feed (Beauchamp, 2017b).

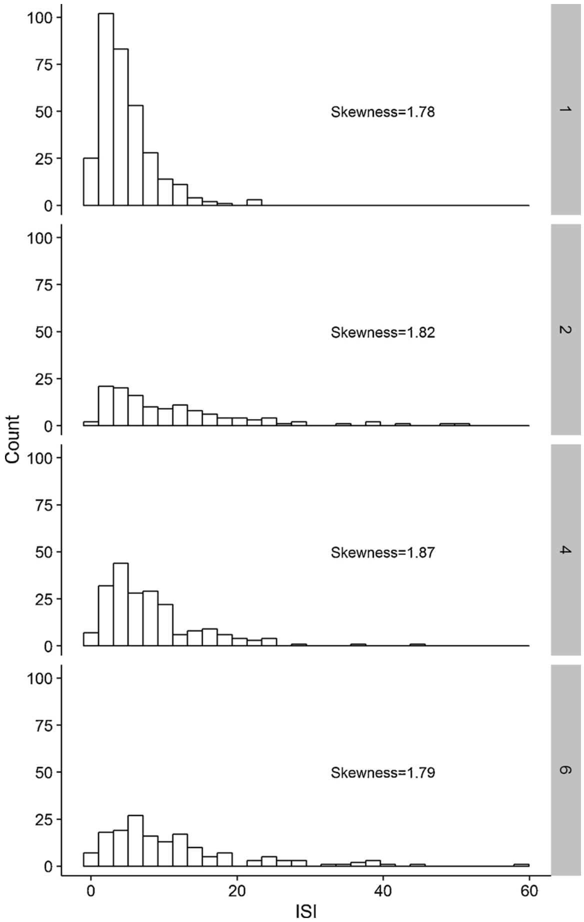

Fig. 2. Distribution of inter-scan intervals in domestic fowls.
The distribution of inter-scan intervals (ISIs) and associated skewness in domestic fowls (n = 13) tested in four different group sizes.

When prey species face stalking predators, the distribution of ISIs is expected to be variable to instill uncertainty in the mind of predators (Scannell et al., 2001; Beauchamp and Ruxton, 2012). One theory predicts that to be truly unpredictable scans should be initiated at a constant rate per unit of time (Bednekoff and Lima, 2002). This would produce an ever decreasing negative exponential distribution of ISIs. There is no support for this prediction in domestic fowls and flamingos as all ISI distributions were humped. Humped ISI distributions also occurred in other species (Sullivan, 1985; Carro and Fernandez, 2009; Pays et al., 2010), but it is not clear whether these prey species only faced non-stalking predators. The fit to scalar timing predictions is not expected to be very strong when prey species face stalking predators and have less need to time fixed intervals. This could be examined in future work with other species.

I studied two relatively large species with rather long ISIs. Distributions of ISIs in smaller species tend to have a smaller mean and often show no hump but rather a peak at the smallest intervals (Elcavage and Caraco, 1983). Scalar timing predicts a gamma-like distribution of ISIs with a right skew as was the case in domestic fowls and flamingos. However, I note that exponential-like distributions of ISIs with a peak at the smallest intervals are compatible with a gamma distribution if the mean is small. Investigations of scalar timing are

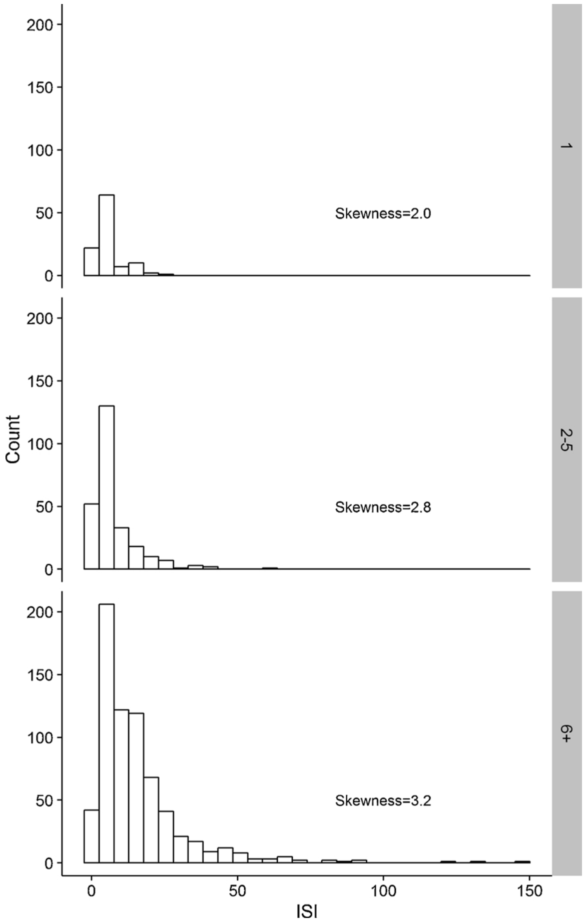

Fig. 3. Distribution of inter-scan intervals in American flamingos.
The distribution of inter-scan intervals (ISIs) and associated skewness in American flamingos observed in three different classes of group sizes in the field.

needed in smaller species not exposed to stalking predators to complement the present findings.

Cognitive processes on timing may well explain why the distribution of ISIs is variable when prey species face non-stalking predators. However, such processes lead to rather sub-optimal behaviour. Short intervals between two successive scans are likely uninformative if the state of the environment changes slowly. Longer intervals are risky because a predator could approach closer before detection. Long intervals, however, are more likely to occur when animals are in larger, more protected groups, which should reduce the impact of very long ISIs. The costs of deviation from scans of fixed duration require more attention. Costs associated with errors in timing have also been discussed for other foraging tasks (Brunner et al., 1992).

The results suggest that scalar timing imposes boundaries on the timing of ISIs, explaining why ISIs are so variable even when they are predicted to be of fixed duration. Adaptive models of vigilance typically specify how much time should be allocated to vigilance in response to changes in predation risk (McNamara and Houston, 1992), but fail to specify how vigilance is achieved from one foraging bout to another. If scalar timing influences the timing of vigilance bouts in several species, future vigilance models should incorporate such processes.

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