Vertical migration timing illuminates the importance of visual and nonvisual predation pressure in the mesopelagic zone

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Abstract

Each day, motile pelagic organisms of all sizes undergo vertical movements tied to sunset and sunrise. Diel migration of animals is thought to result from the competing need to feed in energy rich surface waters while avoiding visual predators. Previous study using a newly adapted autonomous vehicle to measure individual characteristics in scattering layers provided the first measures of the internal layer structure, demonstrating that deep scattering layers can be made up of many topologically scaled, mono-species aggregations, or “schools.” Follow-up measurements presented here show these schools of mesopelagic animals remain coherent during upward migration at dusk. We found that groups of smaller animals began migrating sooner each night than larger individuals, consistent with their relatively lower detectability by visual predators. We also found a correlation with taxonomic differences in swimming capabilities, suggesting that the ability to avoid predators if they are encountered also plays a role in the patterns of migration observed. The presence of acoustic predators, Risso’s dolphins (Grampus griseus), however, altered this pattern for their primary prey, causing squid to remain at depth for approximately 40 min longer than others. The risk of predation by this air-breathing predator decreases with depth, making delaying migration an appropriate response to this largely nonvisual predation risk. Understanding the timing of individual migration patterns provides insights into the bioenergetic and predator–prey processes in the mesopelagic zone that are critical for understanding the ecological and biogeochemical impacts of these high biomass layers in the ocean.

One of the most ubiquitous processes of life in the pelagic realm is diel vertical migration. First described at a global scale through the advent of sonar (Moore 1950; Hersey and Backus 1954), large numbers of motile organisms of all sizes undergo vertical movements tied to sunset and sunrise throughout the world’s oceans and freshwaters (Roe 1974; Kamykowski and Zentara 1977; Dawidowicz and Pijanowska 2018). Thought to be the largest net animal movement on the planet (Longhurst 1976; Hays 2003), vertical migration has profound impacts on ocean ecosystems from the surface to the seafloor, shaping the spatial and temporal structure of pelagic food webs (Brierley 2014), providing a vector for energy that supports pelagic life far below the euphotic zone (Sutton 2013), and accounting for 15%–40% of carbon flux by the biological pump (Steinberg et al. 2000; Archibald et al. 2019), promoting carbon sequestration in the deep sea (Bollens et al. 2011).

The coupling of the vertical movement of pelagic animals to sunset and sunrise indicates that light plays an important role in diel migration (see reviews in Blaxter 1974; Cohen and Forward Jr 2016). Modifications to this behavior resulting from anomalies in the light field caused by solar eclipses (Bright et al. 1972), smoke plumes (Urmy et al. 2016), moonlight (Alldredge and King 1980; Last et al. 2016), and turbidity (Frank and Widder 1997) support the role of light as an important cue for migration. The exponential attenuation of light in water also results in steep vertical gradients of temperature, primary production, and oxygen (Tett 1990). As a result, vertical movements of tens to hundreds of meters in the ocean dramatically alter the habitat animals experience throughout a day, inducing rapidly changing physiological demands along with the energetic costs of movement (Lampert 1989; Dawidowicz and Loose 1992; Loose and Dawidowicz 1994). At the same time, animals are forgoing access to food-rich surface waters approximately half of each day. The widespread occurrence of diel vertical movements (Bianchi and Mislan 2016) and the repeated evolution of this strategy across diverse taxonomic groups suggests that the advantages of migration outweigh the costs. Most typically, diel vertical migration involves the movement of pelagic animals away from food-
rich surface waters during the day (Longhurst 1976). This daytime movement into deeper, darker waters also reduces the acuity of predators that rely on vision (Aksnes and Utne 1997), leading to the hypothesis that diel vertical migration is a predator avoidance strategy where animals only feed at the surface under the cover of darkness (Zaret and Suffern 1976).

Reducing visual predation risk is the most widely accepted but not the only hypothesis for the adaptive significance of diel vertical migration. For example, some animals may benefit from lower metabolic rate at the lower temperatures found at depth when not feeding (McLaren 1974; Cowles 2001; Sims et al. 2006), use the oxygen minimum zone at depth as a refuge from active predators (Vanderploeg et al. 2009), or rely on higher foraging gains from daytime accumulation of resources at the surface (Enright 1977). In typical diel migration, the visual predator avoidance hypothesis may not be mutually exclusive to these alternate hypotheses. However, upward movement at dusk and downward at dawn is also not the only diel migration pattern observed in pelagic systems with some organisms migrating in reverse patterns (Ohman et al. 1983) while others show movement up and down during each crepuscular period, resulting in two migrations each day (Herman 1963). Some species show a mix of migration patterns at a single time or a transition from one pattern to another through time and multiple species in an ecosystem often show multiple patterns. The timing and magnitude of migrations can be affected not only by changes in celestial light levels (Clarke 1970; Last et al. 2016) but also bioluminescence (Clarke and Backus 1964), moon phase (Benoit-Bird et al. 2009a), chemical byproducts of predators (Van Gool and Ringelberg 1998), predator densities (Dawidowicz et al. 1990), food resource levels (George 1983), temperature, and other environmental factors (Enright 1977).

Examining variation in diel vertical migration within a species, in an ecosystem through time, across locations, or across taxa has proven a powerful tool for testing the hypotheses around vertical migration. Most studies have focused on comparing the magnitude of migration and its presence or absence (Lampert 1993). Examining differences in the timing of migration has proven more challenging (Enright and Honegger 1977), largely because of the short time window over which the movement occurs, typically an hour or less surrounding dusk and dawn (Ringelberg 1995). Our understanding is further obscured by the difficulties of identifying the behavior of individuals in samples which generally integrate the patterns of the population or even entire communities (Pearse Jr 2003; but see, for example: Mehrer 2006; Kaartvedt et al. 2007). Using new sampling tools to examine the relationship between the size of individual krill and differences in the timing of their vertical movement, de Robertis (2002) was able to support quantitative predictions of the prevailing hypothesis that individuals migrate to maximize the tradeoff between energy gain and mortality risk from visual predators. Understanding when individuals migrate can allow us to test hypotheses about the adaptive significance, the why of up and down (Enright 1979). Our goal was to examine the tradeoffs affecting upward migration by exploring variation in the timing of ascent in a mixed species midwater assemblage of micronektonic animals. As we continue to expand insights into the adaptive significance of this widespread behavior, we can better examine the effects of vertical migrations on the environment and on the migrators themselves.

Methods

We utilized a novel, autonomous echosounder system (calibrated split-beam Simrad EK60s at 38 and 120 kHz; 512 μs long pulses; 1 Hz pulse rate; source level < 180 dB re 1 μPa [rms]) integrated into an advanced autonomous underwater vehicle (AUV: REMUS 600) capable of sampling at depths up to 600 m to examine the patterns of upward migration in a midwater scattering layer (for a detailed description of the sensors and platform, see Moline et al. 2015). Sampling was conducted in the Catalina Basin, off the eastern coast of Catalina Island, California in September of 2013 during the last quarter of the moon. During this time period, Benoit-Bird et al. (2017), identified three coherent scattering layers in the basin using a combination of acoustics and net tows: a shallow layer centered at 50 m that was dominated by larval fishes and a diverse array of small crustaceans, a midwater layer centered around 300 m during the day but at less than 100 m at night that was numerically dominated by myctophids and krill but also contained various species of squid, and a deep, nonmigratory layer at 450 m made up primarily of dragonfishes, larger squid, shrimp, and large krill. These layers were comprised of discrete, monospecific aggregations approximately 100 individuals across. These monospecific aggregations were adjacent to aggregations of different taxa and individual size, forming horizontally extensive features, “layers” (Benoit-Bird et al. 2017).

In the present study, we conducted surveys at a speed of 2.6 m/s using echosounders mounted on the R/V New Horizon (calibrated Simrad EK60s at 38, 70, 120, and 200 kHz; 512 μs long pulses; 1 Hz pulse rate; source level < 180 dB re 1 μPa [rms]) to define the upper boundary of the midwater layer. These depths allowed targeted deployments of the echosounder-equipped AUV 20–30 m above the daytime depth of the layer. From approximately 90 min before sunset to 90 min after sunset during each of 6 days, the AUV surveyed above the layer at a speed of 1.5 m/s for a total survey distance of 97 km. Proximity provided the resolution necessary to make acoustic measurements of the individual animals that make up layers as they began their upward migration, approximately 10 cm in the vertical and 15 cm horizontally).

Analysis of acoustic data

Acoustic scattering data from both platforms was processed using Echoview software. First, the seafloor and any noise
artifacts were removed. Ship-based data were used here only to provide context for other measurements and were not analyzed further. Acoustic data from 3 to 28 m beneath the AUV, the region with the horizontal resolution necessary to separate individual echoes across the typical range of target densities observed in the measured scattering layers, were first analyzed for single targets, e.g., only one target per acoustic reverberation volume for each pulse (Sawada et al. 1993). Single targets were extracted from both the 38 and 120 kHz data. Echoes consistent with marine mammals were identified based on their frequency response, intensity, and morphology (Benoit-Bird et al. 2009b), their positions noted, and their echoes removed from the dataset for further analyses of the scattering layer. For other targets identified at both frequencies (>90% of all single targets detected), the intensity of the echo at 120 kHz was subtracted from the 38 kHz intensity to provide a measure of frequency response which is related to target identity.

To examine the spatial patterns in echo characteristics, a 100-point horizontal running standard deviation of target strength at each frequency and frequency response was calculated (See Fig. 1). This horizontal scale was chosen as it matches the typical topological scale of individual aggregations (Benoit-Bird et al. 2017). To balance the vertical and horizontal resolution while maintaining the sample size, this calculation was conducted on 5-m vertical windows from 3 m up to 28 m from the AUV. A Kruskal–Wallace test was used to test the effect of range from the transducer on each distribution of standard deviation.

For additional analyses, interpretations were aided by classification of acoustic targets. Targets measured from the AUV were identified as consistent with squid if their target strength at 38 kHz was 3.1 to 10 dB higher than their 120 kHz target strength (Benoit-Bird et al. 2008), as fishes if target strength values between the two frequencies were no more than 3 dB different, and as crustaceans if the differences was –3 to –20 dB. Target strength can be interpreted as a proxy of length (McClatchie et al. 2003) within each taxonomic class (“squid”, “fishes”, and “crustacean”). Conversions to estimated metric length of each class were made using relationships from Benoit-Bird and Au (2001), assuming that the distribution of animals was generally orthogonal to the acoustic beam.

Spatially contiguous groups of targets with low standard deviation values in all three echo metrics were defined as an aggregation. For additional analyses, each aggregation was treated as a sampling unit rather than the individual target to reduce error in classification and length assessment and avoiding pseudoreplication. Averaging the individual characteristics measured in each group reduces the variability in these estimates, increasing our statistical power. The timing of migration for coherent aggregations was referenced to the time of sunset at the study site recorded by the US Naval observatory. A value of zero represents the time of sunset, negative values are minutes before sunset, and positive values are minutes after sunset. The mean length of individuals was estimated for each aggregation using the mean target strength for each aggregation based on the target strength-length relationship appropriate for the taxonomic classification determined from the frequency response for the group. Linear regression analysis was used to examine the relationship between the mean individual length and the timing of vertical movement. Partial regression analysis was used to test for differences in the slope and intercept between taxonomic groups.

To compare the migration timing among taxonomic classes, the effect of length on timing first had to be removed. This was accomplished by examining the migration timing residual for each aggregation, that is the difference from the timing of each group relative to the time predicted by the length-time regression. Additionally, each aggregation leaving the midwater layer was classified for the presence/absence of Risso’s dolphins based on detections within 500 m horizontally and 50 m vertically. This equates to an average of five aggregations of mesopelagic animals in each dimension. The horizontal distance would be covered by the underwater vehicle, and the dolphins which swim at similar speeds, in about 3 min. This timescale is similar to the duration of aggregation of squid in response to Risso’s dolphins (Benoit-Bird et al. 2017). ANOVA was used to assess the effects of taxonomic class and the presence of Risso’s dolphins on the residual of migration timing. Because of large differences in sample sizes, Tukey’s Honestly Significant Difference test for Homogeneous Subsets was used to examine the differences in migration time among treatments.

Results

Surveying above the midwater scattering layer in the period just before and after sunset, we were able to observe tens of thousands of single targets rising from the layer. These targets occurred in spatially connected groups often separated from each other by empty regions as shown in Fig. 1. Using a sliding 100-point window to measure the standard deviation of target characteristics along the track of the AUV, we observed that like the layer they were leaving, vertically migrating animals were found in distinct aggregations with coherent scattering characteristics including a narrow range of both target strength values and frequency response. As shown in Fig. 2, the standard deviation of target characteristics had a bimodal distribution with high values when the sliding window incorporated multiple groups of targets and low values when the window was within a single, coherent aggregation.

Using the echosounder-equipped AUV, we identified a total of 659 aggregations with low standard deviations in target strengths and frequency response categorized as in the process of migration based on their position above the daytime depth of the layer. There was no significant effect of range from the
transducer on the distribution of standard deviations ($H < 0.3$; $p > 0.45$ for all comparisons). Target strength at 120 kHz had more variability within each aggregation than 38 kHz target strength. The frequency difference in target strength had the lowest variability within aggregations, likely because frequency response is less affected by orientation than absolute measures of target strength (Jech 2011). All additional analyses were carried out at the level of the aggregation.

The initiation of upward vertical movement of individual midwater animals was found to occur over a 2-h period. More than three quarters of our observations occurred within the 1-h interval beginning 15 min before sunset and ending 45 min after sunset. The mean length of individuals within each aggregation was estimated using the mean target strength and frequency response for each aggregation. Figure 3 shows the relationship between the length of individuals and the timing of their vertical movement, revealing that larger animals migrated upwards later than smaller animals from this midwater layer. A partial regression analysis showed that there was no significant effect of taxonomic classification on the slope of the regression ($T = 0.91; p = 0.36$) but there was a significant effect on the $y$-intercept ($T = 4.03; p < 0.01$).

The raw migration timing for each aggregation was normalized to remove the effects of mean animal length on the timing of migration of each aggregation. This timing residual value permitted the examination of the effects of acoustic classification, a proxy for taxa, on the timing of migration (Fig. 4). An ANOVA revealed effects of taxonomic group ($F = 1491.09; df = 2, 658; p \leq 0.001$) and the presence of Risso’s dolphins ($F = 2099.86; df = 1658; p < 0.001$) on the migration timing residual and a significant interaction term ($F = 1932.90; df = 2658, p < 0.001$). The homogenous groups analysis (Table 1) showed that there were significant differences in residual migration timing between all pairs of taxa. There was no difference in migration timing between dolphin-present or -absent for aggregations of fishes or crustaceans but squid aggregations in proximity to dolphins migrated significantly later.

**Discussion**

In the Catalina Basin, Benoit-Bird et al. (2017) documented three scattering layers. Here, we focus on the midwater layer, centered at 300 m that underwent diel vertical migration during the study. Using an echosounder-equipped Autonomous Underwater Vehicle (AUV) that can sample in and near the scattering layer provides the resolution necessary to separate individual organisms. This approach revealed that this mixed species assemblage is organized into aggregations of one size and taxonomic group of animals about 100 individuals across (Benoit-Bird et al. 2017). These aggregations abut monospecific aggregations of different animals to form what we
observe from surface sampling as an extensive, continuous layer. By sampling from above the layer near the time of the dusk vertical ascent, here we were able to observe individual animals leaving the layer. Animals within a contiguous, monospecific group with a narrow range of target strength and frequency response values were observed leaving the layer together (Fig. 1). Examining this quantitatively using a sliding measure of variability, we saw a bimodal distribution with low variability when the sliding window was aligned with a coherent aggregation and high variability when multiple aggregations were included.

![Fig 2. Histograms of running measurements of the standard deviation of target strength of individuals leaving the midwater scattering layer around sunset. Standard deviation was measured using a horizontally sliding window of 100 targets in 5 m bins above the layer’s daytime depth. Each frequency and the difference between them showed a bimodal distribution with low variability when the sliding window was aligned with a coherent aggregation and high variability when multiple aggregations were included.](image)

![Fig 3. The estimated mean length of individuals in coherent aggregations measured in the ~ 20 m above the scattering layer’s daytime depth is shown as a function of time relative to sunset rounded to the nearest 5-min interval. Gray dots show the mean value within each time interval while error bars show the full range of values. A total spread of nearly 2 h was observed in the timing of upward vertical movement of midwater animals, similar to observations of the spread of squid migration elsewhere (Kaartvedt et al. 2020). However, more than three quarters of our observations occurred within the 1-h interval beginning 15 min before sunset and ending 45 min after sunset. A linear regression showed a significant positive trend ($p < 0.001$; $R^2 = 0.79$) between time and mean animal size; larger animals tended to migrate later than smaller animals.](image)

Length = 0.11(time) + 5.4
$R^2 = 0.79$
high values when the sliding window incorporated multiple groups of targets and low values when the window was within a single coherent aggregation (Fig. 2).

Coherent small-scale aggregations were observed previously in the midwater scattering layer in the Catalina Basin during the day and at night. That individuals in a group also migrate together suggest that groups may maintain coherence over the entire diel cycle and perhaps even stay together over longer time scales. Both aggregation and vertical migration are thought to be tactics for reducing predation risk. That aggregation behavior persists throughout the day and night suggests the following: that predation pressure persists even in the refuge of the mesopelagic environment during the daytime and in the shallows at night, that the benefits of remaining with the same group over time are substantial, the costs of forming a group are higher than maintaining it, or some combination of these.

The prevailing hypothesis for the adaptive significance of vertical migration is that it serves to balance the tradeoffs of feeding in surface waters while reducing exposure to visual predators. A prediction resulting from this hypothesis is that when predation risk is high, animals that are more conspicuous due to their size or coloration should migrate more extensively to access darker waters during the daytime and the following: that predation pressure persists even in the refuge of the mesopelagic environment during the daytime and in the shallows at night, that the benefits of remaining with the same group over time are substantial, the costs of forming a group are higher than maintaining it, or some combination of these.

The pattern may also be masked by differences in swimming capability that could allow larger animals to ascend more quickly than smaller individuals even as they begin their migration later, more dynamically trading off feeding opportunities with predation risk.

After removing the effects of size, residual differences were observed among taxonomic classes in ascent timing, indicating that visual conspicuousness is not the only factor driving migration timing. In the absence of Risso’s dolphins, squids migrated earliest, fishes next, and crustaceans last. There was a total separation in median values of ascent time across taxa of about 20 min (Fig. 4). These taxonomic groups also have substantial differences in their swimming capabilities. In similarly sized individuals, crustaceans have the lowest sustained and burst swimming speeds, fishes achieve sustained and burst speeds an order of magnitude higher than crustaceans, while squids achieve the highest speeds, ~10% higher sustained speeds and three-fold higher burst velocities than fishes (Benoit-Bird 2004). We hypothesize that the ability to evade predators when they are encountered plays an important role in an individual’s ability to minimize their mortality risk, allowing faster, more maneuverable animals to ascend when light levels are higher. In addition to differences among taxa, swimming speed within a species generally increases with individual size, an effect that could dampen the delay larger animals experience due to their visibility. Earlier ascent could increase individual energy gain by allowing for more time in food-rich surface waters each night and providing access to these food resources before similarly sized competitors.

Table 1. Mean migration time residuals for each condition are shown as homogenous subsets. Within a subset, there is no significant difference in the values as shown by the subset significance values in the table, while between subsets, there is a significant difference at \( p < 0.05 \). Comparisons were made with Tukey’s honestly significant difference test using the harmonic mean sample size.

| Taxon       | Dolphins | N   | 1  | 2  | 3  | 4  | Subset |
|-------------|----------|-----|----|----|----|----|--------|
| Squids      | –        | 102 | −8.0|    |    |    |        |
| Fishes      | +        | 71  | −3.1|    |    |    |        |
| Fishes      | −        | 256 | −3.0|    |    |    |        |
| Crustaceans | +        | 32  | 9.4 |    |    |    |        |
| Crustaceans | −        | 162 | 9.9 |    |    |    |        |
| Squids      | +        | 39  | 25.1| 1.00| 0.93| 0.84| 1.00   |
| Sig.        |          |     |     |    |    |    |        |

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The presence of Risso’s dolphins had no significant effect on the ascent timing of fishes or crustaceans but did delay squid ascent. Risso’s dolphins were present throughout the Catalina Basin during our study, feeding at depths up to ~ 500 m on squid and, to a lesser extent, fishes (Benoit-Bird et al. 2019). That crustaceans do not respond to dolphins is not surprising given that they are not regularly targeted by them. Fishes, however, account for about one quarter of the prey targeted by Risso’s dolphins in the midwater layer but show no response, suggesting they are not able to detect the presence of the predator or that the risk is not sufficient to elicit a targeted response. Aggregations of squids showed a substantial delay in their vertical movement in the presence of Risso’s dolphins, leaving the layer a median of ~ 40 min later. The delay in migration observed reduced the time squid spent at the surface by up to 10%, reducing their potential foraging gains. All of the squid did eventually ascend as no targets were detected from ship-based sampling at the daytime depth of the midwater scattering layer during the night (Benoit-Bird et al. 2019). While dolphins generally remained present in the area, the pressures for squid to eat eventually overcame the pressures to remain deep. The balance of the pressure of avoiding predation while accessing food likely varies seasonally as the length of the night changes. During our study, darkness persisted for approximately 8.5 h but at this site, darkness can be as short as 6.25 or as long as 11 h each night.

Previous analysis has shown that squids also responded to the presence of Risso’s dolphins by tightening their spacing and forming more organized groups or schools both during the day and at night while fishes and crustaceans did not (Benoit-Bird et al. 2017). Squid are apparently able to detect the presence of dolphins and respond using multiple tactics. Dolphins primarily use sound through echolocation rather than vision to hunt (Arranz et al. 2018). It is possible that squids are unable to discriminate the type of predator, erring on the side of caution with a strategy intended to mitigate the risk of visual predation even in the presence of an acoustic predator. However, an analysis of individual tracks of squid showed no strong avoidance of or attraction to the vehicle (Benoit-Bird et al. 2017), indicating some degree of discrimination. Delaying vertical migration could confer advantages other than reducing visibility by staying at lower light levels. Air-breathing aquatic predators, including dolphins, must balance foraging with access to oxygen. Risso’s dolphins have limited time to forage at depth and decide before even leaving the surface which layers they will target (Arranz et al. 2018; Arranz et al. 2019). Remaining at depth when dolphins are present could increase the predator’s access costs and reduce immediate predation risk for the squid. This may be particularly true if dolphins have already been diving to the midwater layer and deeper, as they must have been to be detected by our AUV-based sampling, because dolphins are less likely to make a deep dive after a prior one (Arranz et al. 2019). Staying at depth could also provide squid a better opportunity to escape from dolphins that are physiologically strained; this kind of evasion strategy is common for prey in the absence of refuges (Wirsing et al. 2020).

While it remains unclear how squid detected Risso’s dolphins, the response of squid to the presence of dolphins emphasizes the flexibility of vertical migration. Rather than a fixed pattern cued only by light, migration can be affected by the absence of predators (Gliwicz 1986), chemical byproducts of predators (Van Gool and Ringelberg 1998), food resource levels (George 1983), temperature, and other environmental factors (Enright 1977). To this list, we add the presence of acoustic predators. Non-consumptive effects on prey like the changes in behavior observed in squid are now increasingly recognized for their capacity to shape ecosystem structure and function (Lima 1998). Changes in prey due to fear and vigilance may have impacts on prey populations and ecosystems that rival or even exceed direct predation (Wirsing et al. 2020). Vertical migration is a process fundamentally

![Fig 4](image-url)
driven by fear, highlighting the importance of understanding these nonconsumptive effects in quantifying the role of vertical migration in ecosystem processes including the biological carbon pump.

Conclusion

Understanding the timing of individual migration patterns provides insights into the bioenergetic and predator-prey processes in the mesopelagic zone that are critical for understanding the ecological and biogeochemical impacts of these high biomass layers in the ocean. We observed that aggregations of animals that make up the midwater layer in Catalina Basin remained coherent as they ascended at dusk. This increased our ability to detect differences in the timing of vertical ascent between groups. Smaller, less visually conspicuous animals began their vertical ascent earlier than larger animals with the smallest animals migrating even before sunset. Our observations are consistent with the prevailing hypothesis that the general timing of vertical migration is driven by visual predation risk. We also observed modifications to this timing, with animals capable of higher sustained and burst swimming speeds migrating earlier than less competent swimmers, indicating that the ability to evade predators that may be encountered can also be an important factor influencing migration timing. Finally, while our results are consistent with the overall migration pattern being driven by the risk of visual predators, squid responded to the local presence of an air-breathing, acoustic predator by delaying their vertical ascent, potentially reducing their risk while forgoing food for up to 10% of their nightly feeding time. Our results contribute to our understanding about how the risk of predation structures diel vertical migration. With this understanding, we are able to better understand the cause of vertical movement and potentially, the effects of these daily excursions on the environment and the migrants themselves. Using newly available tools to examine the behavior of individuals revealed much about the when and why of migration.

CONFLICT OF INTEREST

None declared.

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