To hide or not to hide? Refuge use in a fluctuating environment

Many prey spend much of their lives in or near refuges from predation (e.g. holes, crevices, thick vegetation, shells or tubes). Dozens of theoretical and empirical studies have examined how patterns of prey refuge use might reflect a balance between the conflicting demands of feeding and avoiding predators[1,2]. Most of these studies have implicitly taken a static, equilibrium view of refuge use; that is, they have asked the following: given a particular, constant food and predation regime, what proportion of time should (and do) prey spend in refuge? Nature, however, is not static. Predators come and go, and food levels fluctuate. In response to these changing conditions, prey must decide when to move in and out of refuge. Until recently, relatively few studies have quantified the 'dynamics of prey refuge use', or the ability of prey to modulate their hiding behavior in response to fluctuating conditions.

The decision to leave refuge can be particularly important and interesting. From an ecological view, prey emergence rates from refuge can have major effects on predation rates[3]. For example, if an investigator observes that most prey are found in refuge, this could either be because prey go into refuge and rarely come out, or because prey emerge frequently, but are immediately chased back into refuge (or killed) by predators. The latter scenario clearly results in much higher predation rates than the former scenario.

From a behavioral view, the decision to emerge from refuge is fascinating because it requires prey to estimate food availability and predation risk outside of shelter, estimations that are often based on incomplete information about the fluctuating local environment[4]. Poor information can pose a serious constraint on the ability of prey to respond adaptively to local conditions. In theory, for example, uncertainty about the presence versus absence of a dangerous predator can force prey to stay permanently in refuge, even when predators are only occasionally present[4]. Given uncertainty, one wonders whether real, non-omniscient prey are capable of responding accurately and promptly to temporal variations in food and predation regimes.

Fluctuating food levels and hiding behavior of a tubeworm

A recent study by Lawrence Dill and Alex Fraser[5] on hiding behavior of the tubeworm, *Serpula vermicularis*, yields new insight into these issues. Instead of quantifying the proportion of time spent in refuge, Dill and Fraser[5] focused on emergence behavior – the time taken to re-emerge from refuge after a simulated predator attack. And instead of assuming that food availability is constant, Dill and Fraser measured temporal variation in food levels in the field and examined effects of fluctuating food levels on prey emergence behavior in the laboratory. Their results showed that individual tubeworms experience rapid changes in food availability in nature, and that these worms are capable of altering their emergence behavior adaptively in response to short- and medium-term variations in food levels.

Serpula vermicularis is a filter-feeding worm that lives in a calcareous tube cemented to marine intertidal and subtidal rocks. When disturbed, this worm retreats rapidly into its tube. While in hiding, it is safe, but cannot feed. Thus, hiding has a lost feeding opportunity cost. In theory, worms should re-emerge from refuge (resume feeding) sooner if the lost opportunity cost is greater. The lost opportunity cost can be particularly large if food comes in pulses – that is, if food levels are usually low, but occasionally high.

Although behavioral ecologists recognize that temporal variations in food availability ought to be critical in determining behavior, relatively few studies have quantified these variations. Dill and Fraser measured natural fluctuations in food availability by collecting food particles in the worm's natural habitat using a simple, artificial worm (a tygon tube connected to a pump). On each of several days, they took 1 liter samples at 5–30 minute intervals through a tidal cycle. While they did not do quantitative analyses (e.g. time series analyses) on the time-scale of fluctuations in food levels, their data revealed up to 10-fold variations in food availability during a single tidal cycle with up to fourfold changes in adjacent 5–10 minute intervals. These data bolster our intuition that natural food levels vary considerably from day-to-day, from hour-to-hour and even from minute-to-minute.

To quantify effects of varying food levels on worm hiding behavior, Dill and Fraser manipulated food levels and quantified worm re-emergence times after a simulated attack (either a golf ball or a solenoid-generated 'attack' on the side of the worms' laboratory tank). Food was provided in one pulse per day. In one experiment, each tank was given either a high or a low food level for five consecutive days before being switched to the other food level. Simulated attacks were conducted each day, 4 hours after feeding. In almost all cases (95%), the simulated attacks caused worms to withdraw into their tubes. As predicted, the worms re-emerged from their tubes about 50% sooner if they were in the high (as opposed to low) food treatment; i.e. worms that stood to lose more (in terms of lost feeding opportunities) by hiding, hid for a shorter period following a disturbance.

To see if prey also respond appropriately to shorter-term fluctuations in food levels, Dill and Fraser gave their worms either 'high food' or 'water with no food' on alternate days and tested their hiding behavior only one hour after food/water addition. Again, as predicted, worms that were feeding at a high rate at the time of the simulated attack re-emerged from hiding more quickly than worms that were last fed 25 hours ago. This shows that even the 'lowly' tubeworm can evaluate and adjust its hiding behavior based on current feeding conditions, rather than on average, long-term conditions; i.e. that the tubeworm's hiding behavior tracks short-term fluctuations in food levels.

To emphasize, these results go against the usual expectation on how hunger should affect feeding motivation. We usually expect hungrier animals (i.e. those with larger energy deficits) to resume feeding more quickly than well fed ones. Here, worms that experienced the lower food level were presumably hungrier (than those in the high food tanks), and yet they stayed in hiding longer.

Other predictions and other prey

Do other animals exhibit changes in hiding behavior that track short-term variations in predation risk and food availability? This question can be addressed at two levels. First, do prey quickly go in and out of refuge as predators come and go? In particular, do prey typically have short re-emergence times after predators leave the prey's vicinity? Second, do prey alter their re-emergence times in response to short-term changes in food and predation regimes?

Although numerous observations show that prey typically move into refuge shortly after predation risk increases, relatively few studies have quantified re-emergence times after predators leave. In terms of experimental protocols, while many studies have watched prey responses to predator addition, few have followed prey behavior after predators are removed. Dill and Fraser's worms re-emerged from refuge within a few minutes after simulated attacks. Other prey have also been shown to resume activity within seconds or minutes

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after a brief exposure to predators (e.g. hermit crabs[6], caddisfly larvae[7], birds[8]). However, some other prey species take hours or even days to resume full activity after predators are removed (semi-aquatic bugs[4], fish[9], small mammals[10,11]). These prey essentially do not track short-term fluctuations in their predation regime. Instead, for these prey, even an occasional visit from predators can keep them in hiding most or even all of the time.

Even fewer studies have examined factors that alter prey re-emergence behaviors. A recent model generated predictions on optimal re-emergence times for prey with poor information about predation risk outside of refuge[4]. Dill and Fraser's observation that high food availability outside of refuge results in rapid re-emergence from refuge corroborates one of the major predictions of this model. Other major predictions are that prey should wait longer (after predators leave) before re-emerging if: (1) the previous predation regime outside of refuge was more dangerous (higher predator density, attack rates, or capture success); or (2) prey energy reserves are high (e.g. if prey are not hungry).

A few recent studies have corroborated the prediction that prey should take longer to re-emerge from refuge or resume full activity after being exposed to a more dangerous previous predation regime. Sih[4] found this pattern for juveniles of a semi-aquatic bug exposed briefly to cannibalistic adults. Higher predator density or larger predator:prey size ratios resulted in longer delays before juveniles resumed full activity. Johansson and Englund[7] showed that a more intense attack by predatory fish resulted in a longer delay before resumption of activity by tube-dwelling caddisfly larvae. Similar patterns were found for hermit crabs[6], juvenile salmon[12] and calling male frogs[13]. Other studies have shown that hungry prey tend to resume feeding activity sooner than well-fed prey[4,14,15]. As noted earlier, however, Dill and Fraser observed the opposite pattern in their tubeworms – hungrier prey waited longer than well-fed prey before resuming activity.

The bottom line is that we still have much to learn about prey emergence behaviors and prey responses to short-term variations in food and predation regimes. Given the important effects of refuge use on prey fitness, populations and communities, and the likely universal occurrence of temporal fluctuations in food availability and predation risk, more studies like Dill and Fraser's work should prove highly insightful.

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Selfish genetic elements: long-range dynamics predicted by non-equilibrium models

Selfish genetic elements are regions of DNA that can promote their own vertical transmission, usually at the expense of other regions of the genome, thus setting up the possibility of intragenomic conflicts[1-3]. In recent years, the perceived importance of these genomic parasites has dramatically increased: among other things, various authors have proposed roles for them in the origin of sex[3-5], population level sex-ratio deviations[5,6], and patterns of speciation[7,8]. Many selfish genetic elements are polymorphic in natural populations and appear to have relatively stable frequencies over time scales of a few dozen or hundred generations[3,6,9] but their long-range dynamics are not well understood.

Traditional models (for instance, Ref. 10) have generally focused on the frequencies of selfish genetic elements approaching stable equilibria or limit cycles[2]. While there are also many theoretical studies of the evolution of modifiers of meiotic drive systems (see Ref. 2 for a summary and references), comprehensive models of the long-range evolution of selfish genetic element systems have not been formulated. Two recent articles published in *The American Naturalist*[6,9], however, go a long way to establishing such a comprehensive model. In these models, selfish genetic element systems undergo transitions from one phase to the next (see Box 1).

Bs out of line?

For more than a decade, Camacho and his collaborators[9] have studied populational aspects of the supernumerary (B)

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