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Original Article

Hiding behavior in Christmas tree worms on different time scales

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Many animals escape predators by hiding. Hiding decisions are economic in that individuals trade off the physiological costs of hiding with the benefits of increased security. The number of conspecifics may increase competition, security, or attract predators, influencing predation risk. We studied hiding time in Christmas tree worms (*Spirobranchus giganteus*), sessile marine invertebrates, which lived with 0–17 other worms within 20 cm. Competition and predation risk reduction both predict a shorter latency to re-emerge given the necessity to feed and potential for safety in numbers, respectively. In contrast, if grouped worms attract more predators, individuals should hide longer. We experimentally induced hiding in 174 worms and found a significant, positive relationship between hiding time and number of conspecifics. We repeated the test 4 consecutive times in 1 day on a subset of 30 worms that were either solitary or lived with one other untested worm. We found that worms with longer hiding times habituated more quickly than worms with shorter hiding times, and that the individual worm explained 55.8% of the variation in hiding time. When we conducted the trials for 4 days, we found that the individual worm explained 41.75% of the variation, but no evidence of behavioral plasticity. Worm antipredator responses were consistently individualistic, but behavioral plasticity was only evident over short time scales. For sessile marine invertebrates, higher densities may attract predators, enhancing rather than diluting predation risk. Worms that cannot move away from their neighbors, thus seemingly modify antipredator behavior in consistent ways.

Key words: **density-dependent predation risk, hiding time, invertebrate, personality.**

INTRODUCTION

For many species of prey, the most effective method of predator avoidance is hiding in a refuge (Sih et al. 1988). As with other antipredator behaviors, the economic hypothesis proposed by Ydenberg and Dill (1986) can be applied to hiding (Cooper and Blumstein 2015; Martín and López 2015). Many species have the ability to retract or hide within a shell, which has certain costs and benefits with regards to when to initiate and terminate those behaviors (i.e., "the economics of hiding") (Lima and Dill 1990; Dill and Gillett 1991). For prey, decisions of when and how long to hide (or flee) depend on the costs and benefits of remaining out in the open versus retreating (Ydenberg and Dill 1986; Martín and López 1999; Cooper 2015). The efficient use of this strategy is particularly important for sessile organisms, because this may be their only form of antipredator behavior (Dill and Gillett 1991; Dill and Fraser 1997). As most sessile marine species are filter feeders, the main cost of retreating is lost feeding opportunity. If competition for food is high, the cost of delaying retreating may be balanced by the increased calorie intake provided by additional feeding (Ydenberg and Dill 1986). For species that hide rather than flee, emerging sooner to resume feeding could similarly offset the cost of retreating (Hugie 2003).

An important factor that can influence the economics of hiding or fleeing is the presence of conspecifics (Cooper and Peréz-Mellado 2004; Beauchamp 2015). In many prey species, conspecifics actively form groups to reduce their rate of predation and increase their time spent foraging. According to the dilution hypothesis, prey decrease individual risk of predation by forming groups (Hamilton 1971; Bertram 1978). Moreover, prey species in groups can increase their ability to detect predators, as suggested by the detection hypothesis (Pulliam 1973). However, for sessile marine invertebrates, living near conspecifics can impose a greater cost due to increased competition for food. Northern rock barnacles (*Semibalanus balanoides*), for example, show preferential recruitment patterns that lead them to settle in groups (Tourneux and Bourget 1988). Yet, barnacles in groups have significantly shorter hiding times than solitary individuals due to a combination of enhanced foraging competition pressure and risk dilution (Mauck and Harkless 2001). Similarly, Christmas tree worms (*Spirobranchus giganteus*), another sessile marine invertebrate, tend to form groups due to limited coral substrate availability and preferential recruitment patterns (Marsden 1987; Hunte et al. 1990; Marsden and Meeuwig 1990). Christmas tree worms are an ideal system for

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studying antipredator behavior because they have many predators, including wrasses (F. Labridae); butterflyfish (F. Chaetodontidae); surgeonfish, tang, and unicorn fish (F. Acanthuridae); and triggerfish (F. Balistidae) (Vine and Bailey-Brock 1984). Moreover, their sessile nature restricts them to only one escape strategy: hiding. When the area over an individual suddenly darkens or the water pressure changes, Christmas tree worms use their operculum to rapidly retract their spiral crowns into their tube and hide until danger has passed, interrupting feeding activities and respiration (Dill and Fraser 1997; Vinn and ten Hove 2011). Due to the dilution effect, the influence of competition, or perhaps a combination of both, we expect hiding times to decrease in these polychaetes when residing around more conspecifics.

Alternatively, living in large groups of conspecifics may actually increase predation risk. Optimal foraging theory predicts that a predator will spend more time in patches with more prey (Charnov 1976). Previous studies show that larger groups of prey attract more predators (Stamp 1981; Shima 2001; Lindstedt et al. 2006, 2010). For example, predators such as cichlid fish preferentially attack bigger shoals of guppies over smaller shoals (Krause and Godin 1995). However, optimal foraging theory also assumes that predators have perfect knowledge of prey group sizes, which is not always the case. Although other studies have shown that larger groups of prey are simply encountered more often due to random chance, these large groups are still attacked more frequently than smaller cohorts (Lindström 1989; Fordyce and Agrawal 2001; Hebblewhite and Pletscher 2002; Brunton and Booth 2003). Group living can also increase predation risk because larger groups are also more conspicuous to predators (Beauchamp 2014). For sessile marine invertebrates, the inability to move once settlement and recruitment have taken place may heighten this density-dependent predation effect. Therefore, as a competing hypothesis, we would expect individuals living near more conspecifics to have longer hiding times than solitary individuals, to compensate for increased predation risk.

In order to systematically understand the hiding behavior of Christmas tree worms, we examined not only which factors affected hiding time, but also the consistency of the behavior over time. We approached the latter by asking whether differences in behavior between individual worms were consistent over time and context (Réale et al. 2007; Dingemanse et al. 2010). Personality, or “temperament” (Réale et al. 2007), has been observed in a variety of organisms, including invertebrates such as mussels (Wilson et al. 2012), squid (Sinn et al. 2006), crabs (Briffa et al. 2008), and worms (de Bono and Bargmann 1998). Indeed, many such studies focused on consistent differences in antipredator behavior (Reichert and Hedrick 1993; Briffa et al. 2008; Wilson et al. 2012). Whereas many studies of this nature have failed to correctly address time-related change (Biro and Stamps 2015), we aimed to sample worms over both short and long time scales in order to fully account for behavioral plasticity. Additionally, worms that pay the largest costs associated with hiding may be more likely to adjust their behavior with repeated stimulation. Thus, we wished to understand not only the degree to which Christmas tree worms differed in their hiding time response between individuals, but also over multiple time scales.

METHODS

What explains variation in hiding time?

Between 22 January and 7 February 2016, we sampled a total of 174 individual worms from 4 sites in Mo’orea, French Polynesia: UC Berkeley Gump Station reef in Cook’s Bay (−17.487658° S, −149.825322° W), the Hilton Resort reef (−17.484233° S, −149.842275° W), the Motu Fareone and Motu Tiahura reef (−17.488418° S, −149.914913° W), and Temae Beach reef (−17.499367° S, −149.759395° W). Sites were visited during daylight hours between 08:00–12:00 h and 14:00–18:00 h by a group of observers. When a Christmas tree worm was identified, observers stopped a distance of at least 1 m from the worm, to avoid initiating premature antipredator behavior. In order to induce hiding behavior, 1 observer probed each worm with a 2-m long rod until it receded into its tube. The same observer then recorded, with a stopwatch, the number of seconds until full re-emergence (defined as when the individual returned to its original, relaxed state before the disturbance).

After timing the latency to re-emerge, an observer photographed the fully emerged worm (to confirm whorl count) and counted the number of whorls. The number of whorls was used as a measure of both size and age, to account for any confounding factors in hiding time, as found in previous studies of invertebrates (Guerra-Bobo and Brough 2010). Larger animals may pay a disproportionately larger cost by hiding if hiding is not essential, due to the lost foraging opportunity (Guerra-Bobo and Brough 2010). Additionally, studies across taxa show that body size is one of the biggest predictors of how organisms will respond to experimental approaches (reviewed in Cooper and Blumstein 2015). To account for size, whorls were counted for each of the Christmas tree worm’s two stalks (not including the crown) and the larger number was recorded.

Another observer then measured the depth of the worm in the water column, the number of conspecifics within a 20-cm radius of the focal individual, and, if conspecifics were present within this radius, the distance to nearest conspecific. Given the small reach of Christmas tree worm stalks (on the order of a few centimeters), we felt that counting conspecifics within a radius of 20 cm would accurately capture any possible competition or group effect on behavior. We did not test multiple worms from the same group, in order to eliminate possible disturbances from approaching the initial focal worm. Observers also recorded water temperature and wind conditions, however neither varied much over the sampling dates (all values between 28-29.9 °C and 0-4 on the Beaufort Scale, respectively).

How consistent are worms’ hiding times?

We conducted repeated trials on a subset of 30 individually marked Christmas tree worms at the Gump Station reef to determine if worms varied consistently, and if they habituated or sensitized to repeated disturbance. Methods for approaching worms, initiating hiding behavior, and measuring covariates were the same as for the individual measurements. However, to eliminate any effect of the presence of conspecifics (which was found to be significant in the first experiment on individuals), we selected worms with only 0 or 1 conspecifics within 20 cm, because a preliminary analysis showed that there was no difference in hiding times between solitary individuals or those with one other conspecific present ($P = 0.574$ on the initial hiding time of 67 solitary worms and 30 worms with 1 conspecific within 20 cm). We measured the hiding time of each worm for 4 consecutive trials per day, every other day, for a total of 4 sampling dates (16 total trials per individual). After re-emergence, we waited 2 min before resampling the worm. All covariates (depth, conspecifics, temperature, whorls, etc.) were recorded after all four trials were completed each day.

Statistical analysis

Before analysis, we plotted the data and $\log_{10}$ transformed hiding time to normalize its distribution. For the single observation dataset, we fitted a general linear model (GLM) in R Version 3.2.3 (R Core Team 2015) packages Deducer (Fellows 2012) and Java GUI for R (Helbig et al. 2013) to determine if there were significant relationships between $\log_{10}$ hiding time and each of the following factors: number of conspecifics, number of whorls, and depth. Residuals from the model were normally distributed and there were no obvious outliers.

To assess the consistency in antipredator behavior within the 1-day dataset, we fitted linear mixed effect models in R using the packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016). Again, we $\log_{10}$ transformed hiding time to normalize the data. We removed temperature and depth as factors, given the limited range of values for each (28.5–30 °C and 45–85 cm, respectively). We first fitted a random intercept model in order to test if individual explained any of the variation in our dependent variable—$\log_{10}$ hiding time. We calculated the intraclass correlation coefficient for this model using the ratio of Random Intercept Variance/(Random Intercept Variance + Residual Variance). Next, we added the number of whorls as a fixed effect to our random intercept model to see if this explained any of the between-worm variance. We compared these models with a likelihood ratio test. We then fitted a random intercept and random slope model to see if hiding time changed over time. Again, we used a likelihood ratio test to determine whether this was a better model than a random intercept only model. Finally, we compared all of the random effects models to a general linear null model with no random effects using the package RLRsim (Scheipl et al. 2008). We followed the same algorithm for the repeated tests over 4 days, to check for consistency over days rather than just trial and plotted results using ggplot2 (Wickham 2009).

Literature survey

To place our GLM results in context, we reviewed studies on relationships between prey density and predation risk in invertebrates, dividing them into 2 categories: 1) whether prey have the ability to flee from predators or not and 2) if the dilution hypothesis was supported or if there was evidence of greater predation risk for individuals in groups. Our literature search began with studies presented in Seitz et al. (2001) and Beauchamp (2014), and was expanded to citations both within and of those reviews. We performed additional searches in Google Scholar and Web of Science and focused on the first 200 results, sorted by relevance. Search terms included: density-dependent predation, dilution hypothesis sessile, and group dilution predation. For all studies cited, we also examined each respective reference list. Studies on larvae were not included because the ability to flee may be dependent on developmental stage. Papers with parasitism as the method of predation were also excluded. Finally, for studies focusing on mortality due to predation, we only included studies in which proportional mortality for the individual was calculated. We then performed a chi-square test to determine if the ratio of support for the risk dilution hypothesis varied as a function of whether species have the ability to flee from predators or not.

RESULTS

What explains variation in hiding time?

After explaining nonsignificant variation in hiding time accounted for by depth (est = 0.001, P = 0.188) and number of whorls (est = 0.027, P = 0.141) in the full dataset, worms hid significantly longer when there were more conspecifics within 20 cm (est = 0.018, P = 0.004) (Figure 1). This model significantly (P = 0.006) explained 5.6% of variation in hiding time. This finding is consistent with increased predation risk in groups, and in contrast to the dilution and competition hypotheses. The number of conspecifics in a 20-cm radius ranged from 0 to 17, whorls ranged from 3 to 9, and depth ranged from 29 to 205 cm (Supplementary Table S1).

How consistent are worms' hiding times within 1 day?

For the 1-day data set (Supplementary Table S2), the random intercept and random slope model with the fixed effect of trial best

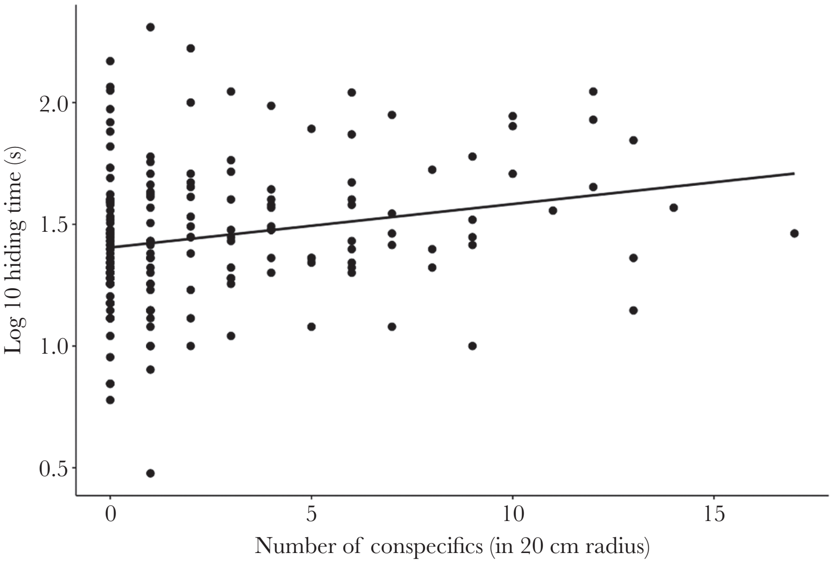

Figure 1
Log_{10}(hiding time) as a function of number of conspecifics within 20 cm radius.

explained variation in hiding time (Table 1a). Thus, individual Christmas tree worms not only had significantly different antipredator responses from each other, but also habituated or sensitized to the benign stimulus at different rates across trials (Figure 2a). We found that worm responses to the stimulus were phenotypically plastic, but not in consistent ways. There was a correlation of −0.75 between the random intercept and the random slope of trial, suggesting that worms with longer hiding times (larger intercepts) habituated more quickly to repeated stimulation than worms with shorter hiding times (Figure 2b). However, worms with low intercepts (shorter hiding time) have large slopes, indicating sensitization over the 4 trials (Figure 2b). Given that the best model had multiple random effects, we estimated from the next best and simplest model (the random intercept model) that 55.8% of variation was explained by individual.

How consistent are worms' hiding times on longer time scales?

In the 4-day data set (Supplementary Table S3), the random intercept model with no fixed effects best explained variation in hiding time (Table 1b). This model showed that 41.8% of the variation in hiding time was explained by individual worm. This contrast suggests that although worms show evidence of phenotypic plasticity over trials on the same day, plasticity was not detectable over multiple sampling days (Figures 3 and 4).

Results from literature survey

Our literature survey (Table 2) found that as the number of adjacent conspecifics increases, invertebrates that cannot flee from predators are more likely to either suffer higher predation risk or to behave in ways that are consistent with higher predation risk (e.g., hide longer; $X_p^2 < 0.001$). In contrast, we found that invertebrates that have the ability to flee are more likely to experience predation risk dilution when in a group.

DISCUSSION

The trade-off Christmas tree worms make between foraging and predation risk is modestly influenced by the number of nearby conspecifics. We evaluated 3 hypotheses that might explain this variation in hiding time: dilution (Hamilton 1971), competition (Rita and Ranta 1998; Grand and Dill 1999), and positive density-dependent predation (Charnov 1976; Stamp 1981), and found the strongest support for increased predation risk in larger aggregations. Worms residing in higher densities of conspecifics tended to hide longer when presented with a benign stimulus.

This finding is supported by our review of density-dependent predation risk in invertebrates. Thus, we may generally expect invertebrates that cannot flee from their predators to be more vulnerable in groups. For invertebrates who cannot flee, often their only antipredator behavior is to hide within a shell or refuge (Dill and Gillett 1991; Dill and Fraser 1997). In contrast, invertebrates who can flee may choose from a wide range of behaviors in response to the presence of a predator, such as fleeing, distracting, hiding, or group defense (Beauchamp 2014). Further, the dilution effect is most effective when the predator cannot successfully consume all the members of the group (Beauchamp 2014). Groups of relatively stationary invertebrate prey, once discovered by a predator, can be more easily attacked and consumed than groups of invertebrate prey who have the ability to flee.

Additionally, the direction of density-dependent predation may also be influenced by external environmental factors such as temperature (Eggleston 1990), substrate (Lipcius and Hines 1986; Eggleston et al. 1992), and dissolved oxygen concentrations (Taylor and Eggleston 1999), or physiological adaptations such as shell thickness (Seitz et al. 2001). The available literature on prey density and predation risk for invertebrates, and the current study, suggest that the dilution effect may be more effective for motile species, whereas increased predation risk in groups is more prevalent for species that are relatively immobile.

We may reasonably assume that Christmas tree worms are able to detect the presense of their neighbors, and therefore group size, based on previous studies focusing on chemical communication. Chemically mediated conspecific communication in tube-dwelling marine polychaetes is known from the settlement literature (Burke 1986; Hadfield and Paul 2001). Specifically, these cues come from the calcareous tubes of nearby conspecifics (Burke 1986; Hadfield and Paul 2001). Another study the marine polychaete *Nereis* (*Neanthes*) *virens* (Sars) found that individuals altered their feeding behavior in response to chemical alarm signals from conspecifics (Watson et al. 2005). However, this particular species has the ability to leave its burrow and swim in the water column, unlike Christmas tree worms. Although we did not observe this type of social communication between Christmas tree worms in the field, previous literature

Table 1

Linear mixed effects models for repeated measurements with random and fixed effects

Model	Variables	Akaike information criterion
(a) 1 day		
Random intercept	log10(HT) ~ (1 | Worm)	−0.2
Random intercept with fixed effects	log10(HT) ~ Whorls + (1 | Worm)	−0.9
Random intercept with fixed effect of trial	log10(HT) ~ Trial + (1 | Worm)	0.6
Random intercept and random slope	log10(HT) ~ Trial + (1 + Trial | Worm)	−3.0[a,b]
Linear null	log10(HT) ~ Trial	41.644
(b) 4 day		
Random intercept	log10(HT) ~ (1 | Worm)	113.3[c]
Random intercept with fixed effects	log10(HT) ~ Whorls + (1 | Worm)	115.2
Random intercept with fixed effects of day and trial	log10(HT) ~ Day + Trial + (1 | Worm)	113.7
Random intercept and random slope	log10(HT) ~ Day + Trial + (1 + Trial | Worm)	114.9
Linear null	log10(HT) ~ 1	292.7

[a] Likelihood ratio test (LRT) compared with random intercept only model ($P = 0.032$).

[b] LRT compared with linear null model ($P = 5.837\mathrm{e}{-11}$).

[c] LRT compared with linear null model ($P < 2.2\mathrm{e}{-16}$).

demonstrates that in at least 2 contexts, marine polychaetes may use chemical signals or cues from conspecifics. Thus, we suspect that they are, to some degree, able to sense conspecific density.

Unlike other species where size had a significant influence on hiding time (Krause et al. 1998; Martín and López 2003; Guerra-Bobo and Brough 2010), this effect was not observed with Christmas tree worms. We believed that measuring the part of the worm visible to predators, quantified by the number of whorls, would best measure size and predict hiding time. However, the number of whorls did not significantly explain differences in hiding time between worms. This may be because size has no effect on worm hiding time, meaning that the economic decision of whether to hide is not dependent on this factor. Alternatively, measuring the diameter of the burrow entrance may have been a better indicator of size (Nishi and Nishihara 1996).

On both short and long time scales, we found that individual worms differed significantly in their average hiding time, a difference that reflects individual variation in personality. However, we also found evidence of phenotypic plasticity in this behavior; Christmas tree worms habituated or sensitized over short time scales (a matter of minutes), but not longer time scales (on the order of days). When this was evident, shyer worms (those who hid for longer) habituated to the presentation of a repeated benign stimulus more quickly than bolder worms (those who re-emerged sooner), and those who were initially bolder sensitized over the 4 trials.

It is not immediately evident as to whether the lack of phenotypic plasticity over longer time scales reflects a biological effect or statistical artifact. Biro and Stamps (2015) argue that the data analyzed to study personality and phenotypic plasticity are often under-replicated and fail to encompass repeated sampling over time. However, these issues can be remedied by accounting for temporal changes in behavior and external confounding factors, in addition to having a large sample size with a sufficient amount of repeated measurements (Biro and Stamps 2015), as was done in this study. When additional repeated measures were added (to include change over 4 days), we found that the random slope and random intercept model, which reflects the degree to which individuals habituated, was no longer the best model to explain variation in worm hiding time. Thus, from one perspective, we may conclude that worms do not exhibit phenotypic plasticity.

However, if we consider the possible influence of confounding biological factors, or more specifically, changes in state over

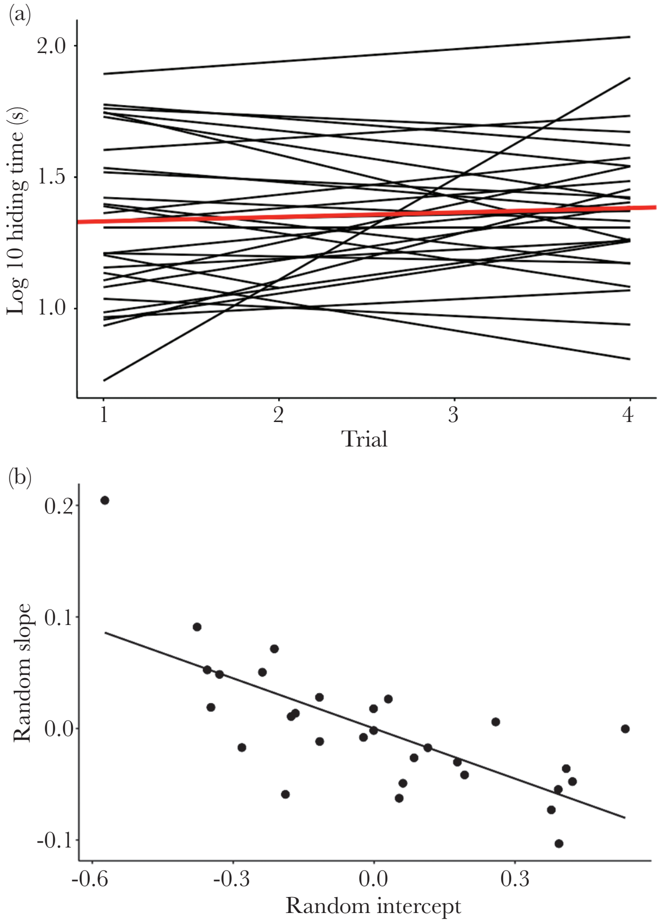

Figure 2
(a) Log_{10} (hiding time) of repeated individuals (n = 30) by trial for 1 day (the first day of sampling); thick red line plots the mean intercept and mean slope across all samples. (b) the correlation between the value of the random intercept and the random slope on the first day.

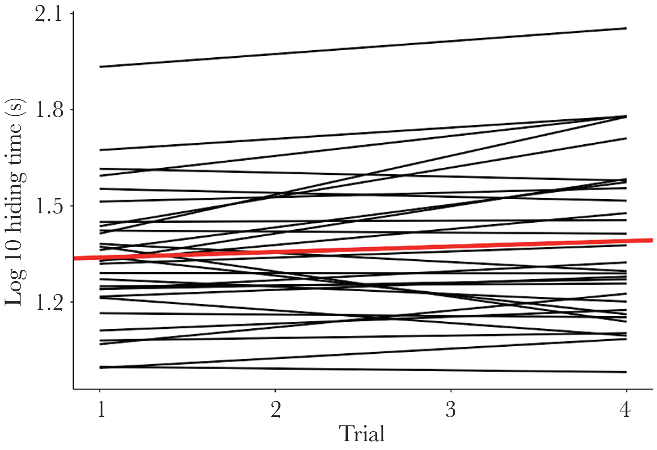

Figure 3
Log_{10} (hiding time) of repeated individuals (n = 30) by trial over 4 days (responses were averaged by trial over all 4 days: e.g., values for Trial 1 are the averages of the response for the first trial only over all 4 days, etc.); thick red line plots the mean intercept and mean slope across all samples.

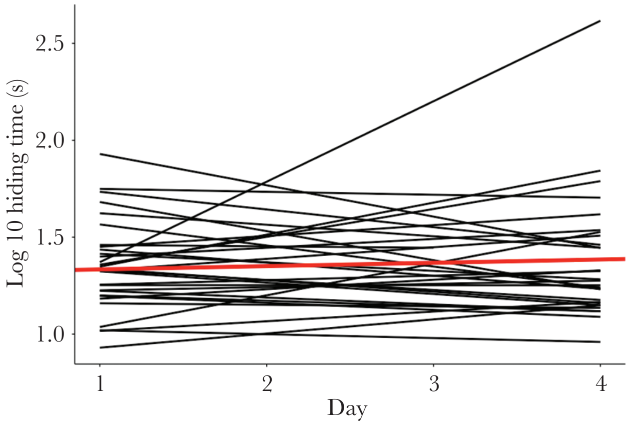

Figure 4
Log_{10} (hiding time) of repeated individuals (n = 30) by day over 4 days (responses averaged for Trials 1–4 on each day: e.g., values for Day 1 are the averages of the responses from Trials 1 to 4 on Day 1 only, etc.); thick red line plots the mean intercept and mean slope across all samples.

Table 2

Results of literature survey of prey density and predation risk for invertebrates

Ability to flee from predator?	Dilution of risk in groups supported *N* = 9	Increased risk in groups (dilution not supported) *N* = 23
No	• Margaritifera *margaritifera*——solitary mussels hid longer than those in groups (Wilson et al. 2012) • Semibalanus *balanoides*——solitary barnacles hid longer than those in groups (Mauck and Harkless 2001) • Anthopleura *aureoradiata*—withdrawal times shorter for those in contact with conspecifics (indirect measure) (Haag and Dyson 2014) • *Geukensia demissa*—mortality increased with density due to competition, mortality from predation decreased with increased density (Bertness and Grosholz 1985) • Paphies *ventricos*—proportion eaten decreased nonlinearly with increased density (Haddon et al. 1987) • *Mya arenaria*, *Ischadium recurvum*—higher proportions of both soft clams and hooked mussels were eaten at low densities when placed together in shallow sand (Ebersole and Kennedy 1995) • *Strombus gigas*—mortality decreased as density increased (Ray-Culp et al. 1999) • *Mya arenaria*—mortality decreased as density increased in mud, even at deep depths (Eggleston et al. 1992) • *Strongylocentrotus droebachiensis*—mean proportion killed decreased with increasing density for both lobsters and wolffish (Hagen and Mann 1992)	• *Protothaca staminea*—mortality increased with increased density (Boulding and Hay 1984) • *Mya arenaria*——soft-shell clams in higher densities experienced higher mortality (Beal et al. 2001) • Macoma *balthica*—mortality proportionally increased at higher density (Mansour and Lipcius 1991) • *Mercenaria mercenaria*—higher predation rates in higher density patches of hard clams (Micheli 1997) • *Tubilaria* larynx—mortality increased with density (MacLeod and Valiela 1975) • *Mercenaria mercenaria*—crabs foraged more efficiently on higher density prey patches (Sponaugle and Lawton 1990) • *Mya arenaria*, *Rangia cuneata*—crabs consumed higher proportion of both soft clams and Atlantic rangia clams in deep sand when placed together (Haddon et al. 1987) • *Mya arenaria*—in 1988 experiment, proportional mortality was higher at higher densities in York River sand (Seitz et al. 2001) • *Macoma balthica*—in 1987 experiment, regardless of sediment type, proportional mortality was higher at higher clam density (Seitz et al. 2001) • *Crassostrea virginica*—proportional mortality rates higher at higher densities for all temperature treatments, though most pronounced in treatments above 14 °C (Eggleston 1990) • *Mya arenaria*—proportional mortality increased at higher densities in both sand and mud, but higher in mud than sand (Lipcius and Hines 1986) • *Mya arenaria*—proportional mortality increased at higher densities in sand (Eggleston et al. 1992) • *Macoma balthica*—with J5 crab predators, clam mortality increased with increased density (Iribarne et al. 1995) • *Mya arenaria*—under both normoxia conditions and hypoxia conditions where clams were acclimated to low dissolved oxygen concentrations, percentage of mortality was higher for lower densities (Taylor and Eggleston 1999) • *Macoma balthica*—mean proportional mortality higher at higher densities (mesocosm only) (Kuhlmann and Hines 2005) *no density relationship in sand/mud in contrast to Seitz et al. (2001) • *Macomona lilliana*—ray foraging increased in high density patches (indirect measure) (Hines et al. 1997) • *Mercenaria mercenaria*—increased proportional mortality with increased density (to limit) (Pollack et al. 2008) • *Artemia salina*—increased proportional mortality with increased density (Pollack et al. 2008) • *Molgula*—proportional mortality highest at highest prey densities (Whitlatch and Osman 2009) • *Ascidiella*—proportional mortality lower at lowest densities (Whitlatch and Osman 2009) • *Styela*, *Ciona*, *and Botryllus*—proportional mortality lower at lowest densities (Whitlatch and Osman 2009) • *Mercenaria mercenaria*—proportional mortality rate increased with increasing density of clams in Virginia and Florida (Long and Hines 2012) • *Arcuatula senhousia*—attracted native predators, indirectly increasing predation on native clams (Castorani and Hovel 2015)

Table 2 *Continued*

	$N = 17$	$N = 3$
Yes	• *Strombus gigas*—conches safer in groups (Ray and Stoner 1994) • *Aphrissa statira*, *Phoebis trite* ("yellows"); Phoebis *argante* ("oranges"); *Daptoneura leucadia* ("whites")—butterflies in groups safer from predation, to limit of 40 (Burger and Gochfeld 2001) • *Halobates robustus*—safer in groups (Foster and Treherne 1981) • *Coleoptera: Scolytidae*—consumption by predator decreased with density (Aukema and Raffa 2004) • *Aphis Varians*—individual predation risk decreased with increasing number of conspecifics nearby (Turchin and Kareiva 1989) • *Uca pugilator*—crabs aggregated when attacked, suggested risk dilution in groups (indirect measure) (Viscido and Wethey 2002) • *Metepeira incrassata*—predation risk decreased for spiders in larger colonies, though may be due to early warning hypothesis rather than dilution (Uetz et al. 2002) • *Daphnia*—proportional number of attacks lower at high densities (Jensen and Larsson 2002) • *Aphidoletes aphidimyza*—probability of mortality decreased with increased colony size (Lucas and Brodeur 2001) • *Metepeira incrassala*—individual risk decreased with colony size, though not to the extent predicted by numerical dilution (Uetz and Hieber 1994) • *Rhyacophila vao*—overall group size benefits due to dilution effect (Wrona and Dixon 1991) • *Austrohelice crassa*—hiding time decreased with increased neighbour density (indirect) (Guerra-Bobo and Brough 2010) • *Callinectes sapidus*—proportional juvenile mortality increased significantly at low densities (Dittel et al. 1995) • *Panulirus argus*—per capita mortality declined with increased group size (Lavalli and Herrnkind 2009) • *Parischnogaster alternata*—predation rate lower in denser areas (Landi et al. 2002) • *Hymenoptera: diprionidae*—members of large groups had significantly lower individual probability of mortality (Codella and Raffa 1995) • *Halobates*—reduced individual risk of attack in larger groups (Treherne and Foster 1982)	• *Gerris remigis*—flight distance from an approaching, potentially cannibalistic adult rose and then fell as group size increased (Dill and Ydenberg 1987) • *Placopecten magellanicus*—mortality increased with increased density (Barbeau et al. 1998) • *Placopecten magellanicus*—predation by crab increased with scallop density (seastar predation density independent) (Barbeau et al. 1994)

the sampling interval, our lack of long-term plasticity may make biological sense. In this context, changes in state can refer to environmental changes or past experiences by the individual that may influence its response to a particular stimulus (Biro and Stamps 2015). Fluctuating environments are likely to enhance the mixture of behavioral phenotypes, because a strategy that is optimal at one period of time may not be optimal at another (Luttbeg and Sih 2010). For example, studies have found that short-term changes in external temperature can affect measures of personality in coral reef fish (Biro et al. 2010), crabs (Biro et al. 2013), and hermit crabs (Briffa et al. 2013). Although we accounted for external variables such as temperature when conducting our 4 trials each day, we cannot know how water temperature (or other factors that were not measured) varied between days of sampling may have affected worm behavior at the time we tested an individual. Environmental changes may also affect the perception of the stimulus in a way that would confound an organism's habituation toward it. For the polychaete *Nereis pelagica*, for example, Clark (1960) found that a slight change in the nature of a repeated stimulus could elicit a reappearance of a given response, masking evidence of habituation. Such state changes may make a repeated stimulus appear novel. Sudden physiological or environmental changes such as these could easily occur between day-to-day sampling, and lead to changes in behavior, leading to different slopes over 1 day, but not over longer periods of time. These microstate changes may be lost in the averaging of responses over 4 days. Thus, it is unlikely that the lack of long-term phenotypic plasticity reflects a statistical artifact and we believe it is more likely to reflect changes in the worm's state over time.

CONCLUSION

We found evidence to suggest that group membership for Christmas tree worms heightens predation risk for the individual. This pattern is further supported by existing literature on sessile invertebrates, but differs significantly compared with patterns for mobile invertebrates. The difference between strategies used by sessile versus mobile prey may reflect life history and physiological constraints. Overall, Christmas tree worm behavior conforms to optimal escape theory (Cooper and Blumstein 2015). For worms in groups, the cost of hiding longer was balanced by the benefit of added safety from predators. In worms facing a repeated benign stimulus, the individuals paying the highest cost (those who initially hid for longer) were most likely to adjust their behavior. Though external factors may be responsible for variation in phenotypic plasticity over short time scales, they did not affect the consistency of worm behavior across longer time scales. These results highlight the significant difference between antipredator behaviors of motile and sessile invertebrates, as well as confirm the necessity of accounting for time-related change in studies of animal personality.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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