

RESEARCH PAPER



WILEY

Predator hunting modes and predator–prey space games

Barney Luttbeg¹ | John I. Hammond² | Tomas Brodin³ | Andrew Sih⁴

¹Oklahoma State University, Stillwater, OK, USA

²Marian University, Fond du Lac, WI, USA

³Swedish University of Agricultural Sciences (SLU), Umeå, Sweden

⁴University of California, Davis, CA, USA

Correspondence

Barney Luttbeg, Oklahoma State University, Stillwater, OK 74074, USA.
Email: luttbeg@okstate.edu

Funding information

US NSF, Grant/Award Number: NSF IBN 0446276

Editor: Jonathan Wright

Abstract

Predators and prey are often engaged in a game where their expected fitnesses are affected by their relative spatial distributions. Game models generally predict that when predators and prey move at similar temporal and spatial scales that predators should distribute themselves to match the distribution of the prey's resources and that prey should be relatively uniformly distributed. These predictions should better apply to sit-and-pursue and sit-and-wait predators, who must anticipate the spatial distributions of their prey, than active predators that search for their prey. We test this with an experiment observing the spatial distributions and estimating the causes of movements between patches for Pacific tree frog tadpoles (*Pseudacris regilla*), a sit-and-pursue dragonfly larvae predator (*Rhionaeschna multicolor*), and an active salamander larval predator (*Ambystoma tigrinum mavortium*) when a single species was in the arena and when the prey was with one of the predators. We find that the sit-and-pursue predator favors patches with more of the prey's algae resources when the prey is not in the experimental arena and that the prey, when in the arena with this predator, do not favor patches with more resources. We also find that the active predator does not favor patches with more algae and that prey, when with an active predator, continue to favor these higher resource patches. These results suggest that the hunting modes of predators impact their spatial distributions and the spatial distributions of their prey, which has potential to have cascading effects on lower trophic levels.

KEYWORDS

hunting mode, predator, prey, *Pseudacris*, space games

1 | INTRODUCTION

How individuals use space shapes ecological dynamics by affecting the strength of interactions between species (Lampert & Hastings, 2016; Schmitz, Miller, Trainor, & Abrahms, 2017). Predators and prey are in many cases expected to shape each other's spatial distributions. The landscape of fear concept predicts that spatial variation in a prey's perception of predation risk affects their space use and foraging decisions (Laundré, Hernández, & Altendorf, 2001). These resulting spatial distributions then may have cascading effects on the prey's resources (Orrock et al., 2010), such as grasshoppers shifting their diet from grasses to forbs in the presence of predators (Beckerman, Uriarte, & Schmitz, 1997).

The predicted strength of the non-consumptive indirect effects that predators have on their prey's resources should depend on the hunting mode of the predator (Schmitz, 2005). "Sit-and-pursue" and "sit-and-wait" predators are expected to cause larger non-consumptive effects than "active" predators because of a combination of (a) their lower movement rates make the cues they produce more indicative of their recent presence than those from "active" predators (Sih, 1992) and reliable cues are a key ingredient for non-consumptive effects (Luttbeg & Trussell, 2013), and (b) they are harder to detect and thus may cause longer antipredator responses in prey (Schmitz, 2005). There has been empirical support for hunting mode affecting the strength of non-consumptive indirect effects (Preisner,

Orrock, & Schmitz, 2007; Schmitz, 2008). In this paper, we investigate whether predator hunting mode also alters the joint spatial distributions of predators and their prey, so that in addition to the informational effects of hunting mode, there might be a spatial game that alters the spatial distribution of the non-consumptive effects of predators.

At the simplest level, prey are expected to avoid locations that have higher predator densities, and predators are expected to favor locations with higher prey densities. Numerous studies have indeed shown that if prey are immobile, predators tend to spend more time foraging in areas with more prey (Godin & Keenleyside, 1984; Sih, 1982), and if predators are immobile (e.g., caged), prey tend to avoid areas of higher predation risk (Caro, 2005; Lima, 1998; Sih, Kats, & Moore, 1992). Surprisingly few studies, however, have examined the joint behavioral responses and space use of predators and prey when both are mobile (Sih, 1984; Lima, 2002; but see Brown, Kotler, & Bouskila, 2001; Hammond, Luttbeg, & Sih, 2007; Hammond, Luttbeg, Brodin, & Sih, 2012; Luttbeg, Hammond, & Sih, 2009).

When both predators and prey are mobile at similar spatial scales, their resulting spatial distributions can be predicted as the outcomes of a 3 trophic level (predator, prey, and resource) spatial game (Sih, 2005). Most 3 trophic level game models assume that predators do not consume the prey's resources, and the resource is immobile. In the absence of predators, when prey are equal competitors, they are expected to follow a simple ideal free distribution theory and match the distribution of their resources (Luttbeg & Sih, 2004). However, if prey tend to match the distribution of their resources, resource levels become a reliable indicator of current and future prey locations. Several game theory models predict that under simple scenarios where predators track prey and prey balance foraging and predation risk, the emergent outcome should be predators strongly favoring patches with more of the prey's resources, while prey only exhibit a weak preference for patches with more resources (Alonzo, 2002; Flaxman & Lou, 2009; Hugie & Dill, 1994; Luttbeg & Sih, 2004; Rosenheim, 2004; Sih, 1998). To emphasize, in these models (with the exception of the model in Luttbeg & Sih, 2004), predator space use responds only to prey, not directly to resources. Still, as long as prey show any tendency, even weak, to be more abundant in patches with more resources, optimally foraging predators prefer sites with more resources because those sites have at least slightly more prey. These predictions depend, however, on several factors including: the strength of predator interference (Hugie & Dill, 1994; Sih, 1998), predator capture success per encounter (Luttbeg & Sih, 2004), state dependence (Alonzo, 2002), refuge availability for prey (Hugie & Dill, 1994), and on how prey optimally balance risk and foraging (Luttbeg & Sih, 2004). Perhaps most importantly, these models assume that predators can track prey accurately and quickly, that is, that they have both the mobility and information to follow an ideal free distribution.

The model predictions are supported by observed spatial distributions and covariates with predator and prey movements.

Predator spatial distributions have been observed to be more correlated with the distribution of prey's resource than prey are, and the movement decisions of predators are affected by the distribution of the prey's resources more than prey movement decisions (Hammond et al., 2012; Hammond et al., 2007; Luttbeg et al., 2009).

While no formal theory has yet been produced on the topic, predator and prey spatial distributions should depend on the relative mobility of predators and prey (e.g., the hunting mode of the predator), and the timeliness and accuracy of the information prey and predators have about their respective locations. Relatively immobile, sit-and-pursue predators cannot easily track the movements of mobile prey. Instead, for these predators that ambush their prey from a close distance, it can be advantageous for them to anticipate the future locations of prey by settling in areas with more of the prey's resources. This then might make the predator's spatial distribution predictable for prey, inducing prey to use areas with more resources far less than they would in the absence of predators. Models suggest that prey that adaptively balance predation risk and feeding needs should weakly prefer areas with more resources even though those areas also tend to have more predators (Luttbeg & Sih, 2004; Sih, 1998). This leads to the predicted pattern of predators strongly favoring high prey resource patches, while the prey tend to be relatively uniformly distributed with respect to their resources.

In contrast, predators that use an active hunting mode to directly track prey may rely less or not at all on the distribution of the prey's resources to inform their movement decisions. If predators respond directly to their prey, and not to their prey's resources, then this weakens the connection (i.e., the conflict for prey) between higher predation risk and higher resource patches.

We contrasted predator-prey space use with predators that differ in their mobility using a multiple treatment experiment with tadpole prey, dragonfly larvae (a sit-and-pursue predator), and salamander larvae (an active predator) (Preisler et al., 2007). Dragonfly larvae are predominantly sit-and-pursue or sit-and-wait predators, but in some cases may become more active predators in the dark (Corbet, 1999). Tiger salamander larvae primarily use an active foraging strategy, where they cruise through the environment and lunge at prey (Hassinger, Anderson, & Dalrymple, 1970). These two predators differ also in predation rates and how they consume the prey (tearing apart vs. consuming the prey whole). Nonetheless, we suggest that contrasting two predators that clearly have different hunting modes is a good start toward understanding factors that affect the outcome of predator-prey games.

We quantified both the spatial distributions and movements between patches of both predators and prey in the following five treatments: tadpoles with no predators, dragonflies (sit-and-pursue predators) with no prey, salamander larvae (active predators) with no prey, tadpoles with dragonflies, and tadpoles with salamanders. Our analyses of factors influencing movements of both predators and prey provide a mechanistic level of behavioral understanding that is unusual in studies of predator-prey space use. Specifically, for

each type of animal, we used their actual patch switching patterns (whether they stay or leave a patch in each of a series of time periods) to discern (via model selection) the effects of prey or predator presence in the arena, and prey or predator abundance in a given patch on the probability of leaving a patch.

In regards to the proportions of time spent in various patches that differ in resource availability, we predict that (1) prey without predators will favor patches containing more of their resources, (2) dragonfly larvae (the sit-and-pursue predator) will favor patches containing more of the prey's resource, and (3) the presence of dragonfly larvae in an arena will cause their prey to not favor patches containing more of their resources. We also predict that (4) the salamander larvae (the active predator) will not favor the prey's higher resource patches and that (5) prey will continue to favor higher resource patches despite the active predator being in the arena.

In regards to the causes of movements we predict that (1) prey without predators present should tend to stay longer in patches with more resources; (2) adding predators to the arena should induce prey to generally move less (to avoid encountering predators), but to leave patches with more predators; (3) with predators present, particularly with sit-and-ambush predators, prey should show a weaker tendency to stay in patches with more resources; (4) sit-and-pursue predators should tend to stay in patches with more resources and/or more prey; and (5) resources should have little or no effect on patch switching by the active predator, but (6) active predators should stay in patches with more prey.

2 | MATERIALS AND METHODS

2.1 | Collection and experimental design

Pacific tree frog tadpoles (*Pseudacris regilla*) were collected from Green Pond at Wantrup Wildlife Sanctuary, Napa County, California using dipnets. They were housed in indoor group tanks (88 × 42 cm, <80 individuals/tank) for 6 days before being used in these experiments, during which they were fed ad libitum commercially available algal disks (Hikari®, 1.4 cm diameter). They were starved for 24 hr before being used in a trial to increase their motivation to feed and reduce variance in motivation. Blue-eyed darter larvae (*Rhionaeschna multicolor*) were collected by dipnets from the Stebbins Cold Canyon UC Reserve in Solano and Napa counties and housed individually in ~0.5 L mesh cups floated in indoor group tanks for 6 days before the start of trials. They were fed ad libitum tadpoles and tubifex worms and starved 12 hr before the start of the trial. Tiger salamander eggs (*Ambystoma tigrinum mavortium*) were collected in Monterey County California and were reared individually first in 10% Holfreter's solution in the laboratory and fed zooplankton ad libitum (Ryan et al., 2012) and upon growing larger were then transferred outside into large plastic bins (60 × 40 cm) filled with 40 L of well water and fed ad libitum zooplankton and tadpoles. Fourteen days before the

start of the experiment, salamander larvae were moved into the same laboratory space as above, held individually in plastic bins (36 × 20 cm) filled with well water, and fed ad libitum tadpoles and tubifex worms. Larvae were also starved for 12 hr before the start of the trial.

These three species historically and currently co-occur throughout the region, and all prefer similar habitats (Alvarez et al., 2013; Ball-Damerow, M'Gonigle, & Resh, 2014). At the location where the frog tadpoles were collected, they co-occur in ponds with dragonfly larvae of many species including *Rhionaeschna multicolor* and often co-occur with the salamander larvae throughout the region (Alvarez et al., 2013). Where the dragonfly larvae were collected, we have observed *Pseudacris regilla* tadpoles to be present. Where the salamander larvae were collected is part of the region where they overlap with *Pseudacris regilla* tadpoles (Alvarez et al., 2013) and *Rhionaeschna multicolor* larvae (Ball-Damerow et al., 2014). All of the animals experienced a photoperiod of 16 hr of light and 8 hr of darkness and water temperatures of 21°C in the days prior to trials. All of the trials were conducted at the Center for Aquatic Biology and Aquaculture on the University of California Davis campus.

We followed the United States Research Council's Guide for the Care and Use of Laboratory Animals. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Animals were collected under CA permit SC-6648. Work was conducted after approval by the University of California at Davis Institutional Animal Care and Use Committee (protocol #05-11741).

The experimental arenas were square plastic tubs (90 × 90 cm) filled with 10.5 cm of filtered well water. The water was changed between each trial in an arena. The arena was composed of 4 contiguous patches (as defined by marks on the outside of the container), each being a square that occupied ¼ of the arena. In the middle of each patch, we placed the prey's resource (algal disks). There were four patch types in each arena with different resource levels: high (2 algal disks; 1.2 g ± 0.04 g), upper medium (1 algal disk; 0.6 g ± 0.02 g), lower medium (1/2 algal disk; 0.3 g ± 0.01 g), and low (1/4 algal disk; 0.15 ± 0.005 g). The spatial arrangements of patch types were randomly determined for each trial. In all of the arenas, sixteen vertical strands of nylon rope with a bolt attached to the bottom were spaced evenly in a grid throughout the arena. The dragonfly larvae use these as perches, and they break up sight lines.

The 4 patches were each 45 × 45 cm, and thus each patch was approximately 20 × 20 body lengths for the tadpole prey and the similarly sized dragonfly larvae. This was fairly large given the typical movement lengths of the tadpoles and dragonfly larvae that we observed. However, the salamander larvae could move rapidly between the patches, and it is quite possible that chemical cues from predation during the trials could have spread throughout the arena. Thus, the three species in the experiment may have differed in how they perceived our four defined patches. Despite these concerns, we still

feel that comparing the patch use of the three species can provide insight into how predator and prey space use shape each other.

The experiment was conducted in six blocks with the first set of blocks on May 3, 2007, and subsequent blocks occurred over the next five consecutive days. For each temporal block, we used 12 experimental arenas and had two replicates for each of the following treatments: (1) 16 tadpoles (T), (2) 3 dragonfly larvae (D), (3) 2 salamander larvae (S), (4) 16 tadpoles with 3 dragonfly larvae (TD), and (5) 16 tadpoles with 2 salamander larvae (TS). In trials, we used fewer salamander larvae than dragonfly larvae because a salamander larva tends to move over a greater area and forage more intensely than a dragonfly larva. In treatments with tadpoles and predators present (TD and TS), the tadpoles were exposed to predators and predation did occur. This experiment was specifically intended to measure prey and predator space use and movement decisions in the presence of the other species; therefore, it was necessary to allow both species to move freely within the arenas. Actual predation is an integral and necessary component to studying these interactions. Tadpole prey responses have been very well studied and support that consumption is needed to produce the maximal ecological and evolutionary responses (e.g., Schoeppner & Relyea, 2005; Schoeppner & Relyea, 2009).

Tadpoles were randomly assigned to the treatments. Tadpoles from the alone treatments ($n = 192$) were weighed after trials ($0.32 \text{ g} \pm 0.14 \text{ SD}$). Head widths are often used as a proxy for size in dragonfly larvae (Benke, 1970) and were here $0.75 \text{ cm} \pm 0.07 \text{ SD}$ ($n = 24$). The snout-vent lengths of the salamander larvae ($n = 19$) were $5.85 \text{ cm} \pm 0.42 \text{ SD}$.

All trials ran from 0900 to 1300 in full light (approximately 400 lux). Thirty minutes before beginning trials, algal disks were placed in their respective patches and were covered with a petri dish. Mesh cups holding individual predators (if they were in the treatment) were placed into the arena. Tadpoles (if they were in the treatment) were released into the arena. After the 30-min acclimation period, the algal disks were uncovered, and the dragonfly larvae and then salamander larvae were gently released from their cups into the center of the arena. Trials were video recorded using a closed-circuit system with a camera above the arena recording to a central DVR. It was not possible to record data blind because our treatment combinations of species were obvious to the observer.

At the end of a trial, tadpoles were removed from the arena and were not used again. Dragonfly larvae were moved to individual mesh cups and given 1 tadpole to consume to re-standardize hunger levels. Salamander larvae were moved to individual plastic containers and given 2 tadpoles to consume to re-standardize hunger levels. After 90 min, any living tadpoles and tadpole remains were removed from the predator containers, and predators were starved for the next 18 hr. Each predator was used in all six blocks (three times with tadpoles and three times without tadpoles). Individuals were kept with previous partners for two blocks, so the grouping experienced treatment with and without

tadpoles present. After every two blocks, all predatory individuals were re-randomized.

2.2 | Measuring patch switching

Using our video recordings, every 15 min we first noted the number of individuals of each species in each patch. We then observed each individual for each species for 30 s and gave them a binary score for whether they switched patches at least once or not.

2.3 | Comparing predator patch switching and predation rates

All statistical analyses were done using R (version 3.2.3) (R Core Team, 2015). We used logistic regression (a generalized linear mixed model, GLMM, with a binomial link function) to test whether the two predators differed in their patch switching rates in the presence of the tadpole prey. Our GLMM had a fixed effect of predator species and a random effect of the trial ID. We also tested whether the proportion of tadpoles that survived the trials differed between the two predator species using a generalized linear model (GLM) with a binomial link function and predator species and experimental block as explanatory variables. The "lme4" package was used for these analyses (Bates, Maechler, Bolker, & Walker, 2015). We report the number of fitted parameters in the model (df) and the Akaike weights (w) for the supported models, which can be interpreted as an estimate of the probability that a model is the best model in the set of alternative models (Burnham & Anderson, 1998).

2.4 | Spatial distributions

Every 20 min (starting 20 min after predators were released), we noted the number of individuals of each species in the four patches. Thus, for each trial, there were 12 observations of the proportion of individuals of each species in each of the 4 patch types. In all trials where a predator was present with prey, the spatial distributions of the prey could have been affected by both the prey's movement decisions and by predation.

For each trial and separately for each species in the trial, we computed the slope of the proportion of individuals observed in a patch versus the amount of prey resource in the patch using a GLM with a binomial link function (logistic regression). For species in each species composition, we report the 95% confidence intervals for the logistic regression slopes noting whether slopes of 0 (no resource level effect) and 1 (resource matching) fall within these intervals. With this conservative approach, we eliminated the pseudo-replication of the repeated sampling within an arena by reducing the data to a single slope value, but preserved the

effect of the continuous variable of different initial resource levels in patches.

We also tested whether the presence of predators affected tadpole spatial distributions. We compared the distributions of slopes, when tadpoles were alone versus when dragonfly or salamander larvae were present in the arena using Wilcoxon Rank Sum tests (because variances significantly differed between the distributions).

2.5 | Causes of patch switching

We assessed what factors best explained when individuals of each of the three species switched patches. We sequentially treated every individual in the arena as the focal individual and calculated the observed number of individuals for each species (excluding the focal individual) in their patch minus the expected number of individuals of each species in their patch given a uniform distribution. For example, if a tadpole was in the same patch as 1 of the 2 salamander larvae in the arena, it was in a patch with 0.5 more salamanders than randomly expected (1.0 observed–0.5 expected). If a species was not in the arena, the observed and expected number of individuals of that species in a patch were both 0, and the difference was 0. This approach allowed us to characterize the number of individuals of a species in a focal individual's patch while being able to combine data from trials with different species present.

We used an exploratory data analysis approach to examine what factors affected the probability that an individual switched patches during a 30-s observation period. For each species, we fit a full statistical linear model and then used the “MuMIn” package in R (Bartoń, 2016) to make simpler combinations of the full model (excluding models where interaction terms were present without both main effects being present). We used Akaike information criterion (AIC) to quantify the relative evidence that the empirical data gave for each of the alternative models (Burnham & Anderson, 1998; Hillborn & Mangel, 1997). Akaike information criterion values were determined using the “lme4” package in R (Bates et al., 2015). We present only the models that produced a $\Delta\text{AIC} \leq 6.0$ based upon idea that models with approximately $\Delta\text{AIC} > 6.0$ are not receiving much support from the data (Burnham & Anderson, 1998). We also excluded models with ΔAIC greater than a simpler version of the model, because this indicates that the model included a pretending variable (Richards, 2008).

For tadpoles, the full statistical model was a GLMM with a binomial link function for the probability of prey patch switching (a mixed logistic model). Fixed effects were the amount of the prey's resource in their current patch (R : 0.25, 0.5, 1, or 2, a continuous variable), the absence or presence of dragonflies (D : 0 if absent, 1 if present) and salamanders (S : 0 if absent, 1 if present) in the arena, the observed–expected number of tadpoles (ΔN), dragonflies (ΔD), and salamanders (ΔS) in the patch, the interaction between the absence and the presence of dragonflies or salamanders with the amount of resources in the patch ($D * R$ and $S * R$, respectively), and the time step of the observation. Random effects were the trial ID nested

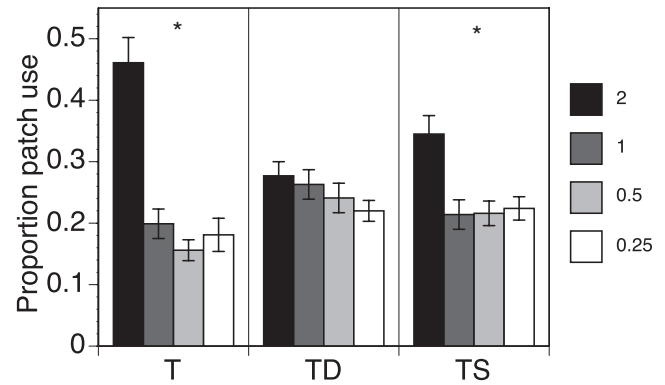


FIGURE 1 Proportions (with SE bars) of tadpoles in the four resource patch types differing in amount of prey resource present for T, TD, and TS treatments. * indicates that the slope of number of tadpoles in a patch versus the resources in the patch significantly differed from 0

within the experimental block. Simpler models with every combination of fixed variables were constructed, but to control for time, we kept it in all of the alternative models.

For dragonflies, the full model was also a GLMM with a binomial link function and the same random effects, but fixed effects were R , the absence or presence of tadpoles (N), the observed–expected number of tadpoles (ΔN) and dragonflies (ΔD), interaction between the absence and the presence of tadpoles with the amount of resources in the patch ($N * R$), and time step. Similarly, for salamanders, the full model's fixed effects were R , N , ΔN , ΔS , $N * R$, and time step.

3 | RESULTS

3.1 | Comparing predator patch switching and predation rates

In the presence of tadpoles, the active salamander larvae patch switching rates (0.151 switches/observation) were significantly higher than the patch switching rates of sit-and-pursue dragonfly larvae (0.028 switches/observation) ($z = 5.263$, $p < .05$). Salamander larvae imposed a higher predation rate on tadpoles than dragonfly larvae ($z = -8.00$, $p < .05$). On average, the two salamanders killed 53.7% ($\pm 4.8\%$) of the prey, whereas the 3 dragonflies killed only 12.5% ($\pm 1.9\%$) of the prey.

While both movement rates and predation rates can affect the spatial distributions of tadpoles, tadpole movement rates were much higher than predation rates and thus probably erased the effects of where mortality occurred. When in arenas with dragonfly larvae, during 30-s observations (every 10 min) 15.2% of tadpoles switched patches (423 out of 2,789 opportunities) and during 20-min periods 0.01% were killed by dragonflies (16 out of 2,075 opportunities). When in arenas with salamander larvae, during 30-s observations 11.8% of tadpoles switched patches (207 out of 1,756 opportunities) and during 20-min periods 4.2% were killed by salamanders (53 out of 1,274 opportunities).

3.2 | Spatial distributions

As predicted, the spatial distributions of tadpoles were significantly affected by the distribution of their resource (i.e., tadpoles were more abundant in patches with more resources) when they were alone and when they were with active salamander larvae, but not when they were with sit-and-pursue dragonfly larvae. When tadpoles were alone, the slope of their patch use ($\bar{x} \pm SD = 0.92 \pm 0.66$, 95% CI [0.50, 1.34]) increased with the resource levels (confidence interval not containing 0) and did not significantly differ from resource matching (Figure 1). When in arenas with active salamanders, their patch use ($\bar{x} \pm SD = 0.39 \pm 0.38$, 95% CI [0.16, 0.63]) increased with the resource levels, but significantly under matched their resources (1 was not within the confidence interval). Finally, when in arenas with sit-and-pursue dragonflies, their patch use did not increase with the resource levels ($\bar{x} \pm SD = 0.15 \pm 0.35$, 95% CI [-0.07, 0.38]). The presence of either predator did reduce the correlation between prey distributions and the distribution of their resources compared with when no predator was present (Wilcoxon Rank Sum test; dragonflies: $W = 125$, $p < .05$, salamanders: $W = 112$, $p < .05$).

The spatial distributions of the sit-and-pursue dragonfly larvae when alone were significantly affected by the distribution of the tadpole's resource, but not when tadpoles were present. When dragonflies were alone, slopes of the logistic regressions of the proportion of dragonflies in a patch versus the amount of the prey's resource in the patch ($\bar{x} \pm SD = 0.48 \pm 0.70$, 95% CI [0.04, 0.92]) were significantly greater than 0, but also significantly less than 1 (Figure 2). However, when with tadpoles, the slopes of dragonflies versus prey resources in the patch ($\bar{x} \pm SD = 0.08 \pm 1.10$, 95% CI [-0.62, 0.78]) were not significantly affected by the prey's resource.

The spatial distribution of the active salamander larvae never appeared to be significantly affected by the distribution of the prey's resource (Figure 3). When alone ($\bar{x} \pm SD = 0.25 \pm 0.64$, 95% CI [-0.12, 0.62]) and with tadpoles ($\bar{x} \pm SD = -0.08 \pm 0.83$, 95% CI [-0.61, 0.45]),

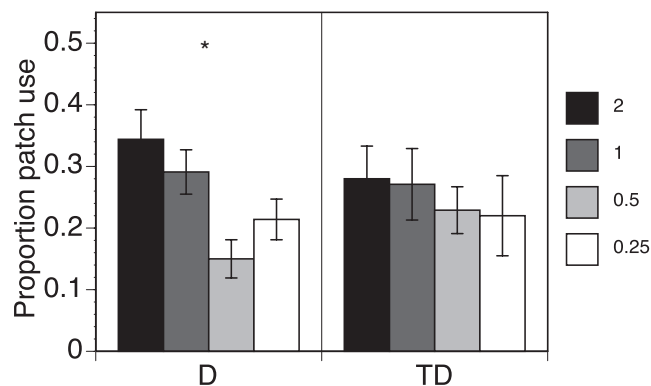


FIGURE 2 Proportions (with SE bars) of dragonflies in the four resource patch types differing in amount of prey resource present for D and TD treatments. * indicates that the slope of number of dragonflies in a patch versus the resources in the patch significantly differed from 0

the slopes of salamanders versus prey resources in the patch were not significantly affected by the prey's resource.

3.3 | Causes of patch switching

Our analyses showed that the probability of a tadpole switching out of a patch was affected by many factors (Table 1). Only two models were supported by the data, and they showed that the probability of a tadpole switching out of a patch decreased when the patch had more tadpoles (ΔN) or resources (R), increased when more salamanders (ΔS) were present in the patch, and decreased when dragonflies (D) or salamanders (S) were present in the arena. The negative effect that resources had on the probability of patch switching ($R = -0.38$) was mostly negated, when dragonflies were present in the arena ($D * R = 0.32$). The best model also indicated that the presence of salamanders ($S * R = 0.31$) in the arena negated the resource effect ($R = -0.38$), but the other supported model did not include this effect. Overall, it appears that the presence of either predator in the arena reduced patch switching, that more salamander larvae in a patch increased the probability of a tadpole leaving that patch ($\Delta S = 0.50$), but more dragonflies in a patch did not. Both models had the presence of dragonflies in the arena reducing the effect of resources on patch switching ($D * R$), but only the top model had the presence of salamanders reducing the effect of resources ($S * R$).

Seven alternative models for the probability of dragonflies switching patches received some support from the data (Table 2). The top 4 models had the probability of dragonfly patch switching being reduced by the presence of tadpoles (N) in the arena and more resources (R) in the patch. There was support for the probability of dragonflies patch switching being reduced, when more tadpoles (ΔN) or more dragonflies (ΔD) were in the patch. According to the analysis, the accumulated probability (summing the Akaike weights) that the prey's resources (R) were in the best model for dragonfly patch switching was 0.88.

Three alternative models for the probability of salamanders switching patches received support from the data. There was support

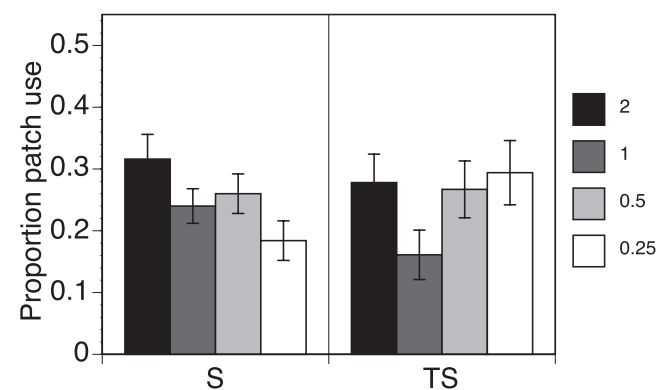


FIGURE 3 Proportions (with SE bars) of salamanders in the four resource patch types differing in amount of prey resource present for S and TS treatments

R	D	S	ΔN	ΔD	ΔS	$D * R$	$S * R$	ΔAIC	df	w
-0.38	-1.07	-1.33	-0.07		0.50	0.32	0.31	0	11	0.89
-0.29	-0.98	-1.02	-0.08		0.50	0.23		4.17	10	0.11

Note: R: resource levels in the patch, D: presence/absence of dragonflies in the arena, S: presence/absence of salamanders in the arena, ΔN : number of tadpoles in the patch—expected number, ΔD : number of dragonflies in the patch—expected number, ΔS : number of salamanders in the patch—expected number, and $D * R$ and $S * R$: interactive effects between R and D and between R and S, respectively. df is the number of parameters in the model, and w is the associated Akaike weight. We only show the models that received much support from the data ($\Delta AIC \leq 6$) and that did not include pretending variables.

TABLE 2 Alternative models and their fitted parameters for the probability of dragonflies switching patches

R	N	ΔN	ΔD	$N * R$	ΔAIC	df	w
-0.43	-1.59	-0.28	-0.31		0	8	0.33
-0.46	-1.56	-0.27			0.49	7	0.26
-0.45	-1.46		-0.30		1.51	7	0.16
-0.48	-1.43				1.85	6	0.13
	-1.57	-0.29	-0.35		3.42	7	0.06
	-1.53	-0.28			4.68	6	0.03
	-1.43		-0.34		5.40	6	0.02

Note: R: resource levels in the patch, N: presence/absence of tadpoles in the arena, ΔN : number of tadpoles in the patch—expected number, ΔD : number of dragonflies in the patch—expected number, and $N * R$: interactive effects between R and N. df is the number of parameters in the model, and w is the associated Akaike weight. We only show the models that received much support from the data ($\Delta AIC \leq 6$) and that did not include pretending variables.

for the probability of salamander patch switching being reduced by the presence of tadpoles (N) in the arena. There was also some evidence that the probability of salamanders switching patches was decreased by the presence of more tadpoles in the patch (ΔN), but only in the top model. There was no evidence that their patch switching was affected by the amount of resources in the patch. The accumulated probability (summing the Akaike weights) that the prey's resources (R) were in the best model for salamander patch switching was 0.

4 | DISCUSSION

Our predictions for what would shape the spatial distributions of tadpoles, dragonfly larvae, and salamander larvae came from a mix of theory on ideal free distributions, predator and prey space games, and the mechanics of predator hunting modes. The simplest prediction, from ideal free distributions, was that in the absence of predators, tadpoles would preferentially use patches with more of their resources. As expected, we found that tadpole space use was significantly affected by their resources. Tadpoles, in the absence of predators, did increase patch use with more of their resources present. In addition, our analysis of tadpole movement rules indicated that tadpoles were less likely to leave a patch, when the patch had more resources (Table 1).

TABLE 1 Alternative models and their fitted parameters for the probability of tadpoles switching patches

TABLE 3 Alternative models and their fitted parameters for the probability of salamanders switching patches

R	N	ΔN	ΔS	$N * R$	ΔAIC	df	w
	-0.76	-0.16			0	6	0.53
	-0.67				0.57	5	0.40
					3.87	4	0.08

Note: R: resource levels in the in patch, N: presence/absence of tadpoles in the arena, ΔN : number of tadpoles in the patch—expected number, ΔS : number of salamanders in the patch—expected number, and $N * R$: interactive effects between R and N. df is the number of parameters in the model, and w is the associated Akaike weight. We only show the models that received much support from the data ($\Delta AIC \leq 6$) and that did not include pretending variables.

From predator and prey space game models, it has been predicted that when a predator's foraging success depends on them anticipating where prey will be in the future that the predators should favor patches that have more of the prey's resources present. Since dragonfly larvae are sit-and-pursue predators and hunt by being in a patch before the prey, we predicted that whether alone or with tadpoles they would favor the high resource patches. We found that dragonfly patch use, when alone, significantly increased with the amount of the prey's resource in the patch (Figure 2). We also found evidence that dragonfly larvae were more likely to stay in a patch when it had more of the prey's resources (Table 2).

However, when tadpoles were present in the arena, dragonfly patch use did not significantly increase with the amount of the prey's resource in the patch, which does not match our predictions. Dragonfly larvae movement was reduced by both the presence of tadpoles in the arena and by the number of tadpoles in their current patch. In their space use decisions, dragonfly larvae are using prey resources and prey cues perhaps in a hierarchical manner, where when no prey cues are detected they are influenced by the distribution of the prey's resource, but when they detect prey they respond to that foraging opportunity by remaining relatively still. If this is true, then perhaps dragonfly space use in the presence of prey would be driven more by the prey's resource if prey density was lower or spatial impediments made them harder to detect. The game theory models make predictions about stable spatial distributions, but current conditions, such as a predator not moving when near a potential meal, might override

stable solutions. We in general need more data on the dynamics of concurrent predator and prey movements.

Predator and prey spatial games have not yet incorporated the effects of predator hunting strategies on predator and prey spatial distributions, but we predicted that when a predator actively hunts prey and uses speed to catch them that the distribution of the prey's resources will have less of an impact on the predator's space use and movement decisions. As predicted, neither salamander patch use (Figure 3) nor movement (Table 3) was significantly affected by the prey's resources either in the presence or absence of tadpoles.

The space game models also predict that when a predator favors or is expected by the prey to favor the prey's higher resource patches that this will lead to a reduction in the prey's preference for their higher resource patches (Flaxman & Lou, 2009; Hugie & Dill, 1994; Luttbeg & Sih, 2004; Sih, 1998). As we just described, dragonflies did not favor patches with more prey resources when prey were in the arena, but despite this tadpoles no longer significantly favored higher resource patches (Figure 1) when dragonflies were in the arena. Also, our analysis of tadpole movement decisions showed strong support for the effect of resource levels ($R = -0.38$) being mostly nullified when dragonflies were in the arena ($D * R = 0.32$, Table 1). Interestingly, there was no support for the number of dragonflies present in a patch affecting tadpole movement; that is, tadpoles did not apparently actively avoid dragonflies. Perhaps the tadpoles either did not detect the presence of a sit-and-pursue dragonfly in their patch or remaining motionless is their response when they detect a dragonfly larvae. This result suggests that we failed to measure (not fine grained enough observations or failed to measure appropriate dragonfly behaviors) the increased predation risk that dragonflies were causing in higher resource patches and this unmeasured difference in risk caused tadpole space use, tadpoles are detecting the presence of dragonfly larvae in the arena and altering their space use in anticipation of higher resource patches being riskier, or both.

Finally, we predicted that since salamander patch use would not be affected by the amount of the prey's resources in a patch that tadpoles would continue to preferentially use their high resource patches when salamanders were present. We found this with the presence of salamanders not causing tadpoles to stop significantly favoring higher resource patches (Figure 1). How much they favored higher resource patches was affected by the presence of salamanders. Our analysis of tadpole movement decisions showed that their preference for higher resources was reduced by the presence of salamanders in the arena ($S * R = 0.27$, Table 1). Tadpoles were also much more likely to leave a patch when more salamanders were present in the patch ($\Delta S = 0.60$, Table 1), which supports the idea that salamander larvae are easily detected by the tadpoles.

We have interpreted our results in terms of differences in predator hunting modes, but because of other differences between the predators more pairs of predators need to be compared. The two predators in our study also differed in their predation rates with the 2 salamander larvae killing approximately 4 times more tadpoles

than the 3 dragonfly larvae. Given that the salamander larvae were a greater danger, it might be expected that they would shape the prey's spatial distribution more, but we found the opposite result, which suggests hunting mode is more important. However, the greater predation rates of salamander larvae could have reduced interference between the prey and thus indirectly affected the spatial distribution of the prey. The two predators also differ in how they consume the prey. The dragonfly larvae tear apart the tadpole prey, while the salamander larvae consume them whole. This likely cause differences in the chemical cues released by predation events and could contribute to the observed space use of the prey and the predators.

The hunting modes of predators have been linked to the size of non-consumptive indirect effects with sit-and-wait and sit-and-pursue predators causing larger effects than active hunters (Preisser et al., 2007; Schmitz, 2008). The explanation has been that predator cues from sit-and-wait and sit-and-pursue predators provide more reliable information than cues from active predators that are more likely to have left the location of the cues. We found that the spatial distributions of a sit-and-pursue predator and an active predator differed and caused differences in spatial distribution of their prey. The landscape of fear concept predicts that a prey's assessed predation risk associated with different locations shapes how they use space and thus alters resource dynamics in those locations (Laundré et al., 2001). Our results showed that sit-and-pursue predators do favor patches with more resources. We saw that this was weakened when the prey was present, but despite this, the prey's preference for higher resource patches was reduced by the presence of the sit-and-pursue predator in the arena. This suggests that sit-and-wait and sit-and-pursue predators might cause a more reliable landscape of fear and thus might contribute to maintaining variation between patches in resource densities by causing prey to not favor more productive patches. In comparison, the active predators were more uniformly distributed, and the prey favored the patches with more resources. This suggests that active predators might have less effect on prey space use and thus in the presence of active predators the prey may be homogenizing resource densities between patches. The landscape of fear from these predators would be more uniform and thus less important for shaping ecological dynamics. More trials are needed to judge the generality and strength of these effects, but our results do suggest that the effect of predator hunting mode on food web dynamics can be a result of predator-prey space games, in addition to informational effects.

ACKNOWLEDGMENTS

We thank Joe Callizo at the Wantrup Wildlife Sanctuary, Shane Waddell and members of the UC Natural Reserve System, Paul Lutes and Erik Hallen at UC CABA, and members of the Sih laboratory for their assistance and discussion. We thank Ella Luttbeg for assistance scoring video data. We thank Jonathan Wright and two reviewers for their help improving the manuscript. This research was funded by a National Science Foundation grant to A. Sih (NSF IBN 0446276), a FORMAS postdoctoral research fellowship to T. Brodin, and a NSF graduate fellowship to J. I. Hammond.

ORCID

Barney Luttbeg  <https://orcid.org/0000-0001-5555-8341>

REFERENCES

- Alonzo, S. H. (2002). State-dependent habitat selection games between predators and prey: The importance of behavioral interactions and expected lifetime fitness. *Evolutionary Ecology Research*, 4, 759–778.
- Alvarez, J. A., Shea, M. A., Wilcox, J. T., Allaback, M. L., Foster, S. M., Pedgett-Flohr, G. E., & Haire, J. L. (2013). Sympatry in California tiger salamander and California red-legged frog breeding habitat within their overlapping range. *California Fish and Game*, 99, 42–48.
- Ball-Damerow, J. E., M'Gonigle, L. K., & Resh, V. H. (2014). Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century. *Biodiversity and Conservation*, 23, 2107–2126. <https://doi.org/10.1007/s10531-014-0707-5>
- Bartoń, K. (2016). *MuMIn: Multi-Model Inference*. R package version 1.15.6.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Beckerman, A. P., Uriarte, M., & Schmitz, O. J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 10735–10738. <https://doi.org/10.1073/pnas.94.20.10735>
- Benke, A. C. (1970). A method for comparing individual growth rates of aquatic insects with special references to the Odonata. *Ecology*, 51, 328–331.
- Brown, J. S., Kotler, B. P., & Bouskila, A. (2001). Ecology of fear: Foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici*, 38, 71–87.
- Burnham, K. P., & Anderson, D. R. (1998). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Caro, T. M. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.
- Corbet, P. S. (1999). *Dragonflies, behavior, and ecology of Odonata*. Ithaca, NY: Cornell University Press.
- Flaxman, S. M., & Lou, Y. (2009). Tracking prey or tracking the prey's resource? Mechanisms of movement and optimal habitat selection by predators. *Journal of Theoretical Biology*, 256, 187–200. <https://doi.org/10.1016/j.jtbi.2008.09.024>
- Godin, J. J., & Keenleyside, M. H. (1984). Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): A test of the ideal free distribution theory. *Animal Behavior*, 32, 120–131. [https://doi.org/10.1016/S0003-3472\(84\)80330-9](https://doi.org/10.1016/S0003-3472(84)80330-9)
- Hammond, J., Luttbeg, B., Brodin, T., & Sih, A. (2012). Spatial scale influences the outcome of the predator-prey space race between tadpoles and predatory dragonflies. *Functional Ecology*, 26, 522–531. <https://doi.org/10.1111/j.1365-2435.2011.01949.x>
- Hammond, J. I., Luttbeg, B., & Sih, A. (2007). Predator and prey space use: Dragonflies and tadpoles in an interactive game. *Ecology*, 88, 1525–1535. <https://doi.org/10.1890/06-1236>
- Hassinger, D. D., Anderson, J. D., & Dalrymple, G. H. (1970). The early life history and ecology of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. *American Midland Naturalist*, 84, 474–495. <https://doi.org/10.2307/2423862>
- Hillborn, R., & Mangel, M. (1997). *The ecological detective*. Princeton, NJ: Princeton University Press.
- Hugie, D. M., & Dill, L. M. (1994). Fish and game: A game theoretical approach to habitat selection by predators and prey. *Journal of Fish Biology*, 45, 151–169.
- Lampert, A., & Hastings, A. (2016). Stability and distribution of predator-prey systems: Local and regional mechanisms and patterns. *Ecology Letters*, 19, 279–288. <https://doi.org/10.1111/ele.12565>
- Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79, 1401–1409. <https://doi.org/10.1139/z01-094>
- Lima, S. L. (1998). Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive and ecological perspectives. *Advances in the Study of Behaviour*, 27, 215–290.
- Lima, S. L. (2002). Putting predators back into behavioral-predator-prey interactions. *Trends in Ecology and Evolution*, 17, 70–75. [https://doi.org/10.1016/S0169-5347\(01\)02393-X](https://doi.org/10.1016/S0169-5347(01)02393-X)
- Luttbeg, B., Hammond, J. I., & Sih, A. (2009). Dragonfly larvae and tadpole frog space use games in varied light conditions. *Behavioral Ecology*, 20, 13–21. <https://doi.org/10.1093/beheco/arn107>
- Luttbeg, B., & Sih, A. (2004). Predator and prey habitat selection games: The effects of how prey balance foraging and predation risk. *Israel Journal of Zoology*, 50, 233–254. <https://doi.org/10.1560/L6QV-UA5T-RDR7-L7QG>
- Luttbeg, B., & Trussell, G. C. (2013). How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. *American Naturalist*, 181, 182–194. <https://doi.org/10.1086/668823>
- Orrock, J. L., Dill, L. M., Sih, A., Grabowski, J. H., Peacor, S. D., Peckarsky, B. L., ... Werner, E. E. (2010). Predator effects in predator-free space: The remote effects of predators on prey. *The Open Ecology Journal*, 3, 22–30. <https://doi.org/10.2174/1874213001003030022>
- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88, 2744–2751. <https://doi.org/10.1890/07-0260.1>
- R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, 45, 218–227. <https://doi.org/10.1111/j.1365-2664.2007.01377.x>
- Rosenheim, J. A. (2004). Top predators constrain the habitat selection games played by intermediate predators and their prey. *Israel Journal of Zoology*, 50, 129–138. <https://doi.org/10.1560/K796-DMB2-546Q-Y4AQ>
- Ryan, M. E., Johnson, J. R., Fitzpatrick, B. M., Lowenstein, L. J., Picco, A. M., & Shaffer, H. B. (2012). Lethal effects of water quality on threatened California salamanders but not on co-occurring hybrid salamanders. *Conservation Biology*, 27, 95–102. <https://doi.org/10.1111/j.1523-1739.2012.01955.x>
- Schmitz, O. J. (2005). Behavior of predators and prey and links with population-level processes. In P. Barbosa, & I. Castellanos (Eds.), *Ecology of predator-prey interactions* (pp. 256–278). Oxford, UK: Oxford University Press.
- Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, 319, 952–954. <https://doi.org/10.1126/science.1152355>
- Schmitz, O. J., Miller, J. R. B., Trainor, A. M., & Abrahms, B. (2017). Toward a community ecology of landscapes: Predicting multiple predator-prey interactions across geographic space. *Ecology*, 98, 2281–2292. <https://doi.org/10.1002/ecy.1916>
- Schoeppner, N. M., & Relyea, R. A. (2005). Damage, digestion, and defence: The roles of alarm cues and kairomones for inducing prey defences. *Ecology Letters*, 8, 505–512. <https://doi.org/10.1111/j.1461-0248.2005.00744.x>
- Schoeppner, N. M., & Relyea, R. A. (2009). Interpreting the smells of predation: How alarm cues and kairomones induce different prey defences. *Functional Ecology*, 23, 1114–1121. <https://doi.org/10.1111/j.1365-2435.2009.01578.x>

- Sih, A. (1982). Optimal patch use: Variations in selective pressure for efficient foraging. *American Naturalist*, 120, 666–685.
- Sih, A. (1984). The behavioral response race between predator and prey. *American Naturalist*, 123, 143–150. <https://doi.org/10.1086/284193>
- Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist*, 139, 1052–1069. <https://doi.org/10.1086/285372>
- Sih, A. (1998). Game theory and predator-prey response races. In L. A. Dugatkin, & H. K. Reeve (Eds.), *Game theory and animal behavior* (pp. 221–238). Oxford, UK: Oxford University Press.
- Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. In P. Barbosa, & I. Castellanos (Eds.), *Ecology of predator-prey interactions* (pp. 240–255). Oxford, UK: Oxford University Press.
- Sih, A., Kats, L. B., & Moore, R. D. (1992). Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology*, 73, 1418–1430. <https://doi.org/10.2307/1940687>

How to cite this article: Luttbeg B, Hammond JI, Brodin T, Sih A. Predator hunting modes and predator-prey space games. *Ethology*. 2020;126:476–485. <https://doi.org/10.1111/eth.12998>