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Meta-analysis of foraging and predation risk trade-offs in terrestrial systems

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Abstract Although there is ample evidence for the generality of foraging and predation trade-offs in aquatic systems, its application to terrestrial systems is less comprehensive. In this review, meta-analysis was used to analyze experiments on giving-up-densities in terrestrial systems to evaluate the overall magnitude of predation risk on foraging behavior and experimental conditions mediating its effect. Results indicate a large and significant decrease in foraging effort as a consequence of increased predation risk. Whether experiments were conducted under natural or artificial conditions produced no change in the overall effect predation had on foraging. Odor and live predators as a correlate of predation risk had weaker and nonsignificant effects compared to habitat characteristics. The meta-analysis suggests that the effect of predation risk on foraging behavior in terrestrial systems is strongly dependent on the type of predation risk being utilized.

Keywords Giving-up densities · Predation · Predation risk · Foraging · Optimal foraging · Trade-offs · Meta-analysis

Introduction

Predation is argued to be a strong selective force shaping the foraging strategies, social behavior, and life histories of most organisms. With respect to foraging behavior, the decision-making system employed by individuals under predation risk is frequently described as a trade-off between acquiring food and avoiding predation (Abrams 1992; McNamara and Houston 1987; Sih 1980). Searching

for and finding food may increase the probability of detection by predators, cause the prey to forage in areas of higher predation risk, or reduce the likelihood that the prey will detect the predator when it attacks. Therefore, animals face a behavioral conflict: increase their exposure to predators or forego foraging opportunities. To resolve this dilemma, animals must assess predation risk and evaluate foraging needs concurrently, balancing the two to maximize fitness. Although studies of individual systems have demonstrated that the relationship between foraging and predator avoidance is an adaptive behavioral trade-off, there has not been a quantitative evaluation of the generality of this relationship in terrestrial systems.

Several models have been developed to predict how short-term foraging behavior is influenced by predation risk (e.g., Lima 1998). Most models assume that prey prefer to minimize predator exposure and encounter rate among choices that keep food availability constant (e.g., Abrams 1993; Lima and Dill 1990). When food availability varies, foragers may adjust their choices to reflect both foraging success and predation risk.

Unless foragers are strongly food-deprived (see Bateson 2002), a general theoretical outcome of trade-off models is that “risky” foraging behavior will vary inversely with increased predation risk and general food availability (Abrams 1993).

Risky foraging behaviors that affect trade-offs between food acquisition and predation risk are very diverse and can affect an animal’s decision on what to eat, how long to feed, where to forage, time allocation through vigilance, and group size and spacing behavior (Janson 1990). Aspects of these predictions have been empirically supported in aquatic systems, insects, and some birds (see Brown and Kotler 2004; Dill 1987; Gilliam and Fraser 1987; Lima and Dill 1990; Millinski 1986; Sih 1987 for reviews). By far, the best studied experimentally among these topics has been how long to feed in patches of differing predation risk.

Charnov’s (1976) marginal value theorem models feeding rates within a patch, and predicts that a forager will discontinue harvesting from a patch when the energetic

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return rate no longer exceeds foraging costs. Brown (1988, 1992) extended the patch use model to incorporate predation risk and alternative activities to foraging. Several predictions follow from his model. First, if two or more equivalent patches have no predation risk, the forager in a nondepleting environment should obey the predictions of the original marginal value theorem. Second, if the predation risk in two patches is the same, then both patches should be abandoned at the same harvest rate. Third, if missed opportunity costs, the energetic costs of foraging, and the energy yield and harvest rate as a function of food density are equivalent between two patches, then variations in the abandonment of patches would reflect differences in predation risk.

Because measuring energy return rates of foragers is both difficult and time-intensive, Brown (1988) recommends the use of a correlate of energy return rate, namely, the giving-up-density (GUD), which is the resource density remaining after an animal has utilized a given patch. The model predicts that foragers should have higher GUDs in higher-risk than in lower-risk patches, reflecting efforts to reduce predation risk by limiting the amount of time in a risky patch. However, a forager's decision to enter a risky patch, and when to leave, may be influenced by its initial state, i.e., current energy reserves (Brown 1988; McNamara and Houston 1987). If two patches differ in both available energy and predation risk (e.g., safer but less energetically profitable or riskier but more energetically profitable) then, if the imperative is to avoid immediate starvation, foragers should be risk-reckless in high reward patches. This prediction is concordant with Sih's (1980, 1982) prediction that as the risk of starvation increases, animals will select more hazardous foraging sites and/or engage in riskier behavior. While GUDs can be an indication of habitat selection, they have also commonly been used to study foraging-predation trade-offs, particularly in rodents, and they offer a quantitative measure of predation-sensitive foraging. The widespread use of GUDs has led to a general agreement that organisms will forgo certain foraging opportunities as predation risk increases. What remains unclear is how strong and widespread these effects are across taxa and whether there are any experimental design features that influence the results.

The objective of this article is to assess the generality of foraging-predation trade-offs in terrestrial systems using meta-analysis to evaluate studies that apply GUDs as a measure of foraging energy return under variable predation risk. A rigorous quantitative analysis can be less sensitive to certain aspects than traditional methods of vote counting or other qualitative syntheses (e.g., age differences, sex differences, and seasonal effects). This is usually due to insufficient number of studies that consistently incorporate or account for particular details. However, qualitative reviews can be misleading and inaccurate by failing to highlight more general differences. As such, meta-analysis may be a more objective and statistically appropriate method to synthesizing the literature (Gurevitch et al. 1992; Gurevitch and Hedges 1999).

I used meta-analysis to address the following specific questions: What is the general pattern and extent of foraging-predation trade-offs in terrestrial systems? Do the effects vary under artificial or natural conditions? Are the effects dependent on the type of predation risk manipulated?

Materials and methods

Data collection

A search of the literature for studies evaluating GUDs under varying levels of predation risk was conducted. The following databases were searched: BasicBIOSIS, Biological and Agricultural Index, BioOne, Biological Abstracts, ScienceDirect, and Web of Science. Search terms included "foraging and predation", "foraging and predation risk", "risk sensitive foraging", "GUDs", "foraging and predation trade-offs", "giving-up-densities", and "giving-up densities and predation risk". Articles were initially screened for the presence of a GUD component. Individual studies were then screened to meet the following criteria. First, the study manipulated predation risk directly (e.g., predator and predator exclusion) or indirectly (e.g., open microhabitat and "bush" microhabitat). Second, the study had an appropriate control. For the purposes of this meta-analysis, the control was designated as the treatment with no predation risk (e.g., predator exclusion) or the treatment considered to be low predation risk for the study system. Third, measures of variance, means, and sample sizes were reported or could be readily obtained from the publication. For the purposes of this analysis, experiment sample size was used, rather than sample sizes of individuals. Fourth, studies that combined two measures of predation risk or other variable without presenting separate results were excluded (e.g., season and predation risk type, illumination, and other predation risk type). Lastly, separate experiments of multiple species reported in a single publication were considered independent.

Statistical analyses

The conventional Hedges's d_+ was used as the metric of standardized effect size. Hedges's d_+ provides a measure of the overall magnitude of the treatment effect, while correcting for small sample size biases (Gurevitch and Hedges 1993; Hedges and Olkin 1985). All statistical analyses used the mixed model approach, given its more realistic assumptions that a given class of studies may share a common effect and that random variation among studies exists (Gurevitch and Hedges 1993). The conventional interpretation of the magnitude of the effect was used, whereby effect sizes of 0.2 were "small", 0.5 were "medium", 0.8 were "large", and any effect greater than 1.0 standard deviations was considered to be "very large" (Cohen 1969; Gurevitch and Hedges 1993). The effect was determined to be statistically significant if the confidence intervals of the effect size excluded zero.

In addition to using (d_+) as a measure of effect size, the analysis was performed using response-ratios (RR). By incorporating two sources of variation, variation among replicates within an experiment and variation among experiments, the mean effect size of log response ratios weigh more heavily than the contribution of within experiment results that have a smaller variance. Consequently, the width of the confidence intervals can be affected allowing a different significance level to be assessed. Hedges et al. (1999) recommends that $\sqrt{n_c}\bar{X}_c/SD_c$ (denoting sample size, mean, and standard error, respectively) or $\sqrt{n_e}\bar{X}_e/SD_e$, whichever is smaller, to be <3.0 to minimize the bias of using $\ln(RR)$. This criterion was met by the data set (over 98% of $\sqrt{n_c}\bar{X}_c/SD_c$ and over 94% of $\sqrt{n_e}\bar{X}_e/SD_e$ were <3.0) making it appropriate to analyze the data using response ratios. Mean RRs reported in Table 1 are geometric (back-transformed) means. MetaWin statistical software (Rosenberg et al. 1999) was used to perform all analyses.

Results

The survey resulted in 31 publications suitable for the meta-analysis, comprising 62 experiments (see Table 1). In most cases, duplication was the result of measurements made on multiple species during the course of the experiment. The majority of experiments were conducted in the field under natural conditions. There was a bias in the published literature towards experiments centered on rodents (over 75%). Overall, increasing predation risk had a very large negative effect on the amount of food consumed, resulting in higher GUDs [$(d_+ \pm CI) -0.99 \pm 0.34$, $df=61$]. The effect size for all studies was heterogeneous based on the significant value of the Q statistic, which tests for homogeneity of the effect size across all studies. The heterogeneity suggested that the data could be partitioned into different classes, such as the location of the experiment (e.g., field vs enclosure) and the type of predation risk being manipulated (e.g., predator, odor, habitat), both of which were reported for each study. As a homogeneity statistic, Q is also a measure of the extent to which the results of all of the studies are in agreement. Therefore, it is possible to partition the effect size into within and between group components (Gurevitch and Hedges 1993; Gurevitch et al. 2000).

The data were subdivided into experiments conducted under field conditions ($n=50$) and those performed in laboratories or in enclosures ($n=12$). While there was heterogeneity within each category, the effect increasing predation risk had on foraging did not differ significantly between these groups ($Q_B=0.68$, $df=1$, $p<0.41$). The average effect was very large for both groups of studies (Fig. 1).

Experiments that used real predators, odor, or habitat characteristics as a surrogate for predation risk did not differ significantly from one another ($Q_B=4.15$, $df=2$, $p<0.13$). While there was heterogeneity within groups ($Q_W=287.18$, $df=19$, $p<0.001$), increased predation risk as a result of

habitat structure had a very large negative effect on foraging [$(d_+ \pm CI) -1.21 \pm 0.48$, $df=39$], odor had small negative effect that was not significant (CI's overlap 0; [$(d_+ \pm CI) -0.22 \pm 0.92$, $df=11$], and the effect of a live predator was not significantly different than zero (CI's overlap 0; [$(d_+ \pm CI) -1.12 \pm 1.16$, $df=9$; Fig. 2]. Analysis with $\ln(RR)$ produced very similar results.

Discussion

The results of the meta-analysis indicate that experimental manipulation of predation risk produced large and significant changes in foraging behavior. By partitioning the data into additional categories, two things became evident. First, the outcome of the experiments did not appear to be significantly impacted by whether the study was conducted under natural conditions or artificial conditions. While there was no significant difference, it appeared as though the mean effect size was larger for experiments conducted in enclosures, whether the data were analyzed as effect size or log response ratios. This result may address concerns in future investigations regarding the validity of experiments conducted under artificial conditions.

The second, and arguably more interesting, outcome was the comparison among different types of predation risk manipulated. The mean effect size (d_+) due to habitat was significant, but overall there was no significant variation among types of predation risk. Unexpectedly, none of the analyses showed a difference among habitat, odor, and actual predators. It is surprising that the presence of actual predators did not appear to have a significant effect compared to less direct indicators of predation risk. While habitat was the only type of predation risk measure that had a significant effect, it may not be prudent to ascribe too much importance to this result, as it may be a consequence of the smaller sample sizes for odor and actual predators. The results do suggest, however, that prey responses are more consistent, if not larger, due to habitat structure. It is possible that habitat cues may significantly increase an animal's perceived predation risk, thus having a greater effect on overall foraging behavior. For a given forager, predation risk may not be a function of the density or presence of a predator, but rather a function of the habitat in which the predator is likely to be found (Boinski et al. 2003). In many instances, a particular type of predator can occur in variable habitats depending on the location, leading to an inability of prey to utilize direct predator information as a reliable indicator of risk. If an individual forager lacks detailed information regarding the density of predators and the probability of an encounter, then assessing predation risk via habitat structure would be more dependable from the forager's perspective. By using habitat structure as a measure of predation risk, foragers may be attempting to increase the probability of successful escape from an attack, rather than attempting to avoid an attack altogether. As a result, actual predator presence or density may be largely irrelevant to foraging decisions. Alternatively, it is possible that significant habitat and

Table 1 Source data for the analysis, location, type of predation risk manipulated, and effect sizes

Publication	Species	Location	Type of risk	d_+	RR
Altendorf et al. 2001	<i>Odocoileus hemionus</i>	Field	Habitat	-0.24	0.89
Arthur et al. 2004	<i>Mus musculus domesticus</i>	Enclosure	Habitat	-1.31	0.78
Bouskila 1995	<i>Dipodomys deserti</i>	Field	Odor	-0.03	1.00
Bouskila 1995	<i>Dipodomys deserti</i>	Field	Predator	-0.28	0.96
Bowers 1988	<i>Dipodomys merriami</i>	Field	Habitat	-1.37	0.51
Brown 1988	<i>Dipodomys merriami</i>	Field	Habitat	0.47	1.17
Brown 1988	<i>Spermophilus tereticaudus</i>	Field	Habitat	-1.27	0.71
Brown 1988	<i>Ammospermophilus harrisi</i>	Field	Habitat	-1.27	0.70
Brown 1988	<i>Perognathus amplus</i>	Field	Habitat	-0.25	0.94
Brown et al. 1997	<i>Gerbillus allenbyi</i>	Field	Habitat	-8.57	0.96
Brown et al. 1997	<i>Galerida cristata</i>	Field	Habitat	9.37	1.31
Brown et al. 1998	<i>Petromyscus collinus</i>	Field	Habitat	-6.34	0.78
Epple et al. 1993	<i>Aplodontia rufa</i>	Enclosure	Odor	-3.84	0.78
Gutman and Dayan 2005	<i>Acomys cahirinus</i>	Enclosure	Habitat	-0.58	0.55
Gutman and Dayan 2005	<i>Acomys russatus</i>	Enclosure	Habitat	-6.19	0.73
Hernández et al. 2005	<i>Odocoileus hemionus</i>	Field	Habitat	-4.82	0.53
Hernández et al. 2005	<i>Odocoileus hemionus</i>	Field	Habitat	-1.12	0.86
Hernández et al. 2005	<i>Odocoileus hemionus</i>	Field	Habitat	-0.40	0.94
Holtcamp et al. 1997	<i>Peromyscus maniculatus</i>	Field	Habitat	0.74	1.43
Jacob and Brown 2000	<i>Microtus arvalis</i>	Field	Habitat	-2.98	0.57
Jones and Dayan 2000	<i>Acomys cahirinus</i>	Field	Odor	0.24	1.02
Jones and Dayan 2000	<i>Acomys russatus</i>	Field	Odor	-18.57	0.71
Kotler 1997	<i>Gerbillus allenbyi</i>	Field	Predator	-25.06	0.57
Kotler 1997	<i>Gerbillus pyramidum</i>	Field	Predator	-3.01	0.09
Kotler et al. 1993	<i>Gerbillus allenbyi</i>	Enclosure	Habitat	0.94	1.04
Kotler et al. 1993	<i>Gerbillus pyramidum</i>	Enclosure	Habitat	-0.02	0.99
Kotler et al. 1999	<i>Sciurus niger</i>	Field	Habitat	-0.10	0.98
Kotler et al. 1999	<i>Procavia capensis</i>	Field	Habitat	1.28	1.40
Kotler et al. 2001	<i>Gerbillus pyramidum</i>	Enclosure	Predator	-0.24	0.89
Kotler et al. 2001	<i>Gerbillus allenbyi</i>	Enclosure	Predator	-0.97	0.56
Kotler et al. 2001	<i>Gerbillus dasyurus</i>	Enclosure	Predator	-2.13	0.80
Kotler et al. 2004	<i>Gerbillus allenbyi</i>	Enclosure	Habitat	-4.99	0.38
Mohr et al. 2003	<i>Mastomys natalensis</i>	Field	Habitat	0.53	1.11
Newman et al. 1988	<i>Sciurus carolinensis</i>	Field	Habitat	-0.16	0.76
Newman et al. 1988	<i>Sciurus carolinensis</i>	Field	Habitat	-0.82	0.77
Newman et al. 1988	<i>Sciurus carolinensis</i>	Field	Habitat	-1.38	0.79
Newman et al. 1988	<i>Sciurus carolinensis</i>	Field	Habitat	-0.17	0.97
Orrock and Danielson 2004	<i>Peromyscus polionotus</i>	Field	Habitat	1.15	1.10
Orrock and Danielson 2004	<i>Peromyscus polionotus</i>	Field	Odor	-0.25	0.84
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Habitat	0.36	2.83
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Habitat	-7.00	0.85
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Odor	-0.47	0.96
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Odor	-0.07	0.99
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Odor	-0.20	0.98
Orrock et al. 2004	<i>Peromyscus polionotus</i>	Field	Odor	-0.10	0.99
Oyugi and Brown 2003	<i>Turdus migratorius</i> and <i>Sturnus vulgaris</i>	Field	Habitat	-0.11	0.99
Powell and Banks 2004	<i>Mus domesticus</i>	Field	Habitat	-0.86	0.81
Pusenius and Schmidt 2002	<i>Microtus pennsylvanicus</i>	Field	Habitat	-6.52	0.39
Stokes et al. 2004	<i>Antechinus flavipes</i>	Field	Habitat	-1.28	0.52
Stokes et al. 2004	<i>Sminthopsis murins</i>	Field	Habitat	-2.62	0.68
Sullivan and Crump 1984	<i>Dipodmys spp.</i>	Field	Habitat	-3.14	0.51
Sullivan and Crump 1984	<i>Dipodmys spp.</i>	Field	Habitat	-0.13	1.00
Sullivan and Crump 1984	<i>Dipodmys spp.</i>	Field	Habitat	-1.72	0.96
Sundell et al. 2004	<i>Clethrionomys glareolus</i>	Enclosure	Predator	0.58	1.02

Table 1 (continued)

Publication	Species	Location	Type of risk	d_+	RR
Thorson et. al. 1998	<i>Sciurus niger</i>	Field	Odor	-0.06	0.98
Thorson et. al. 1998	<i>Spermophilus tridecemlineatus</i>	Field	Odor	-0.35	0.80
Yunger et al. 2002	<i>Octodon degus</i>	Field	Predator	-0.27	0.80
Yunger et al. 2002	<i>Akodon olivaceus</i>	Field	Predator	-2.37	0.89
Yunger et al. 2002	<i>Phyllotis darwini</i>	Field	Predator	6.65	1.86
Yunger et al. 2002	<i>Octodon degus</i>	Field	Habitat	-1.60	0.95
Yunger et al. 2002	<i>Akodon olivaceus</i>	Field	Habitat	-8.11	0.70
Yunger et al. 2002	<i>Phyllotis darwini</i>	Field	Habitat	0.94	1.10

predator interactions may exist and is not accounted for in this meta-analysis.

While increased predation risk due to habitat characteristics had large effects on foraging, variability among studies using habitat as an indication of predation risk was present. For many species, foraging in protective cover considerably reduces their risk of predation (birds: Caraco et al. 1980; rodents: Rohner and Krebs 1996). In general, experiments used in this analysis defined low risk habitat by the presence of cover, while the absence of cover was indicative of higher predation risk. However, for some species, the open may be considered the low predation risk habitat (e.g., crested larks, Brown et al. 1997). In addition, the presence of multiple predators can affect habitat choice. For example, kangaroo rats may assess cover as a “safer” habitat when under predation pressure from owls, but “riskier” when under predation from snakes (Bouskila 1995). Other factors, including illumination and seasonal effects (e.g., Brown 1989 and Brown et al. 1994) may interact significantly with foraging and mediate the impact of predation risk. Unfortunately, the current meta-analysis does not facilitate incorporating the interaction of multiple

predators or the combination of predation risk and other factors.

Although the results provide evidence for large foraging and predation risk trade-offs, approximately 20% of the studies yielded results contrary to those predicted under GUD theory. While the factors mentioned above should be considered, and are implicated in a few studies, there are additional considerations.

Classic foraging theory predicts that animals will maximize fitness by exploiting resources that yield the highest long-term energy gain rate (Houston et al. 1993; Stephens and Krebs 1988). Two significant assumptions underlying this theory are that no other factors influence foraging strategies and that handling times of individual items are fixed (Charnov 1976; Stephens and Krebs 1988). Sih (1980, 1982, 1992) highlights the inadequacy of optimal foraging models that do not account for the minimization of predation risk. Two ways in which real animals may violate these assumptions are (1) changes in diet selectivity and (2) changes in the handling time of individual food items.

Several studies have established that animals may compromise their foraging behavior by simply altering their diet choices and not reducing their intake (Engelhart and Muller-Schwarze 1995; Epple et al. 1993; Pfister et al. 1990; Sullivan and Crump 1984). Because optimal foraging theory predicts that animals rank food choices in

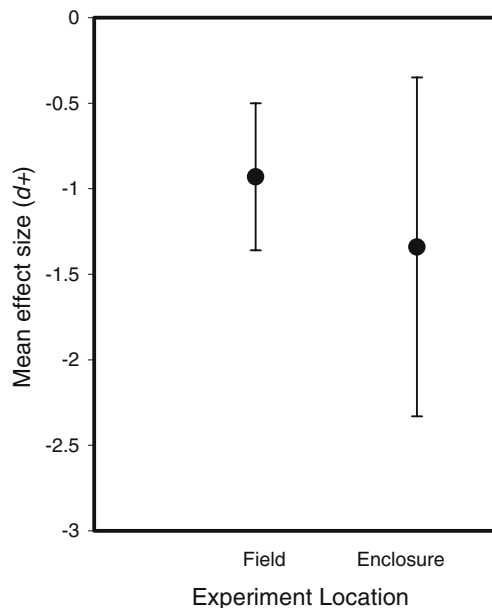


Fig. 1 Comparison of the average effect size, d_+ , (with 95% confidence intervals) in the field and in enclosures

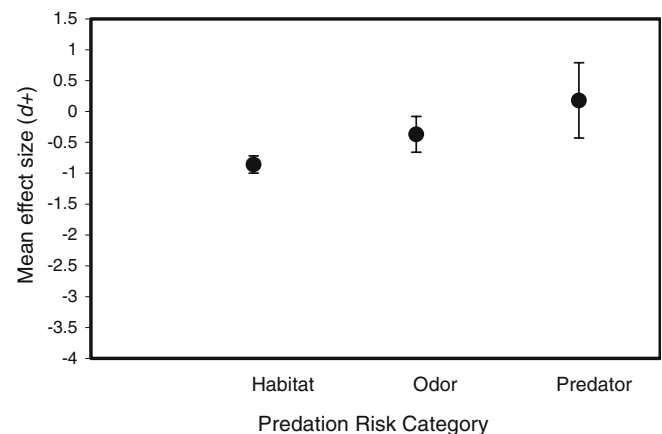


Fig. 2 Comparison of the average effect size, d_+ , (with 95% confidence intervals) categorized by habitat, odor, and predator presence

terms of energetic return, changes in diet selectivity may generate changes in the energy gain curve characteristics, subsequently affecting GUDs (e.g., Bowers 1988; Hay and Fuller 1981; see also Lima and Valone 1986). There is also sufficient evidence that the assumption of fixed handling times per item does not hold. The overall pattern suggests that animals will reduce their handling times under higher predation risk (Holtcamp et al. 1997; Lima 1985; Newman et al. 1988; Valone and Lima 1987). Diminished handling times per item may change the energy yield curve per patch, and in turn, the resulting GUDs may be compressed. Thus, both diet selection and handling times may have complex effects on gain rate characteristics that are not considered in GUD theory.

At present, GUD theory is widely used as a model for quantifying foraging-predations risk trade-offs in a suite of species. However, some assumptions may be violated in studies using GUDs as a quantitative measure of fitness costs, perhaps leading to results inconsistent with theoretical predictions. Price and Correll (2001) tested two of the assumptions associated with the GUD method in kangaroo rats. First, the authors tested the assumption of smooth decelerating gain functions and constant quitting harvest rates. The authors report that gain functions, while generally decelerating, contained nonlinearities, particularly early in the harvest period. While it is anticipated that trade-offs will be made in the decelerating portion of the harvest, their results could have consequences for interpreting quitting harvest rates. For instance, if systematic foraging leads to linear harvest rates until a patch is close to being depleted, then many different predation risk levels will produce the same quitting harvest time and hence, equivalent GUDs. Second, Price and Correll (2001) report that attainment of stable quitting harvest rates was not achieved until the third or subsequent visit to a patch. Thus, observed GUDs might be sensitive to population density and the time available for foraging. In particular, at low forager densities (or strongly restricted activity periods), quitting seed densities may not reflect true GUDs. Both of these assumptions need to be tested more broadly, particularly in instances where the outcome of experiments is inconsistent with a priori predictions of GUD theory.

How important is predation risk to modifying the foraging effort of terrestrial systems? This analysis suggests that studies using GUDs in terrestrial systems demonstrate a significant and large trade-off between foraging effort and predation risk. Habitat structure stands out as a significant and consistent indicator of predation risk to prey. Future experiments may wish to assess what features of habitat are influencing the perceived risk by prey and more stringently test the ability of prey to assess predator density and presence. To gain a more complete understanding, additional experiments that manipulate the state of the forager and predation risk (but see Kotler 1997; Kotler et al. 2004) and account for confounding variables such as handling times, food selection, and seasonal effects are needed. Such studies will contribute valuable quanti-

tative data, leading to a better understanding of how organisms cope with predation pressure. Overall, GUDs provide a solid quantitative tool for detecting and quantifying foraging and predation risk trade-offs.

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