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REVIEW

A practical guide to avoid giving up on giving-up densities

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Abstract The giving-up density (GUD) framework provides a powerful experimental approach with a strong theoretical underpinning to quantify foraging outcomes in heterogeneous landscapes. Since its inception, the GUD approach has been applied successfully to a vast range of foraging species and foraging scenarios. However, its application is not simple, as anyone who has tried to use it for the first time might attest. Limitations of the technique were noted at its conception, yet only the artificiality of the patches, the appropriateness of the food resource, and the possibility of multiple visiting foragers were identified. Here we show the current uses of GUD and outline the practical benefits as well as the often overlooked limitations of the technique. We define seven major points that need to be addressed when applying this methodology: (1) the curvilinearity between harvest rate and energy, (2) the energetic state of the forager, (3) the effect of group foraging, (4) food quality and substrate properties, (5) the predictability of the patch, (6) behavioral traits of the forager, and (7) nontarget species. We also suggest how GUD experiments can be enhanced by incorporating complementary methods (such as cameras) to better understand the foraging processes involved in the GUD itself. We conclude that the benefits of using GUD outweigh the costs, but that its limitations should not be ignored. Incorporating new methods when using GUD can potentially offer novel and important insights into the study of foraging behavior.

Keywords Foraging · Giving-up density · Landscape of fear · Methodological limitations · Practical assumptions · Supplementary approaches

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Introduction

By the time Ernst Haeckel (1873) proposed “Ökologie” as the name of a new, emerging branch of science—modern ecology—foraging was already an established and widely used term that described the process of looking for food, defining where and what an animal chooses to eat. However, the idea of foraging as a mechanism for maximizing fitness was not proposed until the 1960s (Emlen 1966; MacArthur and Pianka 1966). This was followed by the development of optimal foraging theory (OFT), and a myriad of mathematical models have since been constructed to help understand this theory (Stephens and Krebs 1986; Stephens et al. 2007). Early models describing how OFT worked were mostly theoretical (Charnov 1976; Pyke et al. 1977), although some approached foraging from a more practical, yet qualitative perspective (Hay and Fuller 1981). In 1988, Joel S. Brown described an elegant experimental and mathematical approach to quantitatively measure an animal's foraging decisions in the wild based on patch characteristics, using giving-up density (GUD). The GUD framework is underpinned by an extension of the marginal value theorem (Charnov 1976), relying on the existence of food patches as a depletable food source that foragers exploit differentially in order to maximize fitness. Therefore, the amount of food that foragers leave in a patch (i.e., the GUD) reflects the perceived cost of foraging at that patch, such that a lower GUD indicates a lower net cost.

According to this framework, in a depletable patch where harvest rate (H) decreases as more food is consumed over time, the forager should quit the patch when the benefits of harvesting no longer outweigh the costs. This framework incorporates costs associated with predation risk (P), searching and processing (i.e., handling and digesting) resources from that patch as well as thermoregulatory costs (C) and missed opportunities elsewhere (MOC). The concept (Brown 1988) is expressed as:

$$H = C + P + MOC$$

Subsequent authors have made modifications to the initial model, for example, by adding a term that represents the intensity of interference behavior (*I*) experienced by individuals of a given species, in order to explain habitat partitioning (Kotler and Brown 1988),

$$H = C(I) + P + MOC$$

the cost of toxin compounds present in the food (*T*) (Schmidt 2000),

$$H = C + P + MOC + T$$

the benefits of water (*W*) near the patch for desert animals (Shrader et al. 2008b),

$$H = C + P + T(W) + MOC$$

the risk of injury (*RI*) during foraging at the patch (Berger-Tal et al. 2009),

$$H = C + RI + P + MOC$$

and the foraging benefits of information (*FBI*) (Olsson and Brown 2010),

$$H = C + P + FBI + MOC.$$

In a practical sense, most researchers have explored parameters in this framework by building surrogate patches in which food is mixed through an inedible matrix, imposing an ever increasing search cost as food is consumed. As a result, the amount of food left by a forager at one of these surrogate feeders reflects the composite costs associated with the characteristics of the food and the area surrounding the feeder. Some notable exceptions from the use of artificial feeding patches have been the use of the bite diameter at point of wild forage by snowshoe hares (*Lepus americanus*) (Morris 2005), and the ripe fruit left unpicked in a tree by blue (*Cercopithecus mitis*) and red-tailed (*Cercopithecus ascanius*) monkeys (Houle et al. 2006). In these cases, the measured GUD is equally considered to reflect the costs associated with the patch.

Although the framework was originally developed to investigate perceived predation risk while foraging (Brown 1988; Brown et al. 1988; Kotler and Brown 1988), it has since become widely used as a methodological tool to explore other components of foraging behavior. Several previous studies have considered the theoretical strengths and weaknesses of the foraging theory and the GUD framework (Nonacs 2001; Price and Correll 2001; Olsson 2006). Here, we take a more practical approach.

We briefly summarize the literature that has employed the GUD framework in its methodology. Then, we discuss many of the most critical practical considerations for researchers using the GUD framework as part of their experimental design. Our goal in highlighting these issues is to enable future researchers to foresee these potential problems and incorporate suitable protocols to address them. By doing so, we hope to help speed up the development phase of GUD trial methods and prevent ambiguity in the interpretation of results. Addressing these issues should also open opportunities for addressing interesting new questions using the GUD approach. We finish by offering possible approaches that can be helpful in tackling these limitations.

How, and how widely, has the GUD methodology been used?

In order to characterize how the GUD technique has been used, we examined all research papers listed in Google Scholar and published up to February 2013 (inclusive) that cited Joel S. Brown's 1988 original paper introducing the GUD framework. Of the 683 papers citing this work, 28 % (192) used the GUD methodology. Of these 192, 80 % (154) are not authored by Brown, indicating that the method has been widely adopted.

Measuring perceived predation risk remains the focus of most research using the GUD framework (approximately 50 % of GUD papers published to date) (Table 1). Other authors have used GUDs to explore topics affecting harvesting costs (*C*) and missed opportunity costs (*MOC*), ranging from the effect of physiological constraints such as thermoregulation (Bozinovic and Vásquez 1999; Kilpatrick 2003; Orrock and Danielson 2009), immunochallenge (Schwanz et al. 2011, 2012), food secondary compounds (Schmidt et al. 1998; Kirmani et al. 2010; McArthur et al. 2012), and parasite loads (Raveh et al. 2011), to the consequence of interspecific and intraspecific competition (Brown et al. 1997; Abramsky et al. 2001; Ovadia and Zu 2003) and use of information (van Gils et al. 2003; Stenberg and Persson 2005; Amano et al. 2006; Vásquez et al. 2006) and the risk of injury (Berger-Tal et al. 2009) while foraging (Table 1). The typically brief description of the GUD method in these research papers suggests that its application is simple. In practice, it is often not as simple as it appears.

Challenges and opportunities of the GUD framework

Each of the authors of this paper has considered giving up on the GUD technique due to difficulties in

Table 1 Distribution of uses or focal costs of the giving-up density framework among the literature to date

Costs	Term	Number of publications
Predation risk	*P*	108
Foraging cost	*C*	46
Missed opportunity cost	*MOC*	31
Harvest rate	*H*	21
Food toxin cost	*T*	5
Water effect	*W*	1
Foraging benefit of information	*FBI*	1
Risk of injury	*RI*	1
Interference cost	*I*	1
Total publications that use GUD		192[a]

[a] The total number of publications that have used GUD in their methodology appears lower due to some publications encompassing more than one term of the GUD equations

resolving a range of challenges; yet, we decided to persevere and conquer the obstacles, rather than ignoring them and risk compromising the quality of our research. These challenges arise from vital practical issues that take time and ingenuity to solve, but that are essential for correctly interpreting results obtained through this deceptively simple experimental approach. The GUD framework is underpinned by a suite of assumptions which, if met, allow the researcher to measure the final GUD and interpret it as a representation of the study animal's decision-making process while foraging. However, the GUD model allows for multiple inputs into fitness, and there may be many forms of foraging costs; thus, it is not always easy to track what costs are changing. As such, it is vitally important that researchers are explicit about how they approach these challenges and assumptions in their experiments.

It is part of our own initiative to keep track of and share our experience with the challenges and the best practice solutions that arose during our own experiments using GUDs. A current gap in the GUD literature is the recognition of these issues and the suggestion of solutions or approaches for dealing with these aspects of the framework. Brown (1988) himself recognized some of the potential limitations of his approach, namely "(i) the patches are not natural, (ii) the resource may not be appropriate, (iii) the foragers may become satiated, and (iv) the trays may be visited by more than one forager". We believe that there are in fact seven important issues that are rarely articulated by researchers in their methods, yet are key to clarity in the interpretation of a GUD. These are (1) the curvilinearity between harvest rate and energy, (2) the energetic state of the forager, (3) the effects of group foraging, (4) food quality and substrate properties, (5) the predictability of the patch, (6) behavioral traits of the forager, and (7) nontarget species.

Harvest rate and energy gain have a curvilinear relationship

As Brown (1988) originally stated, the patches created for GUD experiments are commonly not natural, and as such, the process of harvesting by the forager has particular characteristics that need to be accounted for. Theoretically, the energy that a forager spends searching in one of these patches increases exponentially with every food item harvested, due to the dependence of harvest rate on the ratio between inedible matrix and food (Fig. 1). As a result, it is expected that at the beginning of a harvesting bout, the energy spent searching is relatively low and increases "slowly" until it reaches an area of "rapid increase," when the food items become scarcer within the matrix. Fine changes in the perceived cost of foraging by the individual can only be perceived during the "fast" phase, making it very difficult, yet nevertheless critical, to create patches with a ratio of inedible matrix to food that would ensure this sensitivity (Fig. 1).

However, the harvest rate (*H*) does not behave in the same way as the relative energy gained (Fig. 2). The relative energy gained by a forager per food item decreases while harvesting the patch. This can be driven by harvesting features such as different efforts required to obtain different food items (e.g., those close to the surface vs. those buried deeply) (Olsson et al. 2001a). As easily harvested food items are removed, only the items that are harder to find remain. Moreover, although the total energy gained while foraging increases, the value that each new food item represents, given the food already consumed, decreases exponentially (Fig. 2). This phenomenon is due to the change in energetic state of the forager as it harvests food. As the individual consumes food, the next food item becomes less crucial in imparting fitness to the consumer. Although this is one of the theoretical foundations of the methodology—since the cost of staying at the patch and continue harvesting should be ever increasing—it also means that there is an intimate link between the specific nutritional

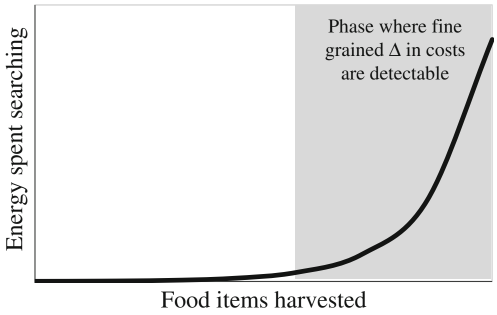

Fig. 1 Conceptual graph showing the dependency between the energy a forager spends searching and the energy gained through the harvesting process in a typical giving-up density framework. The energy spent searching increases exponentially with every food item that it is harvested due to the decrease in food to inedible matrix ratio. The phase where fine changes in the perceived cost of foraging are measurable is shown in the *shaded area*

Fig. 2 Conceptual graph showing the relative energy gained by a forager, per food item, while harvesting. Each new food item harvested is of comparatively less value than the previous one

requirements of the forager exploiting the patch and the GUD. However, in some cases, animals may not change energetic state considerably while exploiting a patch, for example, animals that cache food such as gray squirrels (*Sciurus carolinensis*) (Schmidt and Ostfeld 2008), where the value of the food is of future value, minimizing and even eliminating changes in their energetic state while foraging.

In cases where the energetic state of the forager does change considerably, diminishing returns may be less important since while H may not vary, associated costs such as $C + P + MOC$ can increase, resulting in GUDs that are still meaningful. However, the change in relative energy gained during foraging by one individual (and between individuals, see below) can bias the measured GUD towards those individuals whose state drives them to exploit the patch most thoroughly. This can influence our interpretation of the data, especially in nonmanipulative experiments when comparisons between populations are being made.

Forager state will affect giving-up density

Forager state affects the relative benefits obtained from food items. A classic example is the state-dependent energetic benefits obtained from a meal in vampire bats (*Desmodus rotundus*) (Wilkinson 1984). Wilkinson (1984) found that individual vampire bats that were successful in night feeding could afford to share their meal with starved conspecifics because the relative gain in survival for the starved bats was orders of magnitude higher than the cost incurred by the fed bats sharing their meals. Since foragers would perceive the patch differently according to the amount of food they have already consumed, there is uncertainty in the relative value of the patch for that forager, and yet, this value is assumed to be represented in the final GUD obtained at that patch.

Brown (1992) defines the energetic state of the forager and its marginal value of energy as $\mathrm{d}F/\mathrm{d}e$, where F represents fitness and e net energy, and theoretically demonstrated how it can affect a forager's response to predation risk (P) and missed opportunity costs (MOC). Subsequently, this has been demonstrated empirically. For example, starved Anderson's gerbils (*Gerbillus andersoni allenbyi*) and Egyptian fruit bats (*Rousettus aegyptiacus*) tend to leave lower GUDs than nonstarved animals, presumably because food items are more beneficial to animals in a low energy state (Sánchez et al. 2008a; Berger-Tal and Kotler 2010; Berger-Tal et al. 2010). Similarly, deer mice (*Peromyscus maniculatus*) (Morris 1997; Davidson and Morris 2001) and house mice (*Mus musculus domesticus*) (Ylönen et al. 2002) had lower GUDs when in higher densities, argued to be a consequence of the reduction of the forager's energetic state due to high competition (i.e., environmental food shortage).

Forager state also includes other factors besides satiation, such as a forager's development, physiology, and reproductive state. These states can alter the relative value of the energy gain in a particular patch for a particular individual forager and, as such, alter the GUD that we measure. For example, pink salmon (*Oncorhynchus gorbuscha*) (Webster et al. 2007) and Anderson's gerbils (Raveh et al. 2011), when infected with ectoparasites, reduce their harvest rate and time spent foraging, allocating more time to parasite removal behaviors and, therefore, increasing their GUDs. Immunochallenged white-footed mice show lower GUDs and less patch selectivity, argued to be a result of the increase in energetic demands for anti-infection metabolism (Schwanz et al. 2011, 2012). In spring, during the reproductive season, Anderson's gerbils and greater Egyptian gerbil (*Gerbillus pyramidurn*) show lower GUDs compared to in summer when they are not reproductive, presumably because they favor energy that can go into reproduction against safety (Kotler et al. 2004).

Other aspects of an individual state, such as personality and age, may also be capable of altering GUD. Younger animals may have higher energy requirements for growth (Randall et al. 2002); thus, they may perceive patches as higher in value. Similarly, bolder animals may perceive a lower effect of predation risk and be more liable to stay at a foraging patch longer (Réale and Festa-Bianchet 2003). These elements are yet to be included in the GUD equation.

An individual's state matters because, as identified by Brown (1988), while patches can be visited by more than one forager, the GUD only measures the decision made by the last forager at the patch (or the lowest GUD). It follows then that GUDs may not be representative of the entire population of foragers, but be biased towards those individuals whose state drives them to exploit the patch most thoroughly. Understanding the state of those final foragers is therefore very important for interpreting the final GUD. This is particularly important in nonmanipulative experiments where the aim of the GUD experiment is to detect differences between populations occupying different locations. Populations can vary in their age structure, sex ratio, reproduction, etc., and the locations in which they occur can also vary in their food abundance or predation risk. If the state of the forager is not considered, it would be easy to confound differences in their marginal value of energy with changes in perceived predation risk or indeed many other questions of interest.

Group foraging

Given that patches can be visited by more than one individual, multiple foragers might simultaneously visit a patch. This has implications for the perceived cost of that patch for individuals and the amount of food that is left unharvested. Group foraging can reduce an individual's net predation risk, either because risk is diluted should a predator attack (Hamilton 1971), individuals need not be as vigilant to detect predators when foraging in a group (the "many eyes" effect) (Pulliam 1973), the group can defend a food patch as a unit (group defense) (Alexander 1974; Hoogland and Sherman 1976), predators may be unable to single out and attack a single animal in the group (confusion effect) (Milinski 1977a, b; Landeau and Terborgh 1986), and/or by offering individuals opportunities to take advantage of the "selfish herd" effect and shield themselves against predators (Hamilton 1971). The final GUD may therefore represent the most intense bout of foraging by an earlier group, rather than the decisions of the last forager. However, simultaneous same species exploitation of a patch more commonly leads to interspecific competition. Competition in a patch ultimately decreases the value of that patch (increasing GUDs) by either increasing the cost of foraging (*C*)—risk of injury while fighting conspecifics (also known as cost of interference *I*, see earlier)—or decreasing the cost of foraging elsewhere (higher *MOC*) where competitors may be less abundant. Territorial red squirrels (*Tamiasciurus hudsonicus*), for example, lower their GUDs when territory intruders are removed, which may imply that territorial defense constrains their foraging (Vlasman and Fryxell 2002). Similarly, when densities of Anderson's gerbils are high, there is an increase in aggressive interactions that interferes with foraging, ultimately increasing GUD (by reducing time foraging) even when patch quality is high (high food abundance) (Ovadia and Zu 2003). Further, males of this species visit food patches early during the night and deny access of females to high quality patches; thus, females are forced to exploit low quality patches (decreasing GUDs on those patches) when males are present (Kotler et al. 2005). In birds, spice finches (*Lonchura punctulata*) are able to gather more seeds (lower GUD) when foraging alone than in large numbers, argued to be a consequence of shorter time foraging in groups due to social cohesiveness (Livoreil and Giraldeau 1997).

As in same species groups, when individuals from different species visit the patch, creating mixed species groups, predation risk is theoretically lowered and so is GUD (Pulliam 1973; Powell 1985; Thiollay 1999). However, in practice, interspecific competition is more frequent, leading to aggressive interactions and altering the perceived cost of the patch, thus increasing GUD. For example, sympatric Anderson's gerbils and greater Egyptian gerbils (*G. pyramidurn*) engage in aggressive interactions that interfere with foraging (increasing GUD), and this interference is stronger when competition between species is higher (high abundance of food in patches and high densities of both species), which further increases GUD (Ovadia and Zu 2003). Further, the greater Egyptian gerbil competes mostly with male Anderson's gerbils, indirectly aiding females to overcome males' monopolization of feeding patches (Ovadia and Zu 2003). However, Anderson's gerbils GUD can also show lower GUDs when the greater Egyptian gerbil is present, presumably because the latter lowers food abundance which in turn increases the Anderson's gerbil's marginal value of energy (lowering *P*) (Ziv and Kotler 2003).

There are other examples of interspecific interactions affecting GUDs: nocturnal Cairo spiny mice (*Acomys cahirinus*) impede nocturnal foraging by golden spiny mice (*Acomys russatus*), forcing the latter to forage more intensively during the day and increasing nocturnal GUD (Gutman and Dayan 2005). Olivaceous field mice (*Akodon olivaceus*) show lower GUD when competitor species, degus (*Octodon degus*) and Darwin's leaf-eared mice (*Phyllotis darwini*) are excluded, and for these species, competition has a stronger effect than the presence of predators (Yunger et al. 2002). In contrast, blue monkeys (*Cercopithecus mitis*) are aggressive towards red-tailed monkeys (*Cercopithecus ascanius*), yet they are also less efficient at exploiting fruiting trees (higher GUD), allowing red-tailed monkeys to coexist by exploiting these trees more thoroughly (lower GUD) when both species are present (Houle et al. 2006). In a similar way, southern red-backed voles (*Myodes gapperi*) forage more intensively in their preferred habitat type (decreased GUD) in the presence of meadow voles (*Microtus pennsylvanicus*), presumably to avoid competition in alternative food patches (Morris 2009).

Evidently, the perceived cost of foraging in a particular patch is influenced by the density of the target species and other sympatric species, but also depends on the biology and ecology of the interacting species. More aggressive and territorial species may defend feeding patches, while submissive species may opt to forage elsewhere to avoid injury through aggressive interactions. Therefore, there is a need for greater understanding of exactly which individuals are visiting food patches and contributing to the GUD value. If we do not consider the abundance of the study species and the presence of other sympatric species, these factors may confound our interpretation of differences in GUD between sample populations.

Food and substrate qualities

Characteristics intrinsic to the experimental setup can also affect the GUD obtained. Since patches are artificial, it is crucial to take into account how the food resource and inedible substrate can affect the way a forager perceives the artificial patch. Physical and chemical characteristics of the food have been shown to alter how patches are perceived by altering the cost of foraging (*C*). Increasing nutrient content decreases the GUD left by both large (Kotler et al. 1994; Hochman and Kotler 2006) and small mammals (Brown and Morgan 1995; Leaver and Daly 2003). On the other hand, plant chemical defenses have the opposite effect (i.e., increasing GUD) for small mammals (Schmidt et al. 1998; Fanson et al. 2010), bats (Sánchez et al. 2008a, b), primates (McArthur et al. 2012), and marsupials (Bedoya-Pérez et al., unpublished). Foragers are selective about the type and quality of the food they harvest. For example, the sympatric rock elephant shrew (*Elephantulus myurus*) and Namaqua mouse (*Micaelamys namaquensis*) show species-specific preferences (lowest GUD) for particular food and substrate combinations (mealworms in pebbles for shrews and millet seeds in sand for mice), and these preferences are explained by morphological characteristics that promote coexistence by defining their ecological niche (Abu Baker and Brown 2012). Food preferences can also change across time, for example, village weavers (*Ploceus cucullatus*) switch preferences between millet seeds and peanuts according to the season, argued to be a consequence of an increase in energy requirements for breeding (Molokwu et al. 2011).

Physical characteristics of food items influence handling time and possible future benefits of different types of food, thus shaping GUD. For example, fox squirrels (*Sciurus niger*) show lower GUD in patches that have been supplemented with storable food (unshelled hazelnuts) compared to patches supplemented with nonstorable food (shelled hazelnuts), and this is a consequence of the perceived future value of the food (Kotler et al. 1999). Larger seeds are preferred (lower GUD) by desert gerbils because of their higher encounter rates compared with small seeds, regardless of higher handling time efficiency on smaller seeds (Garb et al. 2000). Swamp wallabies show lower GUD when offered food pellets with low concentration of a volatile plant terpene compared to pellets without the volatile terpene, due to the reduction in handling time achieved when using odor while searching (Bedoya-Pérez et al., unpublished). Handling efficiency can also be a species-specific trait. Thick-billed weaver (*Amblyospiza albifrons*), for example, show lower GUD for a wider range in seed sizes than do four other sympatric species, except the smaller seeds, while bronze mannikins (*Spermestes cucullatus*) showed the opposite trend, with lower GUD when harvesting for the smaller seed size (Soobramoney and Perrin 2008).

Substrate also greatly influences the perceived cost of foraging; as a result, it is critical to test different foraging matrix substrates for each new target species and environment, which can often lead to delays in protocol development. The substrate creates the decline in harvesting rate as a patch is depleted. If this decline occurs too rapidly, or all food items are removed, the GUD obtained is rendered useless. Several studies have highlighted substrate effects on GUD. For instance, several gerbil species show lower GUD when sand is used instead of rocks or loess (Kotler et al. 2001). Moreover, the ratio between substrate and food can also alter GUD; higher food densities result in lower GUD for desert kangaroo rats (*Dipodomys deserti*) (Podolsky and Price 1990) and lesser GUD for spotted woodpecker (*Dendrocopos minor*) (Olsson et al. 1999; Olsson et al. 2001b), while bream (*Abramis brama*) leave higher GUD under this scenario (Persson and Stenberg 2006; Stenberg and Persson 2006). Similarly, water birds increase GUD at greater water depths (Gawlik 2002; Nolet et al. 2006).

In light of these issues, making methodological decisions about food quality and physical characteristics, substrate type, and food-to-matrix ratios can be a titanic task for researchers. For example, high quality food presented in an easily searchable substrate can potentially mask the effects of predation risk (*P*) and missed opportunity costs (*MOC*) by increasing the perceived value of the patch (reducing foraging cost *C*). On the other hand, low quality food may not provide sufficient benefit to foragers to outweigh theses costs (*MOC* and *P*), resulting in low rates of patch visitation (and hence low numbers of replicates for researchers). Under such a scenario, it becomes difficult to determine whether patches are not harvested due to high perceived costs or because they were not encountered by foragers at all. Nevertheless, the GUD framework offers flexibility in its application, providing a variety of ways of solving these problems. For example, presenting an array of food items, either naturally occurring (Lortie et al. 2000) or not, can help determine which is appropriate for subsequent experimentation. Other components of the system can also be manipulated, such as the dimensions of the feeder and the type of substrate.

The predictability of the patch (the “magic pudding” effect)

In Norman Lindsay's (1918) iconic Australian children's tale, the Magic Pudding is a pie that—no matter how often it is cut and a slice taken—magically reforms, allowing its owner to “cut-and-come-again.” For foragers in GUD experiments, artificial food patches have similar “magical” properties. In nature, some food patches (e.g., sand dunes seed patches) may partly replenish daily (Kotler et al. 2002), but others (e.g., shrubs, pasture, or fruiting trees) do not. GUD experiments typically entail the consecutive (daily) replenishment of artificial patches, creating an unnatural predictability to the patch in terms of its quality, location, and periodicity that could all have a marked effect on the GUD by decreasing how the forager perceives the associated costs (*C* and *MOC*). If a forager is able to predict the profitability and the location of a food patch, and the spatial distribution of several patches in the surrounding area, *MOC* and *C* may be perceived more accurately, yet not necessarily reflecting how these parameters are perceived when foraging in naturally occurring patches that may not be predictable. Local foragers may learn about these artificial patches and begin to exploit them more thoroughly, whereas a less predictable (i.e., natural) patch is harder to assess and tends to be either under- or overexploited (Valone 1991; Kohlmann and Risenhoover 1998; van Gils et al. 2003; Vásquez et al. 2006).

Having the possibility of manipulating temporal and spatial predictability during GUD experiments can be advantageous if the aim is to determine how a forager uses previous information during foraging (e.g., recognition time or Bayesian foraging). For example, Inca doves (*Columbina inca*), bobwhite (*Colinus virginianus*), red knots (*Calidris canutus*), and degus use past experience to assess the quality of a patch that they have exploited previously (Valone 1991; Kohlmann and Risenhoover 1998; van Gils et al. 2003; Vásquez et al. 2006). Highly predictable food sources increase the value of foraging and allow the forager to efficiently allocate time to other fitness-enhancing behaviors, partitioning their activity patterns accordingly. Diurnal lesser spotted woodpeckers, for example, feed on highly predictable wood-living insects in dead tree branches, allowing them to allocate more time to foraging in the afternoon (lower GUDs) and spend less time feeding when food abundance increases (thus increasing the marginal value of energy) (Olsson et al. 2000). On the other hand, several other species such as the Namib desert gerbil (*Gerbillus tytonis*) (Hughes et al. 1995) and goldfish (*Carassius auratus*) (Stenberg and Persson 2005) do not vary GUDs in response to patch predictability.

However, where the aim is not linked to the use of information during foraging, then the magic pudding effect must be taken into account; otherwise, predictable patches can misrepresent natural foraging behaviors. How the target species responds to patch predictability may not be known prior to setting up a GUD experiment and can potentially shape GUD results in unexpected ways. Understanding the patterns of patch visitation by individuals can help identify any potential magic pudding effects and help interpret GUD results.

Behaviors that can affect harvest rates

Foragers are capable of employing complex behavioral strategies to overcome the foraging costs associated with a particular patch in order to maximize their fitness (Brown 1999). For example, Anderson's gerbils use antipredator vigilance to limit their exposure to predation risk (reducing P) at the patch, and when vigilance is impeded, their GUDs increase (Embar et al. 2011). On the other hand, when sight lines are blocked, Nubian ibex (*Capra nubiana*) increase their vigilance rates and their GUDs (Iribarren and Kotler 2012). The differences between ibex and gerbils can be explained by the efficiency of vigilance at reducing predation risk; vigilance by ibex is more effective at reducing predation risk than that of gerbils (Brown 1999). In a different example, Cotton rats (*Sigmodon hispidus*) and the eastern chipmunk (*Tamias striatus*) eavesdrop on other species alarm calls while foraging to reduce their own predation risk (again reducing P); this enables them to leave low GUDs while avoiding the costs of vigilance (Schmidt et al. 2008; Felts and Schmidt 2010). Similarly, deer mice alter their food handling strategies (increasing H) in ways that allow them to leave low GUDs even in patches with high cost of injury by fire ants (high C) (Holtcamp et al. 1997). As a consequence of the flexibility in behavioral traits shown by foragers, patches with different perceived value might actually be exploited to the same level (equal GUD), and researches may not recognize the real effects that represent characteristics of the patch.

Nontarget species

Nontarget species foraging from patches is an inconvenient and almost inevitable complication when setting up GUD experiments in a natural environment. The appeal of the GUD methodology is its ability to measure the decisions of free-living animals, but the drawback is that foraging stations may also be available for many species to exploit. However, there is little mention in the GUD literature of how to deal with nontarget species. Most commonly, GUD papers report results only for targeted species, disregarding, and in some case not even mentioning, other species that may have visited the artificial patch; approximately 58 % of GUD papers published to date only reported one species using the patches. The development of strategies to deter nontarget species while maintaining access to the patch for target fauna can prove extremely challenging. Mechanical barriers are not always effective. Accounting for the degree of visitation made by nontarget species in statistical models can sometimes be the only option, although not all species leave signs of visitation and it is difficult to ensure we detect all species that visit the patches.

The seven issues described above illustrate how the final measured GUD reflects many influential processes which most researchers do not explicitly address when describing experimental GUD methodology.

Solutions and additional techniques

One important approach to determine the ultimate causes behind a GUD is to use ancillary measures of forager responses to the experimental setup. A large proportion of all GUD studies to date (approx. 31 %) supplemented their work with additional techniques in order to gather information that allows broader ecological hypotheses to be tested (Table 2).

Table 2 Supplementary techniques and approaches used alongside the giving-up density framework

Aspect addressed	Supplementary technique	Species	Reference
Abundance estimation	Trapping	Anderson's gerbils (*Gerbillus allenbyi*)	Gideon et al. (2005), Kotler et al. (2005), Wasserberg et al. (2007), China et al. (2008)
		Bream (*Abramis brama* L.)	Persson and Stenberg (2006), Stenberg and Persson (2006)
		Brown antechinus (*Antechinus stuartii*)	Kovacs et al. (2012)
		Brushed-tailed mulgara (*Dasycercus blythi*)	Dickman et al. (2011)
		Brushtail possum (*Trichosurus vulpecula*)	Pickett et al. (2005)
		Bush rat (*Rattus fuscipes*)	Kovacs et al. (2012)
		Bushveld gerbil (*Tatera leucogaster*)	Perrin and Kotler (2005)
		Darwin's leaf-eared mouse (*Phyllotis darwini*)	Yunger et al. (2002)
		Deer mouse (*Peromyscus maniculatus*)	Morris (1997), Davidson and Morris (2001), Reed et al. (2005), Rosemier and Storer (2010)
		Degu (*Octodon degus*)	Yunger et al. (2002)
		Eastern chipmunk (*Tamias striatus*)	Rosemier and Storer (2010)
		Eastern wood rat (*Neotoma floridana*)	Reed et al. (2005)
		Grass mouse (*Rhabdomys pumilio*)	Abu Baker and Brown (2010)
		Greater Egyptian gerbil (*Gerbillus pyramidurn*)	Gideon et al. (2005), Wasserberg et al. (2007), China et al. (2008)
		Hispid cotton rat (*Sigmodon hispidus*)	Reed et al. (2005)
		Hispid pocket mouse (*Chaetodipus hispidus*)	Reed et al. (2005)
		House mouse (*Mus musculus domesticus*)	Ylönen and Ronkainen (1994), Arthur et al. (2004)
		Long-tailed pygmy rice rat (*Oligoryzomys longicaudatus*)	Caccia et al. (2006)
		Meadow jumping mouse (*Zapus hudsonicus*)	Reed et al. (2005)
		Merriam's kangaroo rat (*Dipodomys merriami*)	Herman and Valone (2000)
		Oldfield mice (*Peromyscus polionotus*)	Orrock and Danielson (2005)
		Olivaceous field mouse (*Akodon olivaceus*)	Yunger et al. (2002)
		Olive grass mouse (*Abrothrix olivaceus*)	Caccia et al. (2006)
		Ord's kangaroo rat (*Dipodomys ordii*)	Stapp and Lindquist (2007)
		Prairie vole (*Microtus ochrogaster*)	Reed et al. (2005)
		Red squirrels (*Tamiasciurus hudsonicus*)	Vlasman and Fryxell (2002)
		Sandy inland mouse (*Pseudomys hermannsburgensis*)	Kotler et al. (1998), Dickman et al. (2011)
		Southern red-backed vole (*Myodes gapperi*)	Andruskiw et al. (2008), Rosemier and Storer (2010)
		Spinifex-hopping mouse (*Notomys alexis*)	Dickman et al. (2011)
		Striped mouse (*Rhabdomys pumilo*)	Perrin and Kotler (2005)
		Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	Reed et al. (2005)
		Western harvest mouse (*Reithrodontomys megalotis*)	Reed et al. (2005)
		White-footed mouse (*Peromyscus leucopus*)	Schmidt and Ostfeld (2003), Reed et al. (2005), Rosemier and Storer (2010)
Activity estimate	Photographic records (field)	Mule deer (*Odocoileus hemionus*)	Altendorf et al. (2001), Hernández et al. (2005)
	Radio tracking	Anderson's gerbils (*G. allenbyi*)	Kotler et al. (2005), Wasserberg et al. (2007)

Table 2 (continued)

Aspect addressed	Supplementary technique	Species	Reference
		Greater Egyptian gerbil (*G. pyramidurn*)	Wasserberg et al. (2007)
	Sand plots	Anderson's gerbils (*Gerbillus allenbyi*)	Wasserberg et al. (2007)
		Bushveld gerbil (*T. leucogaster*)	Perrin and Kotler (2005)
		Greater Egyptian gerbil (*G. pyramidurn*)	Wasserberg et al. (2007)
		Striped mouse (*R. pumilo*)	Perrin and Kotler (2005)
	Trapping	Cairo spiny mouse (*Acomys cahirinus*)	Gutman and Dayan (2005)
		Common voles (*Microtus arvalis*)	Jacob and Brown (2000)
		Golden spiny mouse (*Acomys russatus*)	Gutman and Dayan (2005)
	Video recording (field)	Natal multimammate mouse (*Mastomys natalensis*)	Mohr et al. (2003)
Behavioral responses	Passive inductive transponder (PIT) tags	Bank voles (*Myodes glareolus*)	Trebatická et al. (2008)
		Gray red-backed vole (*Myodes rufocanus*)	Trebatická et al. (2008)
		Anderson's gerbils (*G. allenbyi*)	Kotler et al. (2010)
	Video recording (captive)	Anderson's gerbils (*G. allenbyi*)	Ovadia and Zu (2003)
		Bank voles (*M. glareolus*)	Liesenjohann and Eccard (2008)
		Goldfish (*Carassius auratus*)	Stenberg and Persson (2005)
		Greater Egyptian gerbil (*G. pyramidurn*)	Ovadia and Zu (2003)
	Video recording (captive)	Red fox (*Vulpes vulpes*)	Berger-Tal et al. (2009)
	Vocalization playbacks	Eastern chipmunk (*T. striatus*)	Schmidt et al. (2008)
		Eastern tufted titmouse (*Baeolophus bicolor*)	Schmidt et al. (2008)
Forager identity	Behavioral observations	Village weavers (*Ploceus cucullatus*)	Molokwu et al. (2011)
Growth measurements	Trapping	Cottid fish (*Clinocottus acuticeps*)	Alofs and Polivka (2004)
Habitat use	Trapping (GIS)	Grass mouse (*R. pumilio*)	Abu Baker and Brown (2010)
	Radio tracking	Pygmy gerbil (*Gerbillus henleyi*)	Abramsky et al. (2005)
		Red squirrels (*T. hudsonicus*)	Vlasman and Fryxell (2002)
	Sand plots	Brushtail possum (*T. vulpecula*)	Pickett et al. (2005)
	Spool-and-line	Bush rat (*R. fuscipes*)	Strauβ et al. (2008)
	Tracking tunnels (fluorescent dye)	Slender-tailed dunnart (*Sminthopsis murina*)	Stokes et al. (2004)
		Yellow-footed antechinus (*Antechinus flavipes*)	Stokes et al. (2004)
Handling time	Behavioral observations	Fox squirrel (*Sciurus niger*)	Kotler et al. (1999)
		Deer mouse (*P. maniculatus*)	Holtcamp et al. (1997)
	Video recording (captive)	Degu (*O. degus*)	Bozinovic and Vásquez (1999)
Harvesting speed	Behavioral tests	Golden-mantled ground squirrel (*Callospermophilus lateralis*)	Smith (1995)
		Least chipmunk (*Tamias minimus*)	Smith (1995)
Morphological adaptations	Retinal histology	Cairo spiny mouse (*A. cahirinus*)	Kronfeld-Schor et al. (2001)
		Golden spiny mouse (*A. russatus*)	Kronfeld-Schor et al. (2001)
Mortality estimate	Radio tracking	Water voles (*Arvicola terrestris*)	Carter and Bright (2003)
Age structure	Trapping	Bush rat (*R. fuscipes*)	Spencer et al. (2005)
Searching pattern	Video recording (captive)	Anderson's gerbils (*Gerbillus allenbyi*)	Dall et al. (2001)
Stress levels	Hormone essay	Cairo spiny mouse (*A. cahirinus*)	Gutman et al. (2011)
		Golden spiny mouse (*A. russatus*)	Gutman et al. (2011)

Pilot studies

The importance of pilot studies cannot be overemphasized and must be factored in to any plan for GUD experimentation. No matter how simple the GUD technique might appear, in our experience, it has never worked immediately and has required some period of tweaking the technique before the main experimental data could be collected. The preliminary information that can be derived from pilot studies allows researchers to calibrate the type of food, the type of substrate, and the overall structure of the feeding station (e.g., tray, container, box, and so on). In combination with techniques such as video recording, pilot studies can also clearly identify which species are foraging in artificial patches and must be further considered as the methodology is developed.

Pilot studies help to fine-tune GUD experiments in order to prevent common initial problems such as GUDs reaching zero or a lack of visitation at feeding stations. If feeders are not visited, increasing the quality or the size of the food offered, or decreasing the amount of substrate, will decrease the costs of foraging (*C*) and the *MOC*, making the feeding stations more attractive to foragers. On the other hand, if GUDs reach zero, the perceived benefits of the patch (*C*) may currently be too high—they can be reduced by increasing the amount of inedible matrix, reducing the amount of food offered, or decreasing the quality or size of the food, or as with goats (*Capra hircus*) and klipspringers (*Oreotragus oreotragus*), adding a physical obstacle (wires and fencing) in feeding stations that makes foraging more difficult and can help prevent foragers spilling inedible matrix from the feeder, thereby keeping the volume constant (Shrader et al. 2008a, b; Druce et al. 2009). This is an important consideration to ensure diminishing returns with continued foraging. In summary, pilot studies are the first practical step to measure and account for specific characteristics of the target species and the system in which the GUD framework will be applied; however, it is not a solution per se, rather it is an approach that enables researchers to refine the method for their research question and system.

Trapping

Trapping has often been used in combination with GUDs to estimate local population density of the target species and to survey the available pool of potential foragers. These data can help researchers to assess the potential for intra- and interspecific interactions that might influence the GUD (Kotler et al. 1998; Reed et al. 2005; Kovacs et al. 2012). Trapping has also been used to estimate a population's age structure (Spencer et al. 2005) and individual's growth and fitness (Alofs and Polivka 2004), which, as we have discussed, might bias sampling if GUDs are left by individuals with the highest energetic requirements (i.e., juveniles, reproductive and/or sick animals). Trapping also allows information to be gathered about the nontarget species in the area. Thus, the information gained through trapping conducted concurrently or prior to a GUD experiment can be incorporated into the analysis and interpretation of GUD results.

Tracking

Tracking (e.g., GPS or radio transmitters) is another common addition to GUD experiments, used to measure activity patterns, time partitioning (Kotler et al. 2005; Wasserberg et al. 2007), and habitat use (Vlasman and Fryxell 2002; Strauβ et al. 2008), which can help address potential effects of inter- and intraspecific competition. Tracking forager activity patterns may identify whether group foraging occurs, but tracking can also reveal the identity of the last forager at a tray, potentially revealing the link between GUD and individual energetic requirements (i.e., age, health, reproductive state). Moreover, real time spent at the patch can be calculated and compared with the GUD in order to determine harvesting efficiency and account for any changes that may have been achieved through behavioral strategies. For example, Kotler et al. (2010) was able to calculate harvest rate and construct harvest rate curves by using time spent in the patch by individuals tracked through the use of passive integrated transponder (PIT tags). Nonintrusive tracking, such as sand plots, have been used to determine forager species identity, nontarget species, and activity patterns (Perrin and Kotler 2005; Pickett et al. 2005).

Behavioral observations

In our opinion, only direct behavioral observations can address the consistent issues of who is visiting and how they allocate their time at the patches to create the final measured GUD. By observing foragers as they exploit the patch, we can measure an entirely new set of data that provides context to the GUD value obtained at the end of an experiment. The value of behavioral observations, taken alongside GUDs, has been demonstrated repeatedly through the use of direct observation (Holtcamp et al. 1997; Kotler et al. 1999; Molokwu et al. 2011), video recordings of captive animals (Smith 1995; Dall et al. 2001; Ovadia and Zu 2003), and importantly, in field experiments (Mohr et al. 2003; Bytheway et al. 2013). Infrared game cameras are being widely adopted in biodiversity surveys and offer the opportunity to capture detailed behavioral observations of animals at GUD patches. Cameras with remote video recording capabilities offer a cost-effective, nonintrusive opportunity to identify which individuals are visiting GUD patches and what they do there in order to demystify the final GUD value.

Conclusions

Even though applying the GUD framework for the first time can be frustrating and discouraging, it continues to offer an elegant and powerful tool to assess an almost infinite array of questions in foraging and predation ecology. However, researchers need to account for its potential limitations and realize that by addressing these limitations, they are opening up opportunities for new and interesting research to decipher how foraging decisions are made. Novel and fascinating questions have already been asked using the GUD, including how foraging partitioning (diurnal vs.

nocturnal) is linked with eye morphology (Kronfeld-Schor et al. 2001), how stress levels due to predation risk affect foraging (Gutman et al. 2011), and how eavesdropping on interspecific alarm calling affects time invested exploiting a patch (Schmidt et al. 2008), just to name a few.

We do not suggest that researchers give up on the giving-up density framework and methodology, but we do think that there is a greater need to identify how these limitations might affect experimental GUD results. The addition of cameras to the GUD method offers a valuable solution that addresses many of the issues we have raised here. This is because it allows researchers to unobtrusively observe the animals at the patch and attempt to relate the behavior displayed and the process of foraging to the final measured GUD, something which was not possible before remote sensing night vision cameras became an affordable option for field ecologists. We exhort our fellow researchers struggling with GUD methods in the field to work through the issues using some of our suggested solutions above and to explicitly address their solutions and approaches to these issues when describing their methodology in future publications.

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