On the value of information: studying changes in patch assessment abilities through learning

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Little is known about how animals acquire and use prior information, particularly for Bayesian patch assessment strategies. Because different patch assessment strategies rely upon distinct capabilities to obtain information, we analyzed whether foragers can alter their foraging strategy when they exploit predictable patches with periodic renewal. For this, we evaluated if learning contribute to increase foraging efficiency by improving patch assessment abilities in degus (*Octodon degus*), a diurnal caviomorph rodent from central Chile. Single degus exploited pairs of depleting patches that were renewed daily. During the initial two days of the experiment, degus exploited patches in agreement with a fixed-time strategy, i.e. at the population level, giving-up densities (GUD) were not distinguishable from density-independence (i.e. consumption proportional to initial patch densities), and richer patches were under-exploited. After day five, degus improved significantly their assessment strategy, showing agreement with Bayesian information updating. However, on day 15 and afterwards, degus foraged patches in agreement with a prescient strategy, because GUDs across patches indicated positive density-dependence and equalization of GUDs. Although highly variable, the GUD ratio between rich and poor patches decreased significantly throughout time. Within-subject data showed that as subjects learned patch qualities they showed a tendency toward GUD equalization and differentiation from density-independence. By the end of the experiment, degus allocated more time to richer patches during the initial period of each trial, and allocated similar amounts of time by the end of trials. Further, the first visit of a session was significantly biased toward the rich patch by the final days of the experiment. The results suggest that assessment abilities can change when exploiting novel but predictable patches. When degus can incorporate adequate environmental information, prior and current information may become accurate enough to make animals exploit patches efficiently.

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To efficiently exploit heterogeneously distributed resources, foragers must recognize resource heterogeneity, obtain information about resource patches, and have a decision process to allocate its efforts according to net benefits (McNamara and Houston 1980, Kacelnik and Krebs 1985, Stephens and Krebs 1986, Valone and Brown 1989, Giraldeau 1997). In many foraging situations, animals have no knowledge about patch quality, and they must assess this quality in order to decide the beginning and/or continuation of patch exploitation. Assessment entails the acquisition of information about patches. Patch information has been divided into two categories (Valone 1991): (1) information acquired during current patch exploitation, and (2) information acquired previously to exploitation. Previous information can be obtained in three ways, via (i) knowledge about the environmental distribution of patchy resources, (ii) information acquired through accurate sensory organs, and/or (iii) previous knowledge (or memory) about predictable patches (Valone 1991).

Depending on what kind of information an individual can use, different efficient foraging strategies have been proposed (Green 1980, McNamara and Houston 1980, Valone and Brown 1989, Valone 1991, Wildhaber et al. 1994, Olsson and Holmgren 1998, van Gils et al. 2003). When the resources of a given patch are unpredictable, hidden and/or difficult to be precisely assessed before exploitation, foraging strategies that use previous and current information are particularly relevant. An individual arriving at a food patch may already have some kind of prior information about the environment, but it may also be able to gather some information about the current patch while exploiting it. Under most conditions the forager would benefit from using both its knowledge about the environment in general and the information obtained during patch exploitation to make appropriate foraging decisions (Green 1980, Iwasa et al. 1981, McNamara 1982, Valone and Brown 1989, Valone 1991, 1992, Rodríguez-Gironés and Vásquez 1997, Olsson and Holmgren 1998, van Gils et al. 2003). Theoretically, the use of information has been undertaken by applying Bayesian statistical decision-making theory (McNamara and Houston 1980, Mangel 1990, Dall et al. 2005). Bayesian decision-making provides a self-consistent rule for updating prior knowledge in view of current experience and has been a fruitful and common approach to model information acquisition (McNamara and Houston 1980, Stephens and Krebs 1986, Mangel 1990, Dall et al. 2005). When prey number varies among patches, a forager attempting to maximize its instantaneous feeding rate might use Bayesian estimation. Such a forager begins with some prior knowledge of resource distribution, and constantly updates that knowledge as it forages.

Given that most natural resources are moderately to highly variable in time and space, studies on patch assessment have been focused on foragers facing patches in a short time scale, normally comprising from minutes to a few days (Valone and Brown 1989, Valone 1991, 1992, Alonso et al. 1995, Olsson and Holmgren 1998, van Gils et al. 2003). No attempt has been made to analyze how foragers track renewing patches on a longer time scale (see Tamm 1987 and Shettleworth et al. 1988 for studies on sampling between patches). This is unfortunate, given our ignorance about how animals form and use previous knowledge. In the case of Bayesian decision-making, there is a lack of understanding about how animals shape their prior information, and what temporal scale is needed to significantly change a prior distribution (Valone 1992). We propose that learning studies of patch assessment where foragers are repeatedly exposed to predictable and periodically renewing patches could help to gain insight about the formation and dynamics of the prior distribution, and in general about the dynamics of previous information on assessment abilities. In this study we evaluated if learning about predictable renewing patches contribute to increase foraging efficiency by improving assessment abilities in degus (*Octodon degus*), a diurnal caviomorph rodent from central Chile.

To study patch assessment we followed the approach developed by Valone and Brown (1989, see also Brown 1988) comprising the use of foraging stations with paired food patches. The approach comprises the offer of a pair of patches with different initial densities of food (thus making one patch richer than the other), and the subsequent examination of the giving-up density (GUD) in each patch, i.e. the remaining quantity of food left by a forager when it ceases foraging after a given period of activity (Brown 1988). Because exploitation rate is a function of resource density, GUD provides a surrogate variable for quitting exploitation rate. Since it is assumed that the pair of offered patches encompasses the same costs, it is predicted that an optimal forager given enough time should equalize the quitting-exploitation rates in both patches, i.e. equalize GUDs (Brown 1988, Valone and Brown 1989). However, animals with no perfect information may use different strategies. The examination of two variables, density-dependence and degree of patch exploitation (sensu Valone and Brown 1989), permits the inference of the type of foraging strategy being used. Figure 1 depicts the pattern of density-dependence foraging (Fig. 1a), and the degree of patch exploitation (Fig. 1b) in a station with a pair of patches, where x, y data points represent GUD points in the poor and rich patch, respectively. Before exploitation, patches are fully replenished (8 g and 12 g of food in the poor and rich patch, respectively, in Fig. 1). After an episode of exploitation (i.e. a foraging trial), a consumer ceases foraging leaving a certain x, y value of GUDs. If a forager exploits both patches in exact proportion to their initial food densities, it will leave an x, y GUD point exactly in the segmented line representing density-independent foraging (Fig. 1a). If a forager exploits proportionally more (or less) prey from the rich patch, it will leave x, y points below (or above) the density-independent line, hence showing a pattern of positive (or negative) density-dependence (Fig. 1a; Valone and Brown 1989). An omniscient optimal forager exploiting this system is expected to exploit the rich patch first (since it has perfect information about patch quality) until food densities are equalized across patches, leaving an x, y point along the continuous line corresponding to GUD equalization, hence showing positive density-dependence. If a forager is not omniscient, as most real animals, then it may under-exploit the rich patch if it does not reach GUD equalization, or it may over-exploit the rich patch if allocates more effort to this patch after GUD equalization (Fig. 1).

Different foraging strategies predict different patterns of density-dependence and patch exploitation (Valone

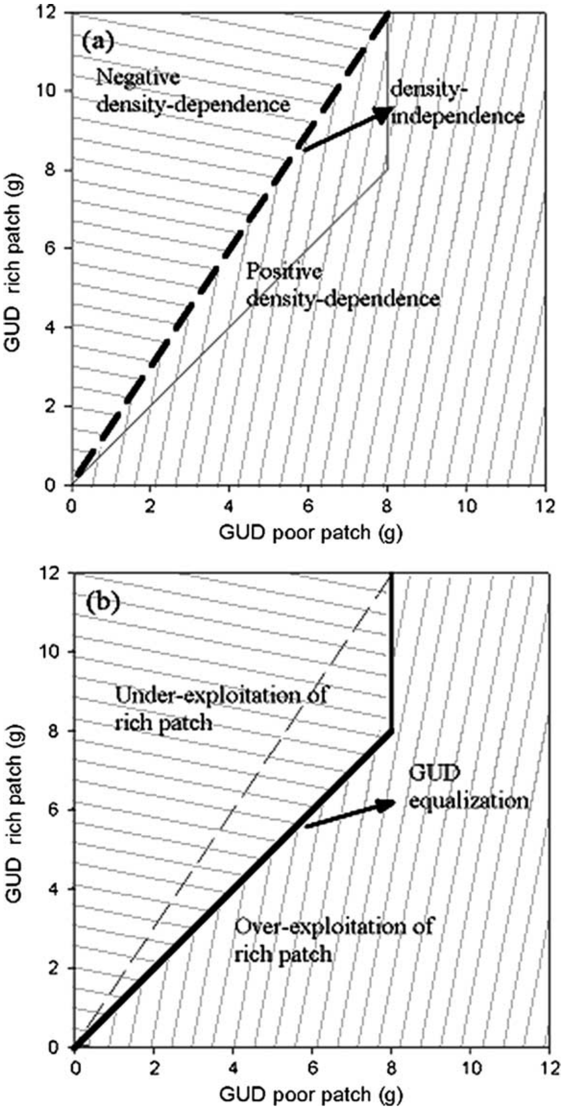

Fig. 1. The paired-patches approach to study patch assessment abilities. Experimental data points are plotted as x,y points, for GUD in the poor and the rich patch, respectively. Initial resource densities are 8 g and 12 g in the poor and rich patch, respectively. (a) The segmented line shows density-independent patch exploitation (i.e., proportional to initial densities). Any point above this line (shading lines with negative slopes) represents negative density-dependent foraging; any point below, positive density-dependence (shading lines with positive slopes). (b) The continuous line shows the predictions for an omniscient optimal forager (i.e. exclusive exploitation of the rich patch until equalization of GUDs). Any point above the GUD equalization line indicates under-exploitation of the rich patch (shading lines with negative slopes); any point below, over-exploitation (shading lines with positive slopes). For comparison, in both figures, the thin continuous and segmented lines show the omniscience and the density-independence predictions, respectively.

and Brown 1989, Valone 1992). Therefore, one can measure a set of animals exploiting stations of paired patches and assess at the population level x, y data points in order to gain insight about the foraging strategy being used (Valone and Brown 1989). For instance, in a fixed-time strategy (Iwasa et al. 1981) the forager devotes the same amount of searching time to each patch independently of patch quality, and hence produces a pattern of density-independent foraging and under-exploitation of the rich patch. On the other hand, a Bayesian forager facing clumped prey distributions shows positive density-dependence and under-exploitation of rich patches (Rodríguez-Gironés and Vásquez 1997, Olsson and Holmgren 2000). Other combinations of density-dependence and degree of patch exploitation characterize other foraging strategies (Iwasa et al. 1981, Valone and Brown 1989). We propose that the approach developed by Valone and Brown (1989) can be used as a diagnostic test for patch assessment, and combined with within trial behavioral data and long-term patch predictability can be a fruitful approach to study the temporal dynamics of information use and changes in patch assessment ability due to learning.

In order to study the influence of learning on patch assessment abilities, we allowed foragers to experience the same arrangement of paired patches repeatedly throughout time. By studying periodically renewing patches it was possible to evaluate if patch assessment abilities change through time and if learning contribute to increase foraging success. Since evidence shows that several species use previous and current information to exploit resources (Hunte et al. 1985, Valone and Brown 1989, Alonso et al. 1995, Olsson et al. 1999, van Gils et al. 2003), we expected that if patch arrangements persist for long periods of time and renew periodically, foragers could learn to increase foraging efficiency. In particular, we expected a shift toward equalization of GUDs, and predominantly positive density-dependence with experience.

Material and methods

Octodon degus is a semi-fossorial herbivorous rodent (ca 160–200 g) that inhabits xeric habitats of central Chile. It is mostly active at daytime, when most activities take place above ground (Fulk 1976, Kenagy et al. 2002). Degus use shrub and open habitats when above ground, and previous studies suggest that shrub habitats provide lower predation risk than open areas (Lagos et al. 1995, Vásquez et al. 2002). Its diet is composed of herbs, seeds, leaves, and other plant materials (Meserve 1981, Meserve et al. 1983). During the annual cycle, degus experience significant changes in climate, food availability, and food quality. Accordingly, degus can modify their foraging physiology and behavior, and their daytime activity budget (Bozinovic 1995, Bozinovic and Vásquez 1999, Kenagy et al. 2002, 2004, Bozinovic et al. 2004). Under natural conditions, degus readily forage on experimental seed patches, and GUDs are reliable indicators of foraging success under different ecological scenarios (R. A. Vásquez, unpubl.). Degus seem to use previous information for patch assessment, and they respond flexibly to predation risk and food abundance, by changing vigilance and foraging allocation (Vásquez 1997, Vásquez et al. 2002, R. A. Vásquez unpubl.).

The protocol includes the use of experimental patches with known initial quantities of food mixed in a fixed amount of substrate, thus making foragers to experience food patches with diminishing returns (Charnov 1976; for examples, see Brown 1988, Kotler and Brown 1990, Schmidt and Brown 1996, Vásquez 1996, Meyer and Valone 1999). In particular, our experimental patches consisted of metallic trays (20 × 20 × 4 cm) filled with a mixture of substrate (1.5 l of fine sand) and food (unhusked sunflower seeds). To evaluate patch assessment abilities, we used the paired-patches protocol designed by Valone and Brown (1989). A pair of identical experimental patches differing only in the initial food density they contained was presented to a single subject. Therefore, a forager experienced a pair of patches with similar features (e.g. area, substrate quantity and quality, predation risk, and microclimate, among others) except by their initial food densities. The patch with higher initial food density is called rich patch, while the other is called poor patch. The pair of patches was placed 10 cm apart in the middle of an experimental indoor arena (1.5 × 1.0 × 0.9 m; length × width × height). The floor was covered with sand to a depth of 4 cm, and a plastic refuge box (25 × 25 × 10 cm) was placed in a corner. Four experimental arenas were used simultaneously. As experimental subjects, we used twenty-four individuals of *O. degus*, captured in a natural population nearby Santiago (Vásquez et al. 2002). This large sample size assured statistical power for our population-level analysis.

To assess the influence of learning, we allowed individual foragers to exploit spontaneously a pair of patches for a continuous period of 21 d. On each daily trial, subjects were allowed to exploit patches for 4–5 h. Therefore, animals were allowed free re-visitation of patches during each session. Animals experienced a partially closed economy (Houston and McNamara 1989), because in addition to the experimental sessions they had access to supplemental food (rabbit commercial pellets) for periods of 30 min two to three times per week. At the beginning of each daily session, patches were replenished with constant amounts of food. Poor patches contained an initial quantity of 8 g of seeds, while rich patches contained 12 g. In order to aid the learning process, the initial density of seeds in each patch was constant during the whole experiment, as well as the spatial position of each patch. After a session, the GUD of each patch was measured by weighing the remaining quantity of seeds left in each patch. Overnight, animals were maintained in individual cages (40 × 30 × 20 cm) with water ad libitum and bedding material.

The evaluation of the effect of repeated exposure to renewing patches was done through a sample population analysis, as well as through within-subject and within-trial (moment-by-moment) behavioral analyses. Our population-level analysis comprised two evaluations. First, we analyzed density-dependent foraging patterns and the ability to equalize GUDs in plots as shown in Fig. 1. We then analyzed data throughout the experiment, identifying those days were a given pattern of exploitation in terms of density-dependence and/or GUD equalization changed significantly and was maintained for more than two consecutive days. Second, we analyzed the ratio of GUDs between rich and poor patches as a function of time. A ratio value of 1 indicates equalization of GUDs.

The within-subject analysis comprised non-parametric Spearman correlations between GUDs among patches. We aimed to analyze a change in behavior with learning experience, hopefully comparing periods with invariable (but dissimilar) patterns of patch exploitation and density-dependence. Population-level results were used to choose these periods. Results allowed within-individual comparisons between the period from day 5 to 11, and the period from day 15 to 21. Therefore, each correlation includes seven data points. We also carried out within-subject comparisons between the observed and expected slopes for density-independence (expected slope = 1.5), and equalization of GUDs (expected slope = 1.0). For this, we calculated linear regressions of GUD points during the mentioned periods for each subject, and used t-tests within subjects to compare slopes.

The within-trial analysis of behavior comprised the examination of patterns within experimental sessions and within subjects. For this purpose, we videotaped experimental sessions of 18 subjects at the beginning of the experiment (between day 1 and 4) and at the end of the experiment (between day 17 to 21). From the video records, we obtained detailed data on patch exploitation through time within each session, including patch visitation time, and events of prey capture. These data allowed analyzing the proportion of time allocated to each patch, as well as to scrutinize the temporal dynamics of patch exploitation within trials by obtaining partial GUDs throughout time.

A caveat on the use of paired patches is worth mentioning. Two patches cannot be assigned to any particular statistical distribution. Even the use of the variance-to-mean ratio is not justified to infer distributions from a sample of two patches or quadrants (Elliott 1977). However, the use of a large realistic distribution of patches was unfeasible due to at least two reasons. First, such an experiment would need prolonged exposure of foragers to the experimental set-up for a single learning session, in order to make animals experience all patches, thus making a whole learning study unmanageably long. Second, a realistic patch distribution would need a larger experimental space, complicating the precise recording of the subject's behavior. However, we are certain that animals experienced all the patches available in their experimental environment, and thus they were allowed to gain information about the actual distribution they experienced. Even in a two-patch environment a Bayesian forager could improve its feeding rate when exposed to prolonged patch predictability. Moreover, we suggest that from a theoretical point of view, it is useful to assess the ability of animals to respond to a given prey distribution, even if it is not a naturally occurring distribution (Valone 1991).

Results

We found significant correlations between GUDs of paired patches for eighteen out of the 21 days of experimentation (Fig. 2a), thus indicating the consistency of foragers at the population level, and supporting predictions of several foraging strategies, including optimal (omniscient) foraging, fixed-time strategy, and Bayesian patch assessment, among others (Valone and Brown 1989). Further, these correlations increased significantly throughout the experiment (Spearman rank correlation, $r_s = 0.52$, $p = 0.02$; Fig. 2a).

The data from rich and poor paired patches show a significant change between the beginning and the end of the experiment (Fig. 2, 3). Although the data is scattered throughout the experiment, during the beginning of the learning period, from day 1 to day 4, the foraging pattern did not differentiate from a density-independence (Fig. 2b). Generally, during the first days of experimentation (with the exception of day 3), rich patches were under-exploited (Fig. 2c). Throughout the days, the proportion of patches with positive density-dependence increased significantly (Spearman rank correlation, $r_s = 0.84$, $p = 0.0002$; Fig. 2b), while the proportion of rich patches under-exploited decreased significantly (Spearman rank correlation, $r_s = -0.77$, $p = 0.006$; Fig. 2c). We considered that a reliable pattern of density-dependence and exploitation was settled once we observed more than two consecutive days with a similar statistical result for each dependent variable (Fig. 2b–c). Thus, we plotted in Fig. 3 only those days where a consistent change was statistically detected, plus the first and final day of the whole experiment. Accordingly, in each of the first two days, we observed that there were many points above as well as below the density-independence line (paired sign tests, $P > 0.2$, for day 1 and 2, Fig. 2b). On the other hand, however, most of the data points were located above the GUD equalization line (paired sign tests, $P < 0.0001$, and $P < 0.0066$, for day 1 and 2, respectively; Fig. 2c). Hence, foragers under-exploited rich patches and did not differ from density-independence (Fig. 3a), supporting a fixed-time foraging strategy (Valone and Brown 1989). On day 5 and afterwards, degus consistently showed positive density-dependent foraging and relative under-exploita-

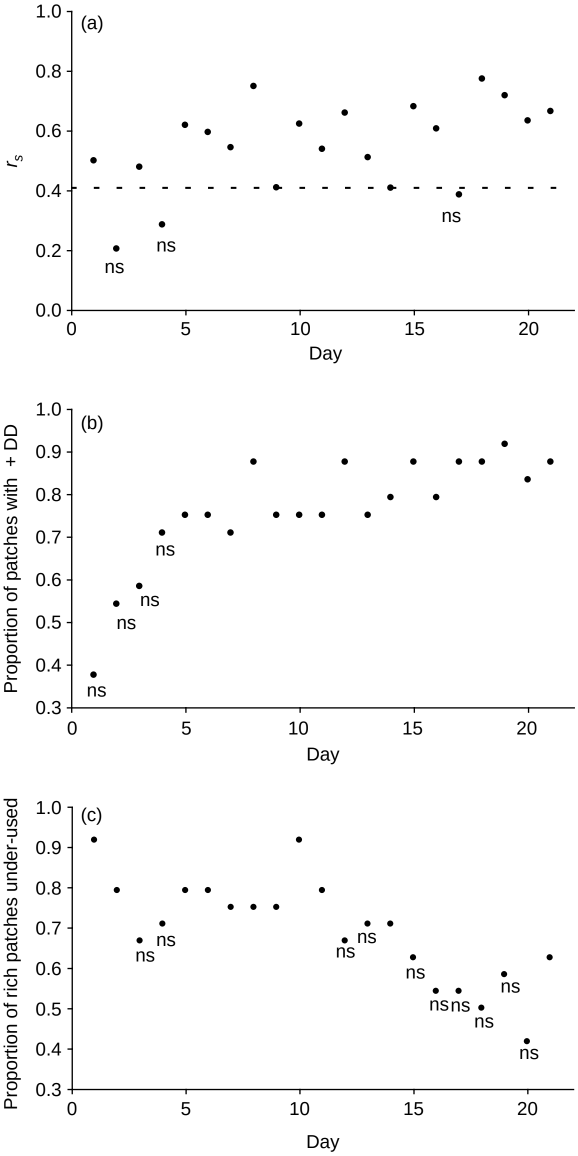

Fig. 2. (a) scatter plot of Spearman correlations (r_s) for giving-up densities between rich and poor patches for each daily session. The continuous line shows the alpha-level for each correlation (Methods). Only three sessions were non-significant. (b) mean proportion of patches with positive density-dependence throughout the experiment. Only the results of the first four days were non-significant. (c) mean proportion of rich patches under-exploited throughout the experiment. Non-significant results were observed predominantly during the end of the experiment. The abbreviation ns indicates non-significant result for the corresponding daily session.

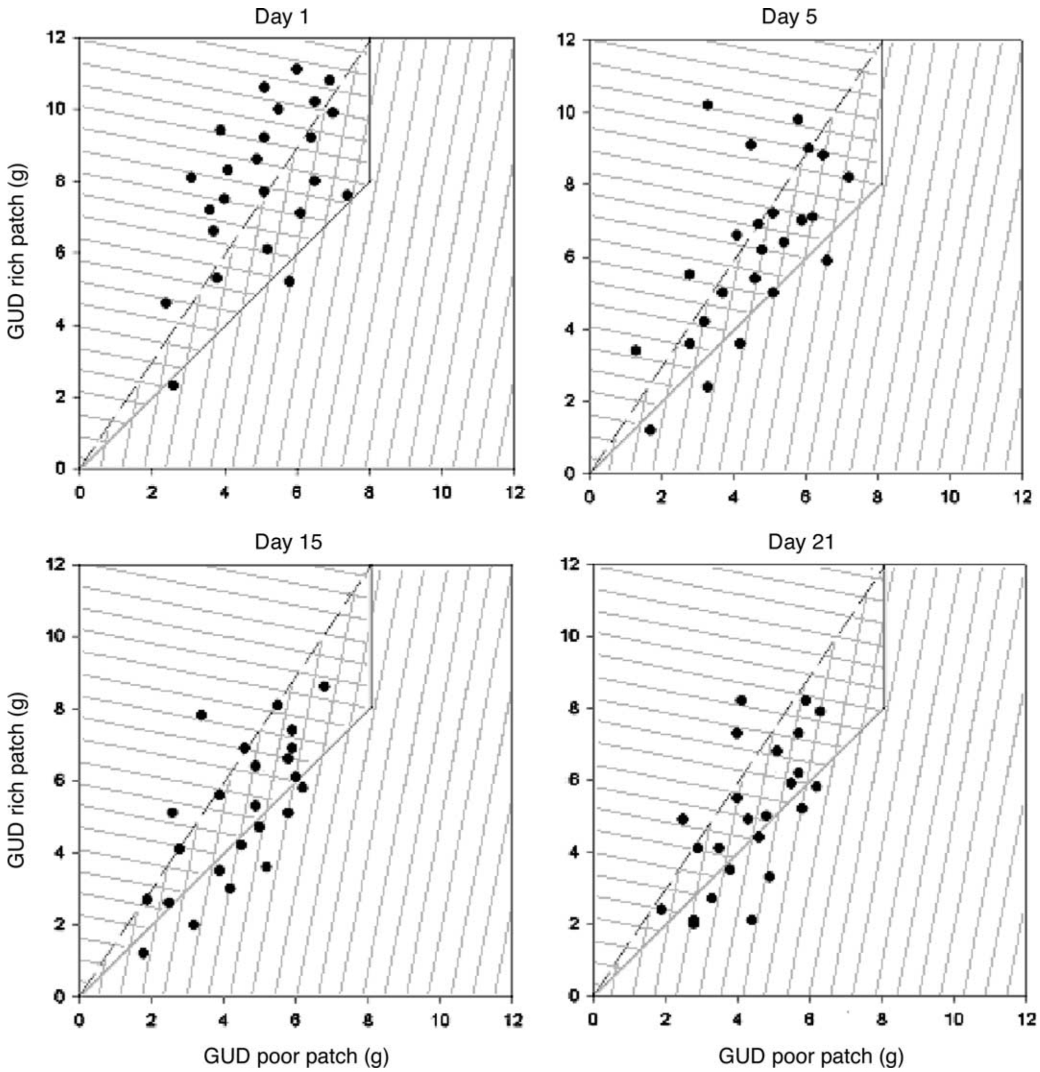

Fig. 3. Results of paired GUDs (in grams left in the rich versus the poor patch) for the first, and last day of experimentation (day 21), and for days 5 and 15 (i.e. when a consistent change was statistically detected). Each dot represents the GUD after a trial of an experimental subject. The continuous and segmented lines show the optimal foraging and the density-independence predictions, respectively. Shading lines with positive slopes indicate the area with positive density-dependence; shading lines with negative slopes indicate the area with under-exploitation of the rich patch.

tion of rich patches (Fig. 2, 3), therefore supporting a Bayesian foraging strategy. Finally, from day 15 and afterwards, degus maintained their pattern of positive-density dependent foraging (i.e. most data points lay below the density-independence line, paired sign tests, $P < 0.0066$, for each day; Fig. 2b), while they exploited rich and poor patches to an overall similar level, thus tending to equalize GUDs (Fig. 2c). This pattern was observed consistently from day 15 to day 21 (Fig. 3), and agrees with a prescient foraging strategy (Valone and Brown 1989). We observed a large variability among individuals (Fig. 4). Some subjects showed no clear pattern throughout time (Fig. 4a), while others revealed that learning made them to exploit patches more efficiently (Fig. 4b).

Figure 5a shows the ratio between GUDs of rich and poor patches throughout consecutive experimental daily trials. In this plot, an omniscient optimal forager should show a horizontal line intercepting a GUD ratio of one (i.e. equalization of GUDs). The ratio of GUDs between rich and poor patches consistently declined throughout the experiment (repeated measures ANOVA on logarithmically transformed data, $F(20,23) = 2.77$, $p = 0.0001$; Fig. 5a), from indifference to a ratio value of 1.5 (i.e. the ratio of initial densities) during the first days, toward indifference to a ratio value of 1.0 (i.e. GUD

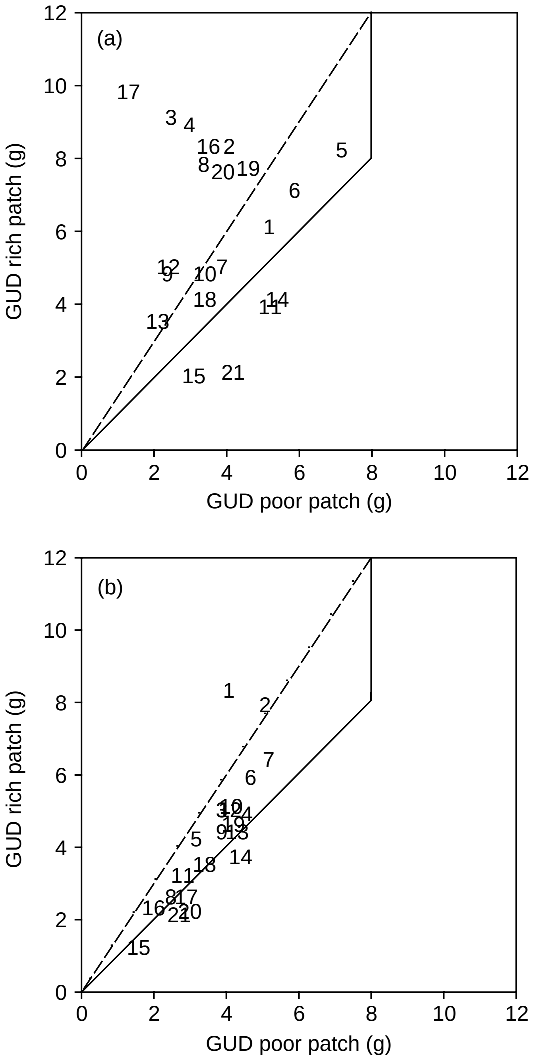

Fig. 4. Results of paired GUDs (in grams left in the rich versus the poor patch) throughout the daily sessions for two different subjects. Each data point is shown by the corresponding day of the experiment (e.g. 5 means fifth day). (a) Subject 19 exemplifies a sub-set of subjects that did not show any learning pattern throughout the experiment. (b) Subject 15 is a representative of those degus who followed a clear learning pattern throughout the experiment, with most data points lying around GUD equalization.

equalization) during the final days of the experiment. Further, seeds consumed in each patch increased during the first 3 days, and then stabilized (Fig. 5b). More seeds were captured in rich patches. Higher food consumption and GUD ratios reaching a value of one indicate that degus increased their foraging efficiency with repeated experience to the experimental environment.

We carried out correlation analyses for each subject comparing GUDs between rich and poor patches. To be consistent with the population pattern observed, we compared subjects from two periods with similar patterns of density-dependence and patch exploitation (Fig. 2b–c), thus we made within-subject comparisons between period from day 5 to 11, and period from day 15 to 21. Spearman rank correlations showed that most subjects had positive relationships between the GUDs of both patches, although eight and ten subjects out of 24, had significant correlations, for days 5–11 and 15–21, respectively. Mean correlations (±SE) were 0.614 ± 0.059 and 0.573 ± 0.067 for periods 5–11 and 15–21, respectively (see Appendix 1 for individual data). We also carried out t-tests within subjects to compare regression slopes with those expected for density-independence, and GUD equalization. The within-subject comparisons of slopes between periods were uneven among subjects. We expected that if animals were incapable of assessing resource density accurately (i.e. if they can not equalize GUDs), the ratio of GUDs should reflect the ratio of patch qualities. During period from day 5 to 11, ten degus differed significantly from the density-independence slope, while only two subjects differed from GUD equalization. During period from day 15 to 21, eight subjects differed significantly from density-independence, and two had different slopes compared to GUD equalization (Appendix 1). When a correction for multiple comparisons is carried out, then only four subjects differ from the density-independent slope during the period day 15–21; the remaining subjects do not differ from the expected slopes of GUD equalization and density-independence (Appendix 1).

Within-trial analyses comprised the evaluation of dependent variables at the initial and final phases of each experimental session, at the beginning (from day 1 to 4) and the ending (from day 17 to 21) periods of the experiment. In order to detect short-term changes in behavior within sessions, from the video records we analyzed the data produced during the initial 25% (i.e. from 0 to 25% of time) and final 25% (i.e. from 75% to 100%) of total experimental time. During the beginning days of the experiment, degus did not allocate different amounts of time to a given patch during the initial and final phases of experimental sessions (Fig. 6; Wilcoxon signed rank test, $P>0.3$). However, after day 17, degus had longer visits to the rich patch at the initial phase of sessions, compared to the time allocated at the final phase of sessions (Fig. 6; Wilcoxon signed rank test, $P=0.046$). The number of visits did not show any difference between phases within sessions, neither at the beginning (Wilcoxon signed rank test, $P>0.4$), nor the ending period of the experiment (Wilcoxon signed rank test, $P>0.2$). From the video records we could also examine the sequence of partial GUDs at successive visits and departures from each patch within sessions (see Fig. 7 for two different subjects). Degus visited both patches several times within any given trial. We observed a high variability between subjects, with some degus

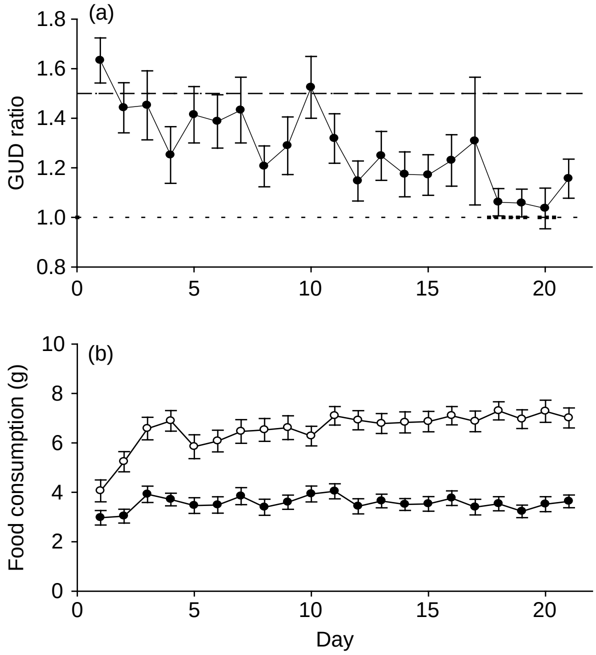

Fig. 5. (a) The ratio of GUDs between rich/poor patches as a function of consecutive daily trials. The segmented horizontal line indicates a ratio = 1.5, i.e. the ratio of initial food densities between patches. The dotted line indicates a ratio = 1.0, i.e. equalization of GUDs across patches. (b) Total food consumption from each patch as a function of consecutive daily trials. Rich and poor patches are show by empty and filled circles, respectively. In each plot, data represents the mean ± SE, n = 24 for each data point.

performing very close to prescient foraging, while other deviating considerable in some sessions (Fig. 7).

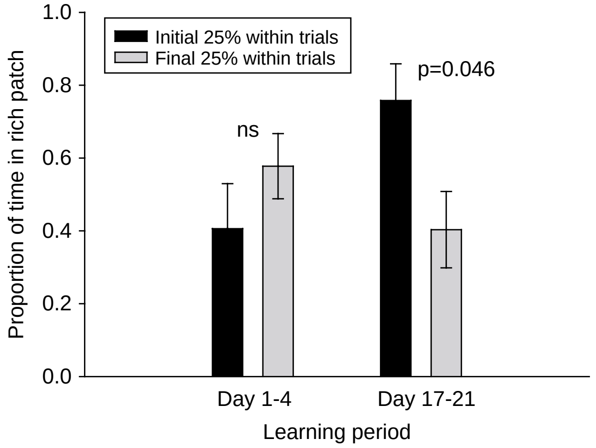

Fig. 6. Within-trial time allocation to the rich patch at the beginning (between day 1 and 4) and at the ending period (between day 17 to 21) of the learning experiment. In each period, the initial 25% of exploitation time (black bars) and the final phase 25% of exploitation time (grey bars) of experiments are shown. Data is the mean (±SE) proportion of time allocated to the rich patch. An ns indicates a non-significant result.

The video records also permitted to analyze the type of patch first visited on the beginning of experimental sessions. This analysis showed that the first visits were significantly biased toward the rich patch after a learning period of several days. During period from day one to four, only 9 subjects out of a total of 24, visited the rich patch first, while during the period from day 17 to 21, 17 degus visited the rich patch first (paired sign test, $p = 0.0215$). Overall, most degus learned to initiate each foraging session from richer patches, although, as mentioned, several subjects were highly variable between trials (see Fig. 7 for two representative subjects).

Discussion

Results revealed that changing patterns of density-dependence and relative exploitation of patches throughout time agree with the notion that foraging strategies for patch assessment can change and improve when resource patches are highly predictable. The population-level as well as the within-trial analysis agreed with this viewpoint. Although the within-subject data did not strongly support this contention, certainly it did show a changing pattern of patch exploitation throughout time, consistent with an improvement of assessment ability. During the beginning period of the experiment, degus exploited patches in a manner consistent with a fixed-time foraging strategy, implying that foragers devoted similar amounts of time to each patch independently of food density. Treating patches with equal or random effort is the optimal strategy when foragers cannot extract information about patch quality (Iwasa et al. 1981, Valone and Brown 1989), because the environment is highly variable, animals have no memory, and/or they require longer experience to attain relevant information. However, after a few days, degus changed their pattern of density-dependence, and foraged patches according to Bayesian assessment. This result suggests that degus were capable of acquiring information about patch quality, and that they used this information for patch assessment. Results also showed that after two weeks of daily trials, degus shifted their foraging pattern once more, evidencing the possession of a finer degree of information about patch quality; they exploited patches in agreement with a prescient foraging strategy (Valone and Brown 1989). Under these conditions, foragers exploited patches in a positive density-dependent pattern, and equalized GUDs across patches, and hence they were using more reliable information about patch quality, information only capable of being obtained through adequate experience. Constantly renewing patches offer reliable information, and hence foragers took advantage of this, improving patch assessment and exploitation significantly. Nevertheless, animals with poor memory capacities could have based their decisions

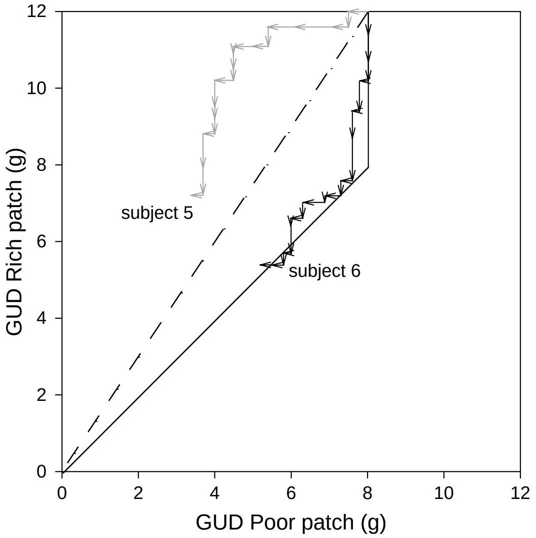

Fig. 7. Within-trial dynamics of patch exploitation for two different representative subjects. As animals visited and abandoned each patch repeatedly, they produced partial GUDs within an experimental session. Grey and black arrows for subject 5 on day 17, and subject 6 on day 19, respectively. Arrows indicate the direction of foraging and the partial GUDs after each visit within a trial. As shown, at the beginning of the trial, subject 6 allocated most, but not all, of its foraging effort to the rich patch, but when GUDs approximate equalization, it continued exploiting both patches more or less in similar proportions; it quitted foraging near GUD equalization, i.e. subject 6 approximates to the behavior expected for an optimal forager with perfect information. On the contrary, subject 5 first allocates significant amounts of effort to the poor patch, and then switches, though not completely, to the rich patch, however, the point of final GUDs is far located from the equalization line.

not in a "longer-term" Bayesian estimation, but using some sort of "within-day" assessment, beginning each foraging day with a prior information only based on the previous day's final distribution. However, our results suggest that degus appear to use such "longer-term" memory to accumulate estimates of patch qualities across several days, and they support the general view that predictable information (in this case constant patch renewal and patch spatial position) offers the opportunity of accumulating more reliable information about resources allowing improvements in feeding performance. An increase in foraging efficiency due to learning was evident in the augmentation of food consumption during the initial days of experimentation, and in the overall trend toward GUD equalization observed throughout the whole experiment. Subjects that nearly equalize GUDs between patches reduce missed opportunity costs (Valone and Brown 1989).

The present study provides some hints about the dynamics of previous information use by showing that patch assessment, and hence prior information, can change in an ecological time scale. Experimental subjects had previous experience with the type of food and patch used, but no previous specific experience with the experimental set-up. Therefore, degus did not have previous information (or prior distribution, for the case of Bayesian updating) about the actual quality of patches. Although most animals might gain some kind of information from a single experience, results suggest that degus required several days of information gathering to improve foraging performance. Consistent with this idea, degus showed a fixed-time foraging strategy at the initial period of the experiment before patches had been properly assessed. After approximately five days, when presumably more information had been gathered, they changed their behavior towards a Bayesian strategy. Degus seem to have formed a prior distribution about the distribution of prey between patches, and they combined it with information about current exploitation to assess patch quality. A study by Valone (1992) reported that black-chinned hummingbirds used prior information after approximately twenty-five experimental patches had been visited, although he did not evaluate the precise temporal dynamics of patch exploitation. From a broadly based definition of information use, we suggest that degus use prior information and current information for their decisions. If this information use agrees exactly with Bayesian updating is still an open question (cf. Kahneman et al. 1982, McKenzie 2003, for various views in the human literature). It is possible that animals in many situations use a decision process that agrees with Bayesian decision-making, but the mechanistic system that governs behavioral decisions might be a neurally-based process, producing certain rules of thumb congruent with different behavioral strategies, depending on the particular conditions and options. Our results suggest the Bayesian behavior observed in previous patch assessment studies could also be the result of short-term evaluations and/or lack of resource predictability (Valone and Brown 1989, Olsson et al. 1999, van Gils et al. 2003). In this vein, Valone (1991) found that given enough environmental predictability, animals become prescient foragers (Valone 1992). In our experiment, as the environment continued to offer predictable daily renewing patches, degus could even improve their knowledge about patch quality, and by day fifteen, subjects equalized GUDs across patches, at the population level. Further, the within-subject data showed that GUDs slopes between patches did not differ from equalization, and more subjects differed from density-independence by the end of the learning period. Accordingly, degus used more precise information about patches to increase their foraging performance, following a prescient strategy. This general pattern was maintained unalterably until the end of the experiment.

Theoretical models of patch assessment normally have assumed that foragers have precise information concerning the probability that a randomly chosen patch from their environment contains a given quantity of prey (Green 1980, Iwasa et al. 1981, McNamara 1982, Olsson and Holmgren 1998). How can this information be obtained? A previous model by Rodríguez-Gironés and Vásquez (1997) analyzed this question using Bayesian updating. In the model, foragers experienced an environment where the number of prey per patch followed a gamma distribution (DeGroot 1986), which makes it possible to choose mean and variance independently. Hence, several prey distributions could be studied simultaneously (e.g. regular, random, and clumped). Foragers started patch exploitation with a prior probability density function for the two parameters of the gamma distribution, and an estimate of the long-term average prey capture rate. In essence, the foragers had information about the likelihood that the mean and variance of the number of prey per patch had certain values (Rodríguez-Gironés and Vásquez 1997). After exploiting a patch, a forager updated its probability distribution. The simulations showed that, given enough time, foragers eventually acquired perfect knowledge about the distribution of prey in the environment (see Fig. 3 in Rodríguez-Gironés and Vásquez 1997). As a general rule, information about the mean number of prey per patch was acquired faster than information about the variance of the distribution. Another pattern that emerged from that study was that learning proceeded faster in poor than in rich environments. In rich environments the long-term intake rate was high and, as a consequence, the quitting threshold point was also high; predators left patches after capturing few preys and could only poorly estimate the richness of the visited patches. As a consequence, they gathered information about the environmental distribution of prey very slowly. In poor environments, on the other hand, patches were exploited virtually to depletion. When leaving a patch, predators had very good estimates of the number of prey that were initially in the patch and they could get a precise idea about the quality of patches with fewer visits (Rodríguez-Gironés and Vásquez 1997). Although that study did not directly answer the question about the origin of the prior information, it provides some ideas about the long-term dynamics of information updating and patch assessment. Interestingly, the results of our experiment showed that after several days, the mean of GUDs were equalized across patches, but the variability of GUDs did not diminish throughout the whole experiment.

Did degus use Bayesian assessment throughout the entire experiment? Degus might have updated their assessment of the prior distribution of resources as they moved back and forth between patches. In a given day, degus would have a different prior distribution each time they entered a patch. If degus recognized patches as different from one another, they should spend relatively less time in the poor patch for each patch visit, because they can obtain precise information about its quality in less time, as suggested by Rodríguez-Gironés and Vásquez (1997). An animal can use long-term memory (sensu Mazur 1998) to accumulate estimates of patch quality through the days, and each time it enters a patch, it can update its long-term estimate of resource distribution. Therefore, throughout time, such a Bayesian forager should improve foraging success and approximate to a prescient strategy (but see below). If patch predictability endures, such a Bayesian forager may be indistinguishable from a prescient forager.

After enough learning occurred (i.e. after two weeks), moment-by-moment analysis on patch exploitation revealed that most degus allocated more time to the rich patch during the initial phase of exploitation within a given trial. By the end of a trial, after both patches had been copiously exploited, degus allocated similar amounts of time to exploiting both patches. The results indicated that a number of subjects allocated their behavior according to patch qualities, initially allocating their exploitation to the rich patch almost exclusively, and once GUDs tended to be equal, they shifted toward exploiting both patches equivalently (Fig. 7). Interestingly, this behavior agrees in general with matching, an empirically based choice rule observed in psychological experiments, where animals have been found to allocate their foraging effort according to patch returns (Wildhaber et al. 1994, Mazur 1998, Shettleworth 1998). If animals used a matching rule they could sampled both patches back and forth, and memorized the location of the rich and poor patch. Therefore after enough learning has occurred, at the beginning of each trial, we would expect animals to bias their foraging effort to the rich patch until GUD are equalized among patches. However, a matching rule does not predict a complete bias toward the rich patch; both patches should be exploited. At the beginning of trials, several degus biased their foraging toward the rich patch, although they continued exploiting the poor patch as well (Fig. 7). However, many subjects did not follow this consistent pattern. Even after two weeks of experience, in some sessions, a number of subjects started patch exploitation biased toward the poor patch (Fig. 7). Although time allocation within trials broadly agreed with the population level results on GUDs, within-subject data did not show a strong trend throughout time, and it was characterized by a high variability. Though we aimed that the within-trial analysis could help explaining population and within-subject results, we note that in some situations this is not the case. For example, in experimental psychology, choice behavior at the whole-trial and at the moment-by-moment level have frequently failed to agree with each other, and the results of one approach have been difficult to translate into the results of the other, making explanations unattainable (see molar and molecular analysis of behavior in Mazur 1998). On the other hand, we suggest that at least partially, the variability observed in GUDs through time within subjects is the result of allowing animals food access while not in experimentation. As mentioned in the methods, we allowed degus free access to supplemental food two to three times a week. This uncontrolled source of food could have influenced significantly the dynamics of food consumption in the experimental sessions (Houston and McNamara 1989). Moreover, it could have hindered a decrease on individual variability around GUD equalization. For future studies, we recommend the use of a balanced food item in strictly closed economy experimental designs, as well as detailed behavioral recording within each trial. Such a design could decrease foraging variability and could be used to assess the precise patch-leaving rule that foragers use (van Gils et al. 2003). More globally, such approach will contribute to the ongoing amalgamation of mechanistic and evolutionary approaches to animal behavior.

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References

Alonso, J. C., Alonso, L. M., Bautista, L. M. et al. 1995. Patch use in cranes: a field test of optimal foraging predictions. – Anim. Behav. 49: 1367–1379.

Bozinovic, F. 1995. Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. – J. Mammal. 76: 627–637.

Bozinovic, F. and Vásquez, R. A. 1999. Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. – Funct. Ecol. 13: 602–610.

Bozinovic, F., Bacigalupe, L. D., Vásquez, R. A. et al. 2004. Cost of living in free-ranging degus (*Octodon degus*): seasonal dynamics of energy expenditure. – Compar. Biochem. Physiol. A – Mol. Integr. Physiol. 137: 597–604.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – Behav. Ecol. Sociobiol. 22: 37–47.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Dall, S., Giraldeau, L.-A., Olsson, O. et al. 2005. Information and its use by animals in evolutionary ecology. – Trends Ecol. Evol. 20: 187–193.

DeGroot, M. H. 1986. Probability and statistics. – Addison-Wesley Publishing Company, Reading.

Elliott, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. – Freshwater Biol. Ass., Sci. Publ. No. 25. The Ferry House, London.

Fulk, G. W. 1976. Notes on the activity, reproduction, and social behavior of *Octodon degus*. – J. Mammal. 57: 495–505.

Giraldeau, L. A. 1997. The ecology of information use. – In: Krebs J. R. and Davies N. B. (eds), Behavioural ecology: an evolutionary approach. 4th ed., Blackwell Science, pp. 42–68.

Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. – Theor. Popul. Biol. 18: 244–256.

Houston, A. I. and McNamara, J. M. 1989. The value of food: effects of open and closed economies. – Anim. Behav. 37: 546–562.

Hunte, W., Myers, R. A. and Doyle, R. W. 1985. Bayesian mating decisions in an amphipod, *Gammarus lawrencianus* Bousfield. – Anim. Behav. 33: 366–372.

Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. – Am. Nat. 117: 710–723.

Kacelnik, A. and Krebs, J. R. 1985. Learning to exploit patchily distributed food. – In: Sibly R. M. and Smith R. H., (eds), Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Publications, pp. 189–205.

Kenagy, G. J., Vásquez, R. A., Nespolo, R. F. et al. 2002. A time-energy analysis of daytime surface activity in degus, *Octodon degus*. – Rev. Chilena Hist. Nat. 75: 149–156.

Kenagy, G. J., Vásquez, R. A., Barnes, B. M. et al. 2004. Microstructure of summer activity bouts of degus in a thermally heterogeneous habitat. – J. Mammal. 85: 260–267.

Kahneman, D., Slovic, P. and Tversky, A. 1982. Judgement under uncertainty, heuristics and biases. – Cambridge Univ. Press.

Kotler, B. P. and Brown, J. S. 1990. Rates of seed harvest by two species of gerbilline rodents. – J. Mammal. 71: 591–596.

Lagos, V. O., Contreras, L. C., Meserve, P. L. et al. 1995. Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. – Oikos 74: 259–264.

Mangel, M. 1990. Dynamic information in uncertain and changing worlds. – J. Theor. Biol. 146: 317–332.

Mazur, J. E. 1998. Learning and behavior (4th ed.). – Prentice Hall.

McKenzie, C. R. M. 2003. Rational models as theories – not standards – of behavior. – Trends Cognitive Sci. 7: 403–406.

McNamara, J. M. 1982. Optimal patch use in a stochastic environment. – Theor. Popul. Biol. 21: 269–288.

McNamara, J. M. and Houston, A. I. 1980. The application of statistical decision theory to animal behaviour. – J. Theor. Biol. 85: 673–690.

Meserve, P. L. 1981. Trophic relationships among small mammals in a Chilean semiarid thorn shrub community. – J. Mammal. 62: 304–317.

Meserve, P. L., Martin, R. E. and Rodríguez, J. 1983. Feeding ecology of two Chilean caviomorphs in a central Mediterranean savanna. – J. Mammal. 64: 322–325.

Meyer, M. D. and Valone, T. J. 1999. Foraging under multiple costs: the importance of predation, energetic, and assessment error costs to a Desert forager. – Oikos 87: 571–579.

Olsson, O. and Holmgren, N. M. A. 1998. The survival-rate – maximizing policy for Bayesian foragers: wait for good news. – Behav. Ecol. 9: 345–353.

Olsson, O. and Holmgren, N. M. A. 2000. Optimal Bayesian foraging policies and prey population dynamics – some comments on Rodríguez-Gironés and Vásquez. – Theor. Popul. Biol. 57: 369–375.

Olsson, O., Wiktander, U., Holmgren, N. M. A. et al. 1999. Gaining ecological information about Bayesian foragers through their behavior. I. A field test with woodpeckers. – Oikos 87: 264–276.

Rodríguez-Gironés, M. A. and Vásquez, R. A. 1997. Density dependent patch exploitation and acquisition of environmental information. – Theor. Popul. Biol. 52: 32–42.

Schmidt, K. A. and Brown, J. S. 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. – Am. Nat. 147: 360–380.

Shettleworth, S. J. 1998. Cognition, evolution, and behavior. – Oxford Univ. Press.

Shettleworth, S. J., Krebs, J. R., Stephens, D. W. et al. 1988. Tracking a fluctuating environment: a study of sampling. – Anim. Behav. 36: 87–105.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press.

Tamm, S. 1987. Tracking varying environments: sampling by hummingbirds. – Anim. Behav. 35: 1725–1734.

Valone, T. J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. – Anim. Behav. 41: 569–577.

Valone, T. J. 1992. Information for patch assessment: a field investigation with black-chinned hummingbirds. – Behav. Ecol. 3: 211–222.

Valone, T. J. and Brown, J. S. 1989. Measuring patch assessment abilities of desert granivores. – Ecology 70: 1800–1810.

van Gils, J. A., Schenk, I. W., Bos, O. et al. 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. – Am. Nat. 161: 777–793.

Vásquez, R. A. 1996. Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. – Ecology 77: 2343–2351.

Vásquez, R. A. 1997. Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. – Rev. Chilena Hist. Nat. 70: 557–563.

Vásquez, R. A., Ebensperger, L. A. and Bozinovic, F. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. – Behav. Ecol. 13: 182–187.

Wildhaber, M. L., Green, R. F. and Crowder, L. B. 1994. Bluegill continuously update patch giving up times based on foraging experience. – Anim. Behav. 47: 501–513.

Appendix 1

Summary of (a) Spearman rank correlations and (b) t-tests comparing observed versus expected slopes for (b.1) density-independence and (b.2) GUD equalization with data of each subject for two periods of the experiment (period from day 5 to 11; and period from day 15 to 21). Bold figures indicate statistical significance. An * indicates statistical significance after sequential Bonferroni′s correction for multiple comparisons.

Period	Subject	(a) Spearman correlation	Observed slope	(b) 1. Density-dependence		(b) 2. GUD equalization	
				t	p	t	p
Day 5–11:	1	0.518	0.995	−1.3140	0.2459	−0.0130	0.9901
	2	0.000	−0.237	−3.5145	**0.0170**	−2.5028	0.0543
	3	0.107	0.112	−5.3375	**0.0031**	−3.4148	**0.0189**
	4	**0.991**	0.993	−4.3997	**0.0070**	−0.0607	0.9539
	5	0.409	0.197	−3.3458	**0.0204**	−2.0619	0.0942
	6	**0.955**	1.318	−0.7961	0.4621	1.3909	0.2230
	7	**0.918**	1.1	−2.6392	**0.0460**	0.6598	0.5386
	8	**0.829**	0.62	−3.6071	**0.0154**	−1.5576	0.1801
	9	**0.883**	1.159	−1.7814	0.1350	0.8306	0.4440
	10	0.396	0.902	−0.7220	0.5026	−0.1183	0.9104
	11	**0.811**	1.898	0.9273	0.3963	2.0923	0.0906
	12	0.718	1.586	0.0648	0.9509	0.4413	0.6774
	13	0.536	1.061	−1.0880	0.3262	0.1512	0.8857
	14	0.09	0.144	−2.4279	0.0595	−1.5327	0.1859
	15	**0.999**	1.348	−1.2840	0.2554	2.9397	**0.0323**
	16	0.649	0.611	−3.6564	**0.0147**	−1.5999	0.1705
	17	0.561	0.935	−1.2311	0.2730	−0.1416	0.8929
	18	0.613	1.334	−0.4406	0.6779	0.8866	0.4159
	19	0.36	0.483	−2.5288	0.0526	−1.2855	0.2549
	20	0.721	0.752	−3.3834	**0.0196**	−1.1218	0.3129
	21	0.739	0.452	−3.8989	**0.0114**	−2.0387	0.0970
	22	0.382	0.676	−1.2490	0.2669	−0.4911	0.6441

Appendix 1 (*Continued*)

Period	Subject	(a) Spearman correlation	Observed slope	(b) 1. Density-dependence		(b) 2. GUD equalization	
				t	p	t	p
	23	**0.847**	0.827	−2.4907	0.0551	−0.6402	0.5502
	24	0.714	0.677	−3.5786	**0.0159**	−1.4045	0.2192
Day 15–21:	1	**0.844**	0.538	−6.7325	**0.0011***	−3.2333	**0.0231**
	2	0.000	0.222	−3.0126	**0.0297**	−1.8339	0.1261
	3	0.75	1.049	−1.8588	0.1222	0.2019	0.8479
	4	**0.779**	0.659	−5.7002	**0.0023***	−2.3112	0.0688
	5	0.685	0.183	−5.7435	**0.0022***	−3.5629	**0.0162**
	6	**0.982**	0.847	−3.7208	**0.0137**	−0.8718	0.4232
	7	**0.786**	1.265	−0.8936	0.4125	1.0077	0.3599
	8	**0.964**	0.994	−5.9611	**0.0019***	−0.0707	0.9464
	9	0.126	0.176	−2.2367	0.0755	−1.3920	0.2227
	10	0.571	1.236	−0.5446	0.6094	0.4869	0.6469
	11	0.324	0.835	−1.7442	0.1416	−0.4328	0.6832
	12	0.679	0.875	−2.0556	0.0950	−0.4111	0.6980
	13	**0.881**	1.093	−1.6252	0.1650	0.3714	0.7256
	14	0.396	0.477	−4.5100	**0.0063**	−2.3057	0.0693
	15	**0.821**	1.204	−1.2642	0.2619	0.8713	0.4235
	16	**0.786**	1.162	−0.9275	0.3962	0.4445	0.6752
	17	0.445	1.169	−0.4449	0.6750	0.2272	0.8293
	18	0	0.321	−3.1828	**0.0245**	−1.8330	0.1263
	19	−0.107	−1.029	−2.0691	0.0933	−1.6600	0.1578
	20	**0.883**	1.463	−0.0996	0.9245	1.2470	0.2676
	21	0.198	0.73	−0.9078	0.4056	−0.3183	0.7631
	22	0.577	0.695	−2.0091	0.1008	−0.7612	0.4809
	23	**0.857**	0.896	−2.0550	0.0950	−0.3538	0.7379
	24	0.536	0.66	−1.9731	0.1055	−0.7986	0.4607