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Patch leaving in humans: can a generalist adapt its rules to dispersal of items across patches?

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We used a computer game to examine three aspects of patch-leaving decisions in humans: how well do humans perform compared to the optimal policy, can they adjust their behaviour adaptively in response to different distributions of prey across patches and on what cues are their decisions based? Subjects earned money by catching fish when they briefly appeared within a pond; the timing of appearances was stochastic but at a rate proportional to how many fish remained. Caught fish were not replaced and ponds varied in how many fish they initially contained (according to three different distributions). At any point subjects could move to a new pond, but travel took some time. They delayed this switch much too long. Furthermore, regardless of the distribution of prey, subjects spent longer at ponds where they had found more items (contrary to optimality predictions in two of the environments). However, they apparently responded not to the number of captures directly (despite this appearing on screen) but to the current interval without a capture, to the interval preceding the last capture, and to the time spent at the current pond. Self-reports supported this order of cue importance. Subjects often left directly after a capture, perhaps an example of the Concorde fallacy. High success rate in the preceding patch decreased residence time and subjects appeared to be learning to leave earlier over the latter two thirds of the experiment. Minimization of delay to the next capture alone might explain some of the suboptimal behaviour observed.

Keywords: Concorde fallacy; delay minimization; evolutionary psychology; giving-up time; incremental rule; marginal value theorem; optimal foraging; rule of thumb; simple heuristic; task switching

Suppose, like one of us, that you sometimes spend a week turning over thousands of leaves on the forest floor searching for slugs. Twenty minutes can often pass without finding one and before then you would probably already have moved on and tried another likely looking hollow. But if you have found one or two specimens in a particular spot, should you stick there because it appears a good spot or move because it is liable to be exhausted? These conflicting arguments must often have concerned our hunter–gatherer ancestors. The answer depends on how evenly prey are dispersed across suitable patches. One can gauge this only from foraging success at nearby spots searched earlier, although prior experience elsewhere with similar prey might help suggest which patch-leaving rules work best.

Optimal foraging theory has provided the optimal solution to the problem, although only once the prey distribution has already been learnt. The classic result is the marginal value theorem (Charnov 1976), that foragers should leave a patch when the current rate of return falls below the mean rate under the optimal strategy. However, this rule becomes only an approximation to the solution when patches contain few discrete items, because stochasticity disrupts estimation of current rate of return. Presently we detail the optimal strategies in this case.

Numerous studies have tested how well animals approximate these optimal policies (Nonacs 2001), mostly in ovipositing insect parasitoids (van Alphen et al. 2003; Wajnberg 2006) but also in fish, birds and mammals

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(e.g. Ydenberg 1984; Redhead & Tyler 1988; Marschall et al. 1989; Kamil & Clements 1990; Kramer & Weary 1991; Agetsuma 1999; van Gils et al. 2003). However, we have found scarcely any tests on humans. In this study we used a computer game, based on fishing at a succession of ponds, to measure how well humans perform compared with the optimal solution. We also investigated the cues and rules of thumb used to decide when to switch patches. Thirdly we tested whether humans adjust their strategy to the distribution of prey, as they should. Humans are a particularly appropriate animal for this test because we are extreme generalists and should surely be adapted to forage on some foods that are evenly distributed across suitable patches and some that are concentrated in a minority. Alternatively, rather than facultatively adjusting, do we gamble on the commonest sort of distribution (probably aggregated) or perhaps use a robust rule that performs reasonably well with all distributions?

Previous Work on Humans

Anthropologists have invoked the marginal value theorem to elucidate a variety of decisions of native peoples: when to leave one hunting or fishing ground, when to move herds to fresh pasture, when to cultivate a new patch of forest (Smith & Wishnie 2000), how far food is processed before carrying it home (Metcalfe & Barlow 1992) and how much a carcass is butchered (Burger et al. 2005). It is also often invoked as a more parsimonious explanation of cases of apparent conservation, because it predicts switching patches before complete depletion (Smith 1983; Smith & Wishnie 2000). However, anthropologists' tests of whether humans really follow the optimality predictions are qualitative and weak (among the stronger examples are Smith 1991 and Aswani 1998).

The patch-leaving analogy has also been invoked by cognitive scientists to model foraging for information (Pirolli & Card 1999; Pirolli 2005). For instance Pirolli (2005) studied when subjects started anew with an Internet search (cf. switching patches) instead of following links within the current web page (cf. foraging within a patch). However, the model that Pirolli (2005) applied to explain these data was unconnected with those considered in behavioural ecology.

The data most relevant to patch-leaving decisions of humans come from operant experiments (Wanchisen et al. 1992; Hackenberg & Axtell 1993). Subjects had to press a key numerous times to get a reward. For one option (progressive ratio) the required number increased with each trial (cf. patch depletion). For the alternative option (fixed ratio) the required number was fixed, and, crucially, choosing this option reset the number of presses required by the progressive-ratio option to the minimum (cf. travel to a fresh patch). Subjects responded adaptively to changes in the fixed-ratio requirement and often found the optimal response. Results were similar when subjects had merely to wait particular times after selecting an option before receiving each reward (progressive interval; Hackenberg & Axtell 1993).

Evidence of Adjustment to Dispersion across Patches

Patch-leaving decisions are known to adjust facultatively to a variety of aspects of the environment (e.g. previous patch quality, prior experience of competitors, perceived mortality risk, travel time: Roitberg et al. 1993; Visser et al. 1992; Cuthill et al. 1994; Goubault et al. 2005; Tentelier et al. 2006; Wajnberg et al. 2006). Also, different species and populations of parasitoid wasps are hardwired to use different patch-leaving rules that would adapt them to different degrees of host dispersal across patches (Wajnberg et al. 1999, 2003). But few studies have tested for a similar facultative adjustment.

Vos et al. (1998) studied switching behaviour in a parasitoid of two congeneric hosts, one with an aggregated dispersion and one more solitary. The cues that were significant in each environment (host) differed appropriately (although the difference was not formally tested). However, the parasitoids might feasibly use host identity as a cue to switch between alternative hardwired rules, whereas our human subjects could learn the distribution and appropriate rules only from their own foraging success on a novel resource. Three experiments involving parasitoids, fish and birds have failed to detect such an ability (Marschall et al. 1989; Dall 1995, chapter 5; Burger et al. 2006). But, although one experiment in blue jays, *Cyanocitta cristata*, also failed to find a difference (Kamil & Yoerg 1985), another suggested greater dependence on time since the last capture when patch quality was more variable (Kamil & Clements 1990). Two other examples also show an ability to change the form of a rule in a way which would enable adaptation to different dispersions (see Theory and Predictions), although other factors triggered the change. Great tits, *Parus major*, switched either after a fixed number of rewards or after a particular giving-up time, depending on whether intercapture intervals were deterministic or stochastic (Ydenberg 1984). And in one insect parasitoid species ovipositions either increased or decreased tendency to switch, depending on egg load (Outreman et al. 2005).

THEORY AND PREDICTIONS

Our experiment involves a solitary forager encountering prey randomly in a patch, with encounter rate proportional to number of prey remaining. Iwasa et al. (1981) showed that, if the forager knows the distribution of the number of items per patch, the a posteriori probability that n items remain depends on only the number of items caught in the current patch (N) and the time spent on it (T). The optimal policy when to switch patches thus also depends on only N and T. There is no additional advantage to remembering time since the last prey capture (I) or timings of earlier captures. Given this, the optimal policy may be calculated by dynamic programming (e.g. Green 1980, 2006; Olsson & Holmgren 1998).

The optimal policy specifies whether to leave or stay given each combination of N and T and its form depends on the distribution of items per patch (Iwasa et al. 1981;