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Giving-Up as a Poisson Process: The Departure Decision of the Green Lacewing

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Predators that forage for aggregated prey appear to require a decision rule for determining the point at which to discontinue their search in a given prey patch and move on to another. Although the optimum rule depends heavily on features of the searching behavior of the predator and the distribution of the prey (Oaten 1977), most previous authors have assumed that the decision must involve an assessment of the capture rate within a patch and a comparison with the mean capture rate in the environment as a whole (Krebs 1978). When the perceived quality of the given patch becomes significantly less than the expected quality of the next one, the predator should leave. Because the time interval since the last prey capture is the most readily available measure of the instantaneous capture rate, it has been suggested that foraging animals may monitor this interval and leave the patch when it exceeds some critical value (Krebs 1978). The "giving-up time," by this argument, should be uniform across patches within a habitat and inversely proportional, across habitats, to the mean prey availability. Although this inference has been supported by empirical studies, Cowie & Krebs (1979) have recently suggested that the correlation could be a sampling artifact. Even if departure from a patch were in-

dependent of the interval between prey encounters, the mean giving-up time would still be shorter, on the average, in a rich environment than in a poor one. A re-analysis of several experiments on patch foraging by predatory insects, described in detail elsewhere (Bond 1980), can be used to test Cowie & Krebs' independence hypothesis.

The predatory larva of the green lacewing, *Chrysopa carnea* Stephens, responds to an encounter with either a prey item or a branch terminus with a transient increase in searching intensity and thoroughness. Under the assumption that an animal's hunger level is its simplest accessible indicator of mean prey abundance, differences in prey availability were simulated by satiating the animals and then depriving them of food for either 2 or 8 h. Contact with prey or a suitable patch substrate was initiated by the experimenter subsequent to the deprivation, thereby separating the effects of prey encounter and prey density and allowing an unequivocal test of the causal prediction. Three separate measures of giving-up time were obtained: the duration of searching within a limited radius after prey contact in an open field, the duration of searching after reaching the tip of a vertical rod, and the time spent feeding on a

Table 1. Giving-up Time Durations and Survivorship Functions

Measure (h)	N	Mean (s)	Ratio	D+	D-	Shape	Signif.
1. Open-field search							
2 h	74	4.8	0.433	0.176	0.022	concave	$P < 0.01$
8 h	66	11.1		0.191	0.017	concave	$P < 0.01$
2. Rod search							
2 h	33	64.4	0.474	0.062	0.022	concave	$P > 0.1$ (NS)
8 h	37	135.8		0.078	0.045	concave	$P > 0.1$ (NS)
3. Feeding							
2 h	16	158.5	0.420	0.199	0.069	concave	$P > 0.1$ (NS)
8 h	17	377.2		0.036	0.120	convex	$P > 0.1$ (NS)

$D+$ and $D-$ are, respectively, the upper and lower Kolmogorov-Smirnov statistics of the given distribution. When $D+ > D-$ the log survivorship function is concave; when $D+ < D-$, it is convex. The expected ratio of prey availability was 0.400.

single prey item. The analogous ratio of prey availability was derived analytically from equations describing the dynamics of food deprivation and repletion (Bond 1980). As may be seen in Table 1, the ratios of the three time measures for 2-h animals to those for 8-h animals were comparable to the derived estimation, even when patch contact was manipulated independently. Giving-up time appears to be causally related to hunger, and thereby to prey availability, in accordance with the theoretical prediction.

Whether the decision to leave the patch is based on a time criterion is an independent question, however. The results could just as easily reflect a Poisson process, in which a random departure probability is set by the level of deprivation. To test this hypothesis, we must examine the probability distribution of the giving-up times. If the departure decision is timed, the distribution should exhibit a central peak, corresponding to the giving-up criterion, and the log survivorship function should be convex, with proportionately fewer observations at the extremes of the range. A linear function, on the other hand, would imply that the giving-up time is simply the expression of a constant, random departure probability. The null hypothesis of linearity was tested using Durbin's modification of the Kolmogorov-Smirnov statistic (Cox & Lewis 1966). The curves for the open-field data were more concave than would be expected by chance, suggesting that more than a single decision process may be involved, but no other significant deviations from linearity were observed (Table 1). Leaving a patch appears to be consistent with a Poisson process, in which the departure probability is determined solely by prey availability.

A Poisson decision process necessarily ignores the information provided by the patch-specific capture

rate, which could be significant if the number of prey per patch were constant, normally distributed, or truncated at some minimum value (Oaten 1977). Unlike vertebrates (Church et al. 1976), insects may lack the ability to judge relative durations, requiring them to adopt a simpler, more approximate decision heuristic. Whether this behavior is actually "suboptimal" clearly depends on the pattern of distribution of the prey. If the number of prey per patch approximated a Poisson distribution, the patch-specific capture rate would be uninformative, and the cost of a probabilistic departure would be minimal.

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