Oikos

o19278

Embar, K., Kotler, B. P. and Mukherjee, S. 2011. Risk management in optimal foragers: the effect of sight-lines and predator type on patch use, time allocation, and vigilance in gerbils. – Oikos 120: 1657–1666.

Appendix A1

Harvest rates curves

Harvest rate curves allow us to visually portray the gerbils' use of their behavioral tools of time allocation and vigilance. The time that foragers spend in each food patch during the night, combined with the GUD data and Holling's disc equation enable us to draw the harvest rate curves. We construct harvest rate curves following Kotler and Brown 1990. Integrating Holling's disc equation(below) yields an equation that relates t, the time spent in a patch, to *h*, the handling time, and *a*, the encounter rate with food items (attack rate). The variables associated with *h* and *a* are both in terms of initial and final resource densities in an exploited patch. Therefore, by regressing the cumulative duration of time spent by gerbils in a patch with the appropriate variables, we obtained estimates for *h* and *a* for the various conditions that the gerbils faced (various combinations of moon phase, cover, fence). Overall, Holling's disc equation provided a good fit to the data. Because of the many combinations, though, estimates of both h and a simultaneously can become unreliable as sample size decreases (Olsson and Brown 2001). Therefore, we used an estimate for *h* of 22.883 obtained under similar conditions from gerbils foraging in the vivarium under standard operating conditions (Mukherjee et al unpubl.). We estimated the various values of *a* by placing the estimated *h*, along with initial and final food densities and foraging times into the equation and extract the slopes of the rearranged single variable equations. We then used the resulting values along with Holling's disc equation to obtain the harvest rate curves. These graphs are summaries that allow a visual assessment of the roles of time allocation and vigilance in risk management as explained below. The curves are based on GUD data and cumulative duration data, and so are the appropriate statistical analyses (Supplementary material Appendix A2).

Comparing the treatments' harvest rate curves and the mean quitting harvest rates among treatments show how the foragers alter their use of time allocation and vigilance to manage risk. Figure A1-1 shows two different harvest rate curves and three different giving up densities. Consider first a forager that manages risk solely through time allocation and two patches that differ solely in risk. In this case, the harvest rate curve itself is unchanging regardless of risk of predation, while point A refers to the safe patch, to which the forager allocated more time, and point B refers to the risky patch, to which the forager allocated less time. That is, the forager allocated more time or less time to the patch, depending on risk. The upper harvest rate curve in Fig. A1-1 depicts this case. Here, the forager devotes more time to safer patches, 'travelling' along the harvest rate curve from the upper right to the lower left as it depletes the patch, and leading to a lower GUD and a lower quitting harvest rate.

Next consider a forager that manages risk solely through changes in vigilance. Such changes in vigilance will lead to different harvest rate curves that rise at different rates and to different asymptotes, depending on how much attention the forager devotes to looking out for predators and how much it devotes to harvesting. The two curves in Fig. A1-1 correspond to a less vigilant animal (upper curve) and a more vigilant animal (lower curve). Such a forager would equalize QHR across patches but the GUD would be lower in the safer patch. That is, it would be less vigilant in and leave the safe at point B, and be more vigilant in and leave the risky patch at point C. In reality, foragers will use changes in both time allocation to manage risk, and graphs such as figure 6 will allow us to visualize how the use of the two tools are combined and altered (vector of the two effects connecting points A and C).

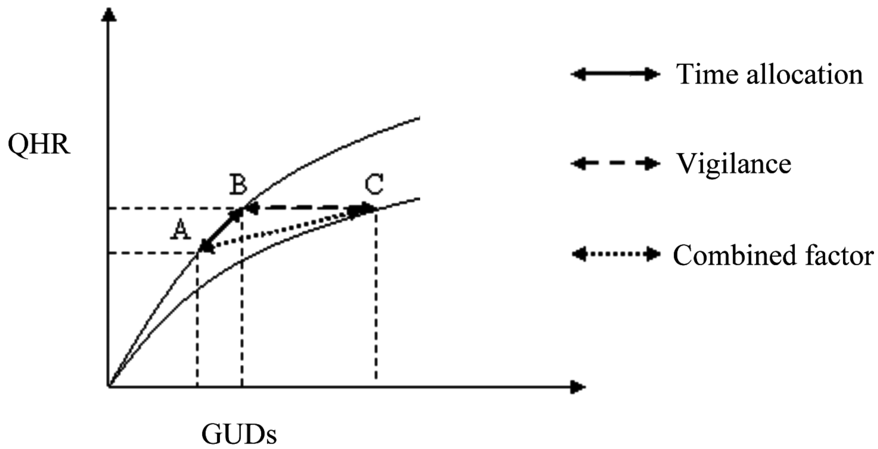


Figure A1-1. The two ways in which a forager can respond to food patches varying in predation risk (after Brown 1999). The arrow connecting points A and B illustrates the use of only time allocation to manage risk between safe (A) and risky (B) patches. The arrow connecting points B and C illustrates the use of Vigilance only to manage risk between safe (B) and risky (C) patches. The arrow connecting point A and C illustrate the joint use of both time allocation and apprehension to manage risk between safe (A) and risky (C) patches.

To plot the harvest curve for a particular set of conditions, we first calculate the QHR and then plot the QHR against the GUD. To do so, we follow the approach of Kotler and Brown 1990. Kotler and Brown (1990) started with Holling's disc equation describing the QHR:

$$QHR = \frac{\partial N}{\partial t} = \frac{aGUD}{1 + ahGUD} \qquad (1)$$

where N is the remaining abundance of resource, *a* is the forager's attack rate, and *h* is the forager's handling time on the resource. They then integrated this equation over the period of patch exploitation to yield the following equation:

$$t=(1/a)[\ \ln (initial/GUD)\ ] + h\ (Initial - GUD) \qquad (2)$$

The first term on the right hand side of the Eq. 2 is the time spent searching for the resource in the patch. This part of the expression incorporates the diminishing return to harvest rate from spending additional time exploiting the patch. As remaining resource abundance in the patch declines, the average time required to search for and find the next item increases. The second term on the right is the time spent handling encountered items. Once the GUDs and the cumulative foraging duration are known, the attack rate *a* can be calculated as the coefficient of the regression of: [t – *h* (initial – GUD)] against [ln (initial/GUD)]. In this study we allowed *h* to equal 22.883 s g^{-1} and obtained values for t and GUD from the experiments described in the main text. Running the regression yields estimates for *a*. Then values of *a*, *h*, and GUD can be plugged back into Eq. 1 to yield estimates of quitting harvest rate (QHR). It also yields the equation for the harvest rate curve for those conditions. We then plot this curve in a state space of quitting harvest rate and giving up density. Finally, we calculate the QHR for the mean GUD for those conditions and plot it on the curve.

Appendix A2

Table A2-1. Analysis of variance results table for giving up density with n = 216 and multiple R^2 = 0.941.

Source	Sum-of-squares	DF	Mean-square	F-ratio	p
Predator	2.954	2	1.477	36.412	<0.001
Moon	25.032	3	8.344	3.062	0.179
Cover	32.828	2	16.414	404.642	<0.001
Fence	4.261	2	2.131	52.527	<0.001
Moon × Predator	2.319	6	0.387	9.530	<0.001
Cover × Predator	0.725	4	0.181	4.466	0.002
Fence × Predator	0.707	4	0.177	4.360	0.002
Cover × Moon	0.084	6	0.014	0.346	0.911
Fence × Moon	0.378	6	0.063	1.555	0.166
Fence × Cover	1.224	4	0.306	7.541	<0.001
Moon × Cover × Predator	0.531	12	0.044	1.092	0.373
Moon × Fence × Predator	0.442	12	0.037	0.907	0.542
Cover × Fence × Moon	1.001	12	0.083	2.056	0.024
Cover × Fence × Predator	0.045	8	0.006	0.138	0.997
Session(Moon)	10.901	4	2.725	67.184	<0.001
Error	5.192	128	0.041		

Table A2-2. Analysis of variance results table for quitting harvest rate with n = 216, Multiple R^2 = 0.743.

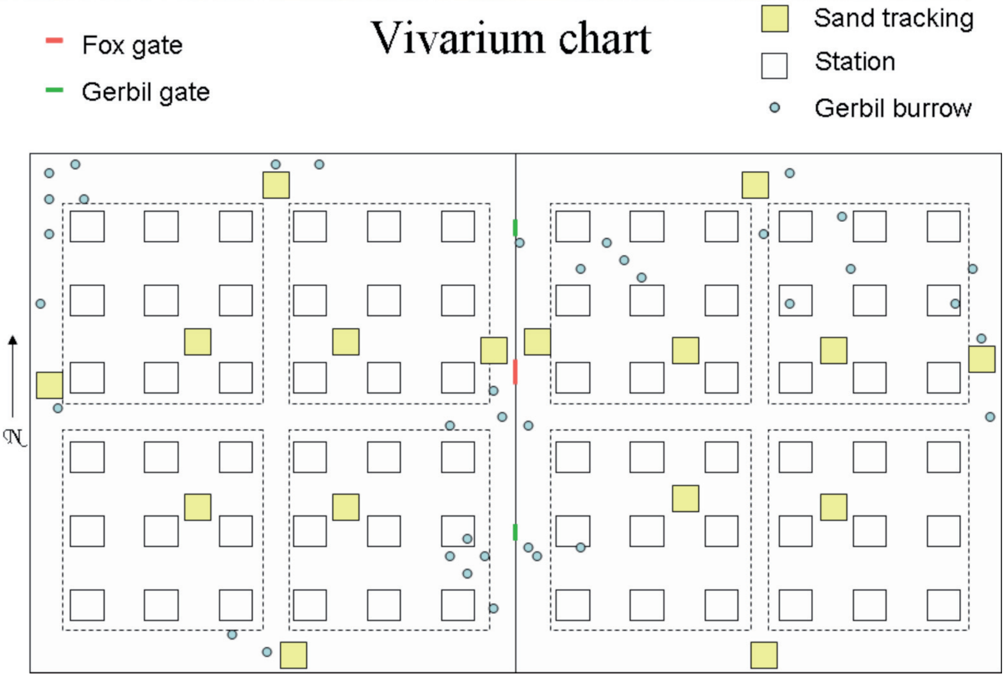
Source	Sum-of-squares	DF	Mean-square	F-ratio	p
Predator	4.908	2	2.454	3.212	0.044
Moon	40.037	3	13.346	10.057	0.024
Cover	21.556	2	10.778	14.108	<0.001
Fence	33.097	2	16.549	21.662	<0.001
Moon × Predator	12.401	6	2.067	2.706	0.017
Cover × Predator	5.900	4	1.475	1.931	0.109
Fence × Predator	10.457	4	2.614	3.422	0.011
Cover × Moon	8.349	6	1.392	1.822	0.100
Fence × Moon	22.692	6	3.782	4.951	<0.001
Fence × Cover	24.742	4	6.186	8.097	<0.001
Moon × Cover × Predator	45.695	12	3.808	4.985	<0.001
Moon × Fence × Predator	16.443	12	1.370	1.794	0.056
Cover × Fence × Moon	18.285	12	1.524	1.995	0.030
Cover × Fence × Predator	13.112	8	1.639	2.145	0.036
Session(Moon)	5.306	4	1.327	1.736	0.146
Error	97.785	128	0.764		

Table A2-3. Analysis of variance results table for time foraged in tray, with n = 199, Multiple R^2 = 0.755.

Source	Sum-of-squares	DF	Mean-square	F-ratio	p
Predator	1.08×10^5	2	5.42×10^4	0.102	0.903
Moon	9.87×10^6	3	3.29×10^6	0.895	0.524
Cover	5.05×10^7	2	2.53×10^7	47.442	<0.001
Fence	2.05×10^7	2	1.03×10^7	19.290	<0.001
Moon × Predator	5.04×10^6	6	8.41×10^6	1.578	0.160
Cover × Predator	3.65×10^6	4	9.13×10^6	1.714	0.152
Fence × Predator	3.13×10^6	4	7.83×10^5	1.470	0.216
Cover × Moon	4.07×10^6	6	6.78×10^5	1.274	0.275
Fence × Moon	6.41×10^6	6	1.07×10^6	2.005	0.071
Fence × Cover	1.88×10^7	4	4.71×10^6	8.846	<0.001
Moon × Cover × Predator	3.53×10^6	12	2.94×10^5	0.552	0.875
Moon × Fence × Predator	1.68×10^6	12	1.40×10^6	0.263	0.994
Cover × Fence × Moon	2.46×10^7	12	2.05×10^6	3.842	<0.001
Cover × Fence × Predator	1.94×10^6	8	2.42×10^5	0.455	0.885
Session(Moon)	1.47×10^7	4	3.68×10^6	6.905	<0.001
Error	5.91×10^7	111	5.33×10^5		

Appendix A3

Pictures and illustrations of the experimental setup



The vivarium is an outdoor cage 17 × 34 × 4.5 m divided into halves. The predators are released into it in the evening and removed in the morning. There is a big window stretching between the two gerbil gates to allow the owl free access to the whole cage. There are 36 experimental stations per side. The nine combinations of cover and fence treatments were randomly arranged within each block (dotted squares in the above illustration).

Examples of cover and fence treatment at the experimental stations. The three cover treatment options are no cover, low cover and high cover. The three fence treatment options are no fence, mesh fence and black opaque fence. Together they make up nine treatment combinations. Here we show (A) Mesh fence with no cover, (B) No fence with low cover and (C) Black opaque fence with high cover.

Picture D shows that the high cover allows relatively free access to terrestrial predators as well as the flying ones.