general arousal, whether through hormonal or neural pathways, facilitate sexual behavior in male rats by reducing the number of intromissions and time required for ejaculation (*19*). Anticipatory endocrine responses, which contribute to general arousal, may prepare the male for sexual encounters and therefore have considerable adaptive value, especially for prey species, by ensuring that a male is adequately aroused to mate effectively and quickly (*20*). In addition to behavioral effects, conditioned systemic elevations in testosterone may participate in the regulation of androgen-dependent functions at several loci, including the accessory reproductive structures (*21*). Thus, anticipatory endocrine responses to conditioned stimuli may be an important functional antecedent of sexual behavior and thereby contribute significantly to the regulation of reproductive behavior and certain physiological aspects of pituitary-testis function.

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Optimal Behavior: Can Foragers Balance Two Conflicting Demands?

Abstract. *According to much current theory, organisms should be able to balance the conflicting demands of the need to feed efficiently and the need to avoid predators while feeding. In an experimental conflict situation, it was possible to evaluate the relative fitnesses associated with the available choices and to compare the observed behaviors with predictions derived from fitness considerations. A backswimmer,* Notonecta hoffmanni, *was capable of balancing these two conflicting factors adaptively.*

In recent years, feeding has been viewed as a behavior molded by natural selection into an optimal state (*1*). In general, optimal foraging theory has taken the maximization of the net rate of energy intake to be the appropriate goal for foragers (*2*). An important assumption of this view is that other factors that can affect an organism's fitness do not affect the optimal foraging strategy. Considerable evidence suggests, however, that at least one such factor, the risk of being eaten while feeding, is important in altering the behavior of foragers (*3*). In particular, either foragers alter their behavior in a way that reduces the risk of predation (*4*) or alterations are greater in response to greater risks of predation (*5*). If the demands of maximizing feeding rate and minimizing the risk of predation conflict (for example, if a forager's predators and prey are found in the same place at the same time), foragers must choose a strategy that is an adaptive (*6*) compromise between these two demands. I attempted to quantify relative fitness in order to examine the hypothesis that feeding behavior represents such an adaptive compromise.

I studied the behavior of an aquatic insect, *Notonecta hoffmanni*, which is commonly found in stream pools and ponds where it feeds on both aquatic prey (such as mosquito larvae) and terrestrial prey trapped on the water's surface (such as adult flies). In the absence of predators, all size classes of *N. hoffmanni* seem to prefer similar sorts of prey and microhabitats (*7*). In addition, the main predators on (and perhaps the main cause of death of) young *N. hoffmanni* are larger conspecifics (*7*). Thus, juvenile *N. hoffmanni* are commonly placed in a situation in which the demands of feeding and avoiding predators conflict. To clarify my terms, predators (adult *N. hoffmanni*) eat foragers (young *N. hoffmanni*) and both eat prey (adult flies).

I conducted experiments in a chamber with a controlled environment at 24°C under a regime of 12 hours light and 12 hours dark. Experimental tubs (38 by 56 cm filled to a depth of 13 cm) were divided into a central region and an edge region through the use of a wooden frame (28 by 46 by 15 cm). The frame rose above the water's surface and constrained surface prey (a strain of wingless adult fruit flies, *Drosophila melanogaster*) to one of the two regions. The sides of the frame were either covered with fiber glass window screening, thereby restricting notonectids (both foragers and predators) to one region or the other, or left open, allowing notonectids to move freely between the two regions.

I experimentally created a conflict situation in which the central region (HH) had high prey density (0.11 fly per square centimeter) but high risk of predation (three adult notonectids), and the edge region (LL) had low prey density (0.03 fly per square centimeter) but low risk of predation (no adult notonectids). In experiment 1, I assessed the relative fitnesses associated with time spent entirely in one region or the other by con-

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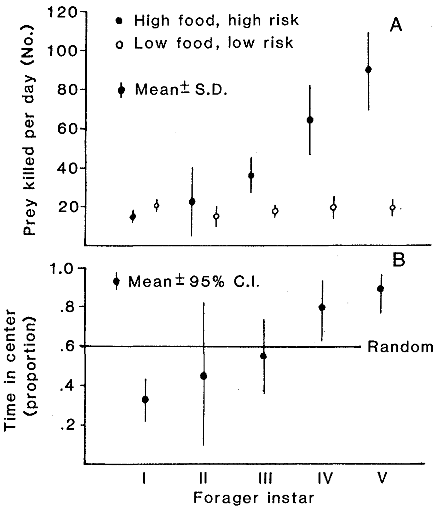

Fig. 1. (A) The number of prey killed per day by foragers of a particular instar when constrained to either the HH central region (●) or the LL edge region (○). Differences are significant for instars I, III, IV, and V ($P < .05$, Mann-Whitney U test). (B) Proportion of time a particular instar spent in the central region when given a choice between the two regions. The value .6 is random because .6 of the area of the experimental tub is in the center. Points above the line represent greater than random use of the HH central region.

straining foragers to either region and measuring survivorship and feeding rates. Feeding rates can be used to estimate developmental rate and future fecundity (*8*) such that the costs and benefits of mortality and feeding can be converted into the common currency of fitness. However, because survivorship was quite high (97.3 percent per day) and did not significantly differ between the edge and central regions [$\chi^2(1) < 2.01$, $P > .25$ for all instars], my single measure of relative fitness is feeding rate. Although foragers were rarely killed by predators, the need to avoid predators reduced their feeding rate (*9*). Thus the relative fitness associated with the two regions could be evaluated by comparing the feeding rate in the central region where prey are plentiful but predators must be avoided to that in the edge where prey are scarce but foragers need not avoid predators.

Using these data, I predicted on the basis of fitness considerations how foragers should use space when given a choice between these two regions, and in experiment 2, the barriers to notonectid movement were removed. Because 86 percent of the prey were restricted to the center, predators (who also eat flies) spent 92.6 percent of their time in the central region and did close to 100 percent of their foraging there. Thus, even in the absence of constraints on predator movements, the spatial distribution of prey and predators in the two experiments were almost identical.

Foragers were tested for 24 hours in groups of six, and both experiments were replicated six times for each of the five nymphal notonectid instars. Observations were made at approximately 30-minute intervals (ten observations in daylight, generally between 1300 and 1800 hours, and eight in the dark, generally between 1900 and 2300 hours) on the use of space by each predator and forager. After 24 hours, survivorship and feeding rates were recorded.

I predicted that (i) foragers would spend a greater than random proportion of their time in the region associated with significantly higher feeding rates, and (ii) the greater the relative advantage associated with a region, the greater the preference would be for that region. If H and L are the relative feeding rates associated with regions HH and LL, respectively, prediction (i) merely requires that when H is significantly greater than L, region HH should be preferred (and vice versa). Prediction (ii) requires that a measure of the relative advantage associated with a region HH [for example, $(H - L)/L$] be significantly positively correlated with a measure of the preference for that region (for example, proportion of time spent in HH).

When constrained to either region, the feeding rates of first instar notonectids were significantly ($P < .05$, Mann-Whitney U test) higher in the LL region, even though food is far more dense in the central region (Fig. 1A). In the central region, first instar notonectids avoided adults and thus reduced their feeding efficiency (*9*). For the same reason, second instars did not feed at significantly different rates in the two regions despite the higher prey density in the center. Third, fourth, and fifth instar notonectids fed at a significantly higher rate in the HH central region where prey were more dense. That the presence of adult notonectids had a larger effect on first and second than on older instars can be explained by the greater susceptibility of these younger instars to adult predation (*10*).

On the basis of these data, first instars given a choice should allocate a greater than random proportion of their time to the LL region; second instars should allocate their time randomly between the two regions; and third, fourth, and fifth instars should spend a greater than random proportion of their time in the HH region. When given a choice, all but the third instar fit the predictions (Fig. 1B). This is a powerful result for two reasons. To corroborate the predictions, three of the instars (I, IV, and V) required significantly nonrandom use of space in a specified direction, and two instars (I and II) required significant changes from their use of space in the absence of predators (*11*).

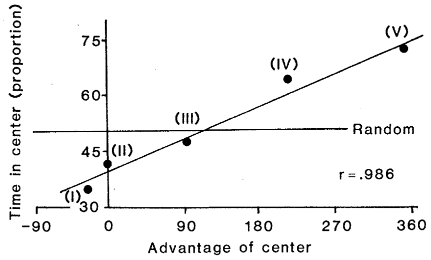

Fig. 2. The linear regression between a measure of the relative advantage associated with time spent in the central region [$(H - L)/H \times 100$ where H and L are the feeding rates in the central and edge regions, respectively] and a measure of the preference for the center when given a choice between the two regions (angular transformed proportions of time spent in the center). Instar numbers are shown in parentheses.

As expected under the second prediction, the correlation between the relative advantage of the central region and the preference for that region was significant (Fig. 2) ($r = +.986$, $y = 39.70 + 9.47x$, $P < .01$). The measure of the relative advantage associated with the center explained 97 percent of the variance in the mean proportion of time spent by a particular instar in that region. Overall, juvenile *N. hoffmanni* appear capable of adaptively balancing the conflicting demands of feeding efficiently and avoiding predators.

These results have an implication for the use of optimality theory to explain or predict the behavior of foragers. Previous modeling studies have generally considered only the forager's need to maximize its net rate of energy intake (*2*). In many situations, however, understanding the behavior of foragers requires that we consider the need to avoid predators. Models that include both of these factors should prove useful. Some attempts have been made at building such models (*12*) but much remains to be done.

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Effect of Urban Sources on Acid Precipitation in the Western United States

In their report of acid precipitation near the Continental Divide, Lewis and Grant state (*1*, p. 176) that they expect the air at their measurement site "to receive only sporadic and limited contamination from nearby urban sources of pollution." Although we agree that the movement of air from the Denver front range metropolitan area into the mountains may be termed sporadic, our observations of such upslope episodes indicate that they may have a determining effect on the results of Lewis and Grant, especially since Lewis and Grant collected the sum of dry and wet deposition.

We have made continuous measurements of gas-phase NO, NO_2, and HNO_3 in the same area of the Como Creek watershed as that used by Lewis and Grant, from January to July 1979 (*2*). We find that the concentrations of these pollutants are up to 100 times higher in periods of upslope air movement from the east than during periods of clean air movement from the west. Over a sampling period of a week, the interval at which Lewis and Grant emptied their precipitation collectors, we find that the average concentrations of NO, NO_2, and HNO_3 are determined by their high concentrations in upslope periods. This result was also found by Noxon in his study of NO_2 concentrations near the Divide (*3*).

Lewis and Grant state (*1*, p. 177) that "no local, sizable sources of pollutants are properly situated" to account for their observed pH trend. Their only apparent support for this conclusion is the meteorological study by Barry (*4*). Because of the long sampling interval used by Lewis and Grant, it is vital that they consider not only the probable frequency of pollution episodes, based on the local meteorology, but also the severity of such pollution relative to the clean air which they purport to study. Our observations indicate that the average pollutant concentrations at their sampling site are so dominated by intermittent transport from urban sources that their measurements cannot be the basis for generalizations about precipitation in the western United States as a whole.

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We look forward to the publication of the NO_x observations alluded to by Kelly and Stedman; such data will provide a welcome addition to our knowledge of materials transport in the vicinity of the Continental Divide in Colorado.

Kelly and Stedman are mistaken in their implication that their observations of eastward upslope air movement contradict some aspects of our recent report of acid rain near the Continental Divide (*1*). We have not promoted the idea of long-distance transport from the west of the Divide but merely urge that it be considered as a contributor, possibly even a major one, of acidic materials to the Como Creek watershed. Even in view of Kelly and Stedman's observations, we must remain skeptical that the acid precipitation phenomenon can be essentially accounted for by upslope movement of air from the east until this has been demonstrated quantitatively on an annual basis. The seasonal pattern of storms in this area is such that the frequency of upslope air movements is highest during the fraction of the year (January through July) studied by Kelly and Stedman.

By selecting for quotation from our report portions of sentences without the accompanying qualifiers, Kelly and Stedman have unfortunately made our comments on sources of acidity appear more tendentious than they were intended to be. Our report did not purport to be a summary of the condition of bulk precipitation for the entire western United States, nor does it deny the possibility of significant westward-moving upslope contributions to acidity in the Colorado Rockies. In fact, in our report we explicitly stated that regional urban sources to the east of the Divide (Denver) are one possible source. We view the study of Kelly and Stedman as providing useful information verifying the potential importance of sources to the east of the Divide.

As we now see it, the evidence could be summarized as follows. (i) Contrary to expectations prior to the publication of our report, bulk precipitation in the Como Creek watershed (6 km east of the Continental Divide) is affected by substantial amounts of strong mineral acids almost all weeks of the year. (ii) Urban pollution from Denver is one potential source of the mineral acids in precipitation near the Continental Divide, but very forceful and frequent year-round upslope movements are required, against strong prevailing weather patterns in certain months, in order to account fully for the acidity. (ii) Upslope movement definitely does occur at some times of the year and is perhaps more important in transport than previously suspected if the patterns observed by Kelly and Stedman are typical. (iv) A quantitative balance sheet for the sources of the strong mineral acids at the Como Creek site cannot be drawn as yet, and any conclusion that the acidity is principally from the east or the west would be premature.

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