were directly applied onto the leaves. Infective conidia of *E. graminis* were evenly dusted over the alkaloid-treated leaf segments and incubated at 20°C and a 14-h light period for 70 h. As can be seen from the table, QA and gramine significantly suppress the germination of *E. graminis* conidia, as compared to controls. Furthermore the number of appressoria and secondary hyphae were also reduced. Both the free alkaloid bases and the salts were effective.

These results could be confirmed in another set of experiments. Microscope slides were coated with agar on which conidia readily germinate and develop into appressoria (fig. 1). However if the agar contained suitable concentrations of alkaloids, a marked inhibition of germination and further development could be observed (fig. 1b). Half-maximal inhibition was recorded at alkaloid concentrations between 1 and 5 mmol/l (equivalent to 0.02–0.1%) (fig. 2). The inhibitory concentrations of QA against mildew are lower than those recorded against other phytopathogenic fungi[14] but are in the same range as against gram-positive bacteria[14]. The actual concentrations of QA in lupins fall in the range of 5–20 mmol/kg in leaves, of 5–40 mmol/kg in stems and of 100–200 mmol/kg in seeds and seedlings[19,20]. Furthermore QA are concentrated in a strategically suitable position in peripheral tissues[20], especially the epidermis and subepidermal layers, which have to ward off a microbial or herbivore attack. It is thus likely that QA can account for the resistance of alkaloid-rich ('bitter') lupins against powdery mildews. Since no defense is absolute it is not surprising to find a specialized mildew, *E. pisi*, infecting lupins as well as other Leguminosae; a mildew, however, which according to preliminary observations (Wink unpublished) can degrade QA.

Our results support the assumption that QA have a broad spectrum of biotoxic properties, the mechanisms of which are still unknown. There is growing evidence that most alkaloids and other toxins, often thought to be evolved in response to specific and specialized herbivores, may be broad spectrum defenses, just like tannins and other digestion-inhibitors. A challenging question is whether we can exploit the properties of alkaloids to protect cereals against powdery mildew, either by selecting plants with a high concentration of the natural indole alkaloid of cereals, i.e. gramine, or by spraying plants with exogenous alkaloids.

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Object retrieval preferences of Norway rats: an evolutionary generalization of behavior

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Summary. Prior studies have shown that object retrieval (including food hoarding) by domestic rats can occur in the context of different motivations. The present experiments show that retrieval preferences related to two motivational systems, feeding and gnawing, are ordered by object features related to either or both systems. Object retrieval in this species is apparently guided by a generalized value system. The capacity to order alternatives across specific motivational systems has evident selective advantage and may reflect a general adaptive principle.

Key words. Hoarding; economic value; motivational integration; evolutionary adaptation.

Norway rats (*Rattus norvegicus*, fam. Muridae)[1–4] and other rodent species (e.g. *Rattus fuscipes* (fam. Muridae)[5], *Mesocricetus auratus* (fam. Cricetidae)[6], *Cricetomys gambianus* (fam. Cricetidae)[7], *Neotoma cinerea* (fam. Cricetidae)[8], *Sciurus vulgaris* (fam. Sciuridae)[9], *Tamiasciurus hudsonicus* (fam. Sciuridae)[10], *Geomys bursarius* (fam. Geomyidae)[11], *Heterocephalus glaber* (fam. Bathyergidae)[12] transport a variety of objects on occasion to their homes or other sheltered locations. That transport of this kind is related to hoarding and food storage has been argued previously[5,13,14]. For *Rattus* species there is evidence that such transport, or 'object retrieval', can occur in association with more than one motivational system. In these animals the following properties of objects can support retrieval preferences: sweetness, wateriness, partibility, novelty[4,5,14–16]. The associated motivational systems are feeding, drinking, gnawing and exploring. This variety of relationships to object retrieval must have arisen from multiple selection pressures acting at command levels in the retrieval system. However, the above results do not show the degree to which retrieval preferences based on different properties of objects can be coordinated. The present experiments suggest that for domestic *R. norvegicus*, these preferences are always ordered consistently, i.e., that objects of different kinds are retrieved in conformity with a scaling process that can always be represented in one dimension. This implies that retrieval in this species is governed by a unified system that is related to more than one motivational context.

This report describes the choices of domestic rats within the behavior sequence that produces retrieval. To impose choice behavior on this sequence, a Y-maze was used for the 'hoarding alley'; rats could then choose between objects presented in the two arms by entering one arm or the other. The pair of objects presented on a single trial was drawn from a set of three or four alternatives, which allowed properties of choice based on sets of pairs to be examined. (The size of the set of all alternatives was limited because of the time required to present all possible pairs by positions and to allow subjects to approach asymptotic behavior.) The objects in these experiments had either of two of the attributes that induce retrieval in this species: sweetness and partibility[4,14]. These attributes are easily distinguished and related to different motivational systems. Since this work was concerned with preferences based upon these attributes, other factors known to be important in foraging and food storage, which might be effective here (e.g. probability of encounter including effects of patch depletion, and ease of pursuit and handling[17–19]) were equalized or minimized . In three separate experiments either or both attributes were varied quantitatively, to determine whether the same regularities would be found when retrieval was based on one attribute or the other, or when it involved comparisons between the two.

The analysis herein follows a two-part strategy. First, an ordering is demonstrated for the number of objects retrieved along with corresponding orderings of choices and durations of oral behavior. Having shown that choices correspond to retrieval preferences, this aspect of the animals' behavior is examined in more detail using probabilistic choice theory[20,21], to further delineate the valuation process. The relevant aspects of this theory will be briefly discussed.

A probabilistic model of binary choices associates a real-valued monotonic function, a 'utility function', with choice probabilities, for pairs of alternatives drawn from a larger set. The probabilities of choosing alternatives a or b from one such pair are commonly denoted $p(a,b)$ and $p(b,a)$, respectively[20]. Models differ in how they specify the relation between choice probabilities and the utility function, u. The Weak (Binary) Utility Model states only that $p(a,b) > \frac{1}{2}$ if and only if $u(a) > = u(b)$. In contrast the Strict Utility Model asserts that $p(a,b)$ is equal to the ratio of $u(a)$ to $u(a) + u(b)$[20]. In the present work the importance of justifying a binary utility model of any sort is that this allows us to infer that something (however abstract) is maximized. This is implied by the representation of choice by a monotonic function, so that the outcome chosen is always associated with the larger value of $u(x)$.

Although there is no way to evaluate these models completely, entailments hold between them, and between a given model and certain properties that choice probabilities can exhibit[20,21]. The properties examined in this study included two categories of 'stochastic transitivity' and the product rule. Only the former will be described, since probability estimates deviated from the product rule in a systematic fashion. Suppose that for all triplets x, y, and z, $p(x,y)$ and $p(y,z)$ are $> = \frac{1}{2}$. Then weak stochastic transitivity (WST) holds if $p(x,z) > = \frac{1}{2}$. Strict stochastic transitivity (here SST) holds if $p(x,z)$ is greater or equal to the larger of the former two probabilities, and if strict inequality holds when the former probabilities are each geater than $\frac{1}{2}$[21,22]. SST is equivalent to the property of 'simple scalability', defined thusly: there are real-valued functions F and u such that for any alternatives x and y,

$$p(x,y) = F[u(x), u(y)]$$

'where F is strictly increasing in its first argument and strictly decreasing in the second'[22]. Simple scalability implies that choices reflect the difference between differences in u, without implying a linear scale.

Of most interest here are the entailments that hold between WST and the Weak Utility Model. For a finite set of alternatives each implies the other. In addition, WST is implied by SST, and the Weak Model is implied by the Strict Model. The latter is not implied by any type of stochastic transitivity (although it is implied by the product rule, which is therefore consistent with a linear scale for utility).

It seems well-established that utility models in and of themselves are not sufficient to describe the processing of complex decisions by humans, i.e. those involving multiattribute alternatives and uncertain (risky) outcomes[23,24]. It is not the purpose of the present paper to dispute this, even for rats. This work does indicate that utility models can be useful for the more modest goal of describing a valuation process in a simple riskless situation, where the difficulties of information analysis for the subject are minimized.

Wistar rats were obtained from the John Curtin School of Medical Research at the Australian National University in Canberra. Rats in each experiment were given six daily retrieval trials per week for 2–4 months, depending on the possible pairings of objects in that experiment and the time required to obtain a stable level of behavior for choices and number of objects retrieved. The apparatus for each animal consisted of its home cage and a Y-maze (one of six) used only by that animal while it was run. The mazes had clear Perspex tops and inner walls, and were open at the stem (20 × 18 × 17.5 cm) so that a maze could be placed against the cage during a trial. Each type of object used on a trial was placed at the end of a separate arm (43 × 19.5 × 17.5 cm) in sufficient quantity to avoid depletion before the end of the trial. All rats were fed ad libitum throughout an experiment. Other conditions conformed to earlier studies[4,14]. Rats were run singly and behavioral events were recorded on Rustrak tape. Each trial continued until the animal had

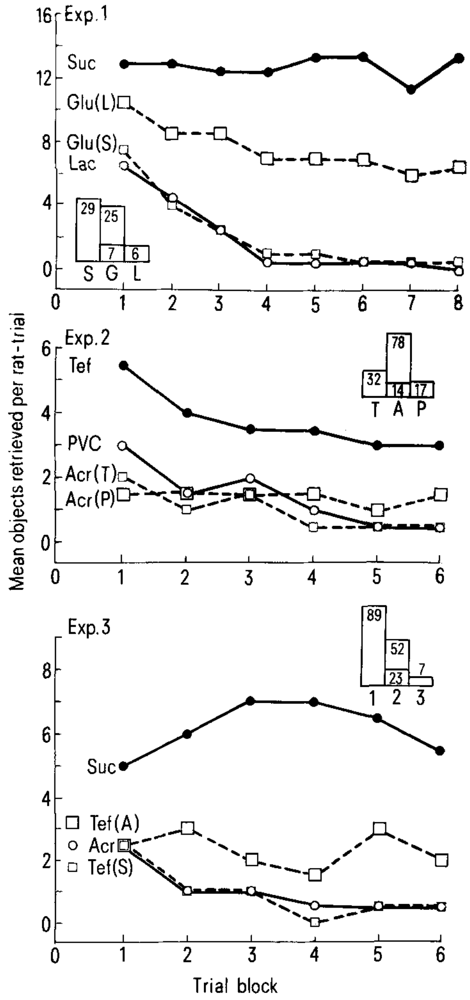

Figure 1. Number of objects retrieved in the three experiments. In each experiment separate graphs of the object that was second in the preference hierarchy show the mean retrievals when it was the preferred object (e.g. GLU(L) refers to glucose pledgets retrieved when glucose was paired with lactose) and when it was nonpreferred. Histograms show the mean duration of oral behavior in seconds per retrieval for each object in the last two trial blocks, with data for the second object again shown separately. (Longer times always correspond to retrieval preferences.) In experiment 3 numbers under the histogram reflect the fact that the second and third objects were not the same for all rats (see text).

ceased to retrieve objects for 5 min. The period in the trial chosen for data analysis was that between the time that both kinds of object had been contacted with the snout and the time that the last object was retrieved. Placement of objects was balanced across trials with respect to position, so that for a set of three objects, six daily trials were required to present all pairs in both positions. Experiments were therefore organized in terms of such trial-blocks.

Three sets of objects were used. Those in experiment 1 were dental pledgets soaked in 4% sucrose, 5% glucose or 5% lactose (w/v). Studies of judged sweetness (by humans) and licking preference (by rats) suggested that this would be the order of preference, from most to least[25,26]. Solutions were prepared 30 h before each session, objects 1–2 h before an individual trial. Objects in experiment 2 were, in order of decreasing partibility (volume gnawed/time), cylinders of polytetrofluorethylene (Teflon), polyvinylchloride (PVC) and polymethylmethacrylate (Acrylic) of similar size (13 mm dia, 16 mm (Teflon) or 18 mm length) and weight (from 2.6 (Acrylic) to 3.5 (Teflon) g). Objects in experiment 3 consisted of a sweet object (an Acrylic cylinder coated with sucrose), a partible object (Teflon), and a nonsweet object of limited partibility (Acrylic).

Figure 1 shows the mean number of objects retrieved per rat-trial (within the period analyzed) for each object in each block of the main experiments. Every rat showed a consistent ordering of retrieval preferences. With set 1 this was sucrose > glucose > lactose for all subjects. With set 2 it was Teflon > Acrylic > PVC for all. (This ordering is not consistent with the hypothesis that preferences among familiar non-food objects depend only on the degree of partibility). With set 3 seven rats showed an ordering of Acrylic and sucrose > Teflon > Acrylic, while one rat preferred Acrylic to Teflon. Two-tailed paired comparison t-test on means for the last two blocks of each experiment yielded significant results for all three pairs of objects in experiment 1 ($p < 0.001$ (probabilities hold for all pairs if not noted)), and experiment 3 ($p < 0.02$) and for the two pairings with Teflon in experiment 2 ($p < 0.05$; for the Acrylic-PVC preference, $0.1 > p > 0.05$).

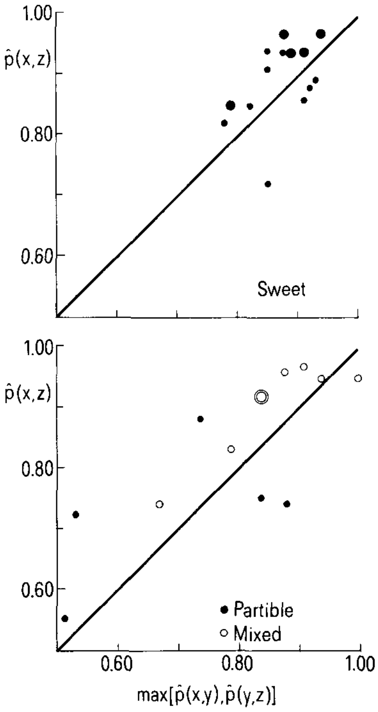

Figure 2. Evaluation of strict stochastic transitivity for the last two trial blocks of each experiment. Subjects from experiment 1 are shown in the upper graph together with five subjects (large circles) from another sweetness experiment that was similar (eight blocks) except for the inclusion of an empty arm as a fourth alternative (hence 12 trials per block). Filled circles in the lower graph are for experiment 2, outline circles for experiment 3.

As expected[4,5,27] the retrieval preferences corresponded to the relative durations of oral behavior (chewing, licking, gnawing) that followed retrieval, and to relative choices. Therefore the remaining analyses are based on the ordering of retrieval preferences by each rat rather than on object types, although this affects only the 'odd' rat in experiment 3. These analyses are all based on the last two trial blocks of each experiment.

One-tailed paired comparison t-tests for the mean duration of oral behavior per retrieval were significant for all three pairs in experiment 1 ($p < 0.02$), and for the first vs second and second vs third objects in experiment 3 ($p < 0.05$; too few of the nonpreferred objects were retrieved with the other pairing to derive statistical results). The tests for experiment 2 were not significant ($p > 0.10$), although the differences were in the expected directions (fig. 1). Choice was defined as an initial entry into a maze arm (four feet in the arm) after emerging from the cage into the alley. One-tailed t-tests for relative choice of the arm with the preferred object, with $H_0 = 0.50$, were significant for all pairs in experiment 1 ($p < 0.001$), 2 ($p < 0.05$), and 3 ($p < 0.001$).

For the analysis of choice properties, estimates of choice probability were also based on averages across the last two blocks of each experiment (four trials per estimate). The analysis was limited to the first eight choices in each trial after contact, to ensure greater similarity in the number of choices for all pairings and in the time to make them. (In fact the degree of transitivity would have been the same for all but two rats if all choices had been used.) Probability estimates for the three pairs of objects were consistent with WST for all animals in all experiments. Most rats showed a greater degree of order in their choices. In figure 2 $\hat{p}(x,z)$ is compared with the maximum value of $\hat{p}(x,y)$ and $\hat{p}(y,z)$ for each subject. Most points lie above the diagonal lines of the graphs, and are therefore consistent with SST and simple scalability. Evidently choices of rats in this situation can be represented by a utility function, and there is also evidence for sensitivity to the degree of difference in utility. The similarity of the results in each experiment suggests that the processes which underlie this scaling capacity can operate across all attributes that induce retrieval, i.e. that retrieval of objects of different types is mediated by a common system.

Although the maximization in evidence here cannot be compared directly with models of *optimization* in behavior, it is relevant to this general approach. It suggests a greater degree of abstraction in the evaluation of alternatives than is assumed by any model of optimal foraging[17–19], for example, in that it cannot be referred to an energy currency in a simple fashion. This is especially pertinent in view of results in this and earlier studies[4,5,14], which show that the properties of objects which are mapped into the domain of utilities are related to oral stimuli and responses. These findings are consistent with the hypothesis that retrieval behavior evolved from a feeding or foraging system to which optimization models should apply.

More general models of optimization such as McFarland's[28–30] or those stemming from the analysis of operant behavior[31,32] may be sufficient to explain the maximization in evidence here. However, these models are more concerned with partitioning the entire behavioral repertoire of an animal than with the delineation of a specific behavioral system that has achieved broad applicability. For example, the use of McFarland's model would result in the dissection of this system into sweetness-retrieval, partibility-retrieval, etc. to conform with the classificatory requirements of this approach[29]. Important organizational and evolutionary problems would then be obscured.

This work shows that a behavioral system can evolve for making decisions across a number of situations that lead to related goals (i.e. all involve oral behavior) but not to a single endstate. To account for the evolution of such a system, I would suggest a 'common skill' hypothesis: If a behavioral capacity can be used in a variety of motivational contexts that are sometimes concurrent, there will be selective pressures for the development of a system to order these contexts. In the present case, object retrieval was the common skill (or a common skill) that served as a foundation for the evolution of a generalized value system. This system allows these, and perhaps other rodent species[5-13], to choose between objects that are related to different motivational systems, but that can be treated in a similar manner with respect to transportation. Object retrieval may therefore stand somewhere between response systems dedicated to a single goal, that are often designated as species-typical behavior, and those that are largely instrumental in character. The latter by implication may have arisen in the same fashion as retrieval.

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Sex pheromone blend of the codling moth, *Cydia pomonella:* Evidence for a behavioral role of dodecan-1-ol[1]

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Summary. Pheromone glands and effluvia of the codling moth female contain *E*-8,*E*-10-dodecadien-1-ol as main component, accompanied by its geometric isomers, the corresponding acetate and aldehyde (both in gland extracts only), *E*-9-dodecen-1-ol and saturated alcohols of 10 to 18 carbons. Dodecan-1-ol as the most abundant secondary component (about 30% of the female blend) acts in the wind tunnel by widening the dose range over which codling moth males are optimally attracted to *E*-8,*E*-10-dodecadien-1-ol.

Key words. Codling moth; *Cydia pomonella;* sex pheromone; male attraction; *E*-8,*E*-10-dodecadien-1-ol; dodecan-1-ol; synergism; wind tunnel; chemical analysis.

Cydia pomonella L. (Lepidoptera: Tortricidae, Olethreutini) is a worldwide pest on apple, peach and walnut[2]. *E*-8,*E*-10-Dodecadien-1-ol (*E*8*E*10-12:OH; other short forms see table) was established as a male attractant for this species, based on electroantennographic (EAG) data and synthesis[3], and subsequently identified in female extracts[4,5]. Although this compound is extremely effective, behavioral observations suggest that other female products are involved in courtship of *C. pomonella*[6,7]. Additional components related to *E*8*E*10-12:OH were identified in female glands[7,8]; however, evidence for the behavioral role of any of these has been lacking, with the exception of an inhibitory effect observed for *E*8*E*10-12:Ac[9,10]. Here we present results of analysis of *C. pomonella* female extract and effluvia, and first evidence for a role of 12:OH in the sexual activity of males.

Materials and methods. Insects were reared on an artificial diet[11]. Extraction of sex glands of 3-day-old virgin females (made in the early scotophase), and analyses by gas chromatography-mass spectrometry (GC-MS) and GC with EAG detection (GC-EAD) on Silar 10c and SP-1000 were done as described for *Adoxophyes orana* F.v.R.[12]. For determination of double bond positions in monoenic alcohols, the extracts were reacted with trifluoroacetic anhydride and then with dimethyl disulfide (DMDS)[13,14]. Preliminary experiments aimed at collection of effluvia indicated that recovery from charcoal (Grob filters, Brechbühler AG, Schlieren, Switzerland) of *E*8*E*10-12:OH and aldehydes was very poor (circa 10%) in contrast to saturated and monounsaturated hydrocarbons, alcohols and acetates (circa 60%). On the other hand, nearly 50% of *E*8*E*10-12:OH released from a cover