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Full Papers

Time-energy budgets and optimization*

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Summary. Since the process of natural selection entails a comparison of phenotypes and choosing of the best, optimality theory appears appropriate to identify selection pressures. Optimality theory does *not* test whether an organism is designed optimally - it assumes it. The ingredients of a complete optimization model are outlined and two approaches are exemplified. Both time-energy-budgeting and Pontryagin's maximum principle lead to semi-quantitative predictions about, e.g., an animal's behavior; they merely entail an inequality formalism. A discrepancy between prediction and test would not yet show a behavior to be maladaptive since several other explanations are possible. Animals optimize their behavior over intervals ranging from less than a second to months or years. It is unknown whether, with a long interval, the animal makes use of the opportunity to revise its decision(s). Present optimal foraging models predicting, e.g., diet breadth are too simple in that foragers a) may not always maximize energy intake, as postulated, b) have to allow for nutrient, toxin and remedial content of food items, and/or c) have to allow for interaction of items, annihilating their ranking along a unidimensional scale of profitability.

Time-energy budgets and optimization

Natural selection is a process which maximizes 'inclusive fitness' or some other suitable quantity. In maximizing its inclusive fitness an animal cannot do better than survive; 'trying harder' does not yield greater rewards. Even the best genotype cannot live forever since there are certain constraints. From this it becomes clear that by 'optimal' one does not mean the commonplace sense of 'the best design'. The process

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of natural selection is a matter of comparing variant phenotypes in terms of their survival value and the choosing of the best. Comparison and choosing the best are maximization or optimization principles; hence, the notion of optimality seems to be inherent in evolution.

What does optimality theory test? It does *not* test whether the animal is designed optimally - it assumes it[34]. The problem is: How does the design we observe contribute to fitness? In other words: What are the selective forces that have contributed to, or that presently shape, for example, the behavior under investigation? Optimality theory helps us to 'picture' the theoretically best behavior against which we measure the performance of the real animal. Two of the approaches will be outlined in this paper. Optimality theory is to be applied to a problem if the animal 'fights against nature'. If the animals's behavior depends on what others in the population do, then game theory, as applied by Maynard Smith and Price[33,35], is the appropriate tool.

A complete optimization model consists of the following 4 components (table 1):

1. A state space, i.e. a description of state variables, internal and external to the animal. Feeding, for example, changes the hunger state and at the same time lowers food abundance, an external state variable. Measurement of a state variable allows us to predict the state at some time in the future. This description is necessary but it will hardly ever be complete; much intuition is still necessary to identify even a minimum number of state variables. Questions relevant to this task are enumerated in table 1.
2. A set of observed strategies or of observed phenotypes (table 1) the survival values of which we want to evaluate. This is related to finding a 'fitness set'[29,30] which defines the genetic and ecological conditions of phenotypes, each of which is best adapted to a particular sub-niche. Maynard-Smith[34] argued in favor of speaking of a 'phenotype set' instead, because of the group selectionist connotation of 'fitness set'. The strategy set or the phenotype set is based upon what individuals really do, prior to and separable from an estimation of their fitnesses[47].
3. One or more optimization criteria which we need to define in order to know what quantity should be maximized (table 1). In general, we cannot make straightforward predictions about fitness - that currency in which we would ultimately like to assess survival value. Nor can we measure it satisfactorily[31]. Rather we have to content ourselves with more indirect sub-criteria like net energy intake, number of copulations or offspring, and so on.
4. The constraints of the behavior under study (table 1). Again, knowledge has to come from a study of the animal and its ecology. It may turn out that some of the state variables are in fact constraints. A stringent constraint is the genetics or the population structure of our species which is often unknown. Both of these will determine the type of equilibrium to which a population will move. No method exists for construing optimization models when the constraints exhibit chaotic or discontinuous behavior[47].

Optimality models have the advantage of replacing intuitive guesses about perfection of traits with quantitative predictions the generality of which can be tested. A particular model can be tested either by a direct test of its assumptions, or by comparing its prediction with observation. In testing a model, we are *not* testing the idea that nature optimizes, but rather the specific and explicit hypotheses implied by the model's components (1-4).. When a model fails to predict a particular behavior correctly, the behavior could be maladapted. However, this conclusion is justified only if several other explanations are ruled out. These may be a) evolutionary lag, i.e., the animal has not (yet) tracked its changing environment, b) one or more of the model's components (1-4) have been incorrectly identified or inadequately assessed; c) there may be a multi-stable equilibrium, e.g. a polymorphism with a number of solutions to the animal's problem, not all of which are optimal. This could be due to compensating benefits in respects unrelated to the trait under study.

Table 1. The components of a complete optimization model and some of the questions that can be asked about them

1. State space: How does behaviour change the state in time?
2. Strategy set, phenotype set[a]: How many strategies (phenotypes) are there?
3. Optimization criteria: Which quantity should be maximized?
4. Constraints[b]: Is it possible to enumerate all of the constraints?

[a] The phenotype set is related to Levins'[29,30] fitness set; at its worst it contains an assumption about what can evolve, at its best it describes all observable strategies or phenotypes coping with a problem for the organism.

[b] Sometimes identical with state variables, e.g. hunger: as a constraint, it must not exceed a certain level that may be fatal; as a state variable, hunger affects feeding and thereby itself.

Time-energy budgets

With the above 4 essential components of the model in mind, we can ask the question: How does an animal maximize its net energy intake, and how does it allocate its time optimally. These are the optimization criteria. At the same time energy and time are constraints restraining every behavioral activity. It is the limitation of energy and time that makes us consider how the animal is budgeting both (see the review by Pulliam[51]).

In a study of foraging behavior of winter flocks of yellow-eyed juncos *(Junco phaeonotus),* Caraco[8,9] considered time to be the central constraint. These granivorous songbirds forage singly or in groups of various sizes and each single bird has to make a decision as to whether to stay alone or join a flock. A flock offers the advantage of making more time available for feeding by saving time in looking out for predators. The advantage of being in a flock varies with dominance status; dominant birds profit from the increased vigilance more because subordinates have to look around more to cope with supplanting attacks from dominants.

The essential components of a time budget model, not explicitly enumerated by Caraco, are set out in table 2. The decision any one bird has to make is either to stay alone or to forage in a group of optimal size. Predator avoidance is achieved by scanning.

The maximization of energy intake and predator avoidance are sub-criteria of optimization that cannot be independently fulfilled. The bird clearly can not feed without ever looking around for predators (fig. 1); nor can it only scan without feeding. There is a 'trade-off' between both demands that are combined in a value function $V_{(x,y)}$ represented by indifference curves: even with intense foraging y there is still come scanning x, and even with long scanning there is still some feeding. Hence, there is only partial substitution of one demand by the other. Another reason for assuming nonadditivity of x and y is that at low levels of predator avoidance a bird should sacrifice more of its foraging to increase its scanning time than at high levels and vice versa. As one goes 'northeast', survivorship on the indifference curves increases.

The causal chain of events is as follows (fig. 2): Food and predators act as external stimuli; attention given to both is determined by a 'trade-off' mechanism of a multiplicative value function

$$V_{(x,y)} = x^{w_1} \cdot y^{w_2}$$

where w_1 and w_2 are 'weighting factors'. Note that predators need not be present as a stimulus for scanning to occur. The evaluation by $V_{(x,y)}$ leads then to a decision to pursue one or the other form of behavior: to stay alone or feed in a flock. This decision must be 'consistent' or rational for optimization to occur[36]. At this point the causal machinery becomes subject to natural selection via fulfillment of the sub-criteria foraging and predator avoidance (below dashed line in fig. 2). In the long run, both of these serve the long-term criterion of winter survival and, finally, fitness. Note that time-energy budgeting of the model regards time as invariant, in contrast to more dynamic models looked at later on in this paper. It is extremely important to remember some assumptions of the model by Caraco[8]:

1. Total time in the group T_T is the sum of feeding, scanning and fighting times (fig. 3). However, it is entirely feasible that a bird continues scanning while picking up a seed or while chasing another bird. We do not know to what degree these activities overlap in time.
2. Time spent scanning T_D is not a function of predator presence. It has been shown recently, howev-

Table 2. Essential components of optimization of feeding and predator detection in yellow-eyed juncos (implicit in 8). Numbers 1-4 correspond to the set of components listed in table 1

1. Depletion of food patches; number of birds in patch
2. Choice of optimal feeding group size
3. Maximization of $\left.\begin{array}{l}\text{net energy intake y}\\ \text{+ predator avoidance x}\end{array}\right\} V_{(x,y)}$
4. Total time in group T_T; maintenance costs

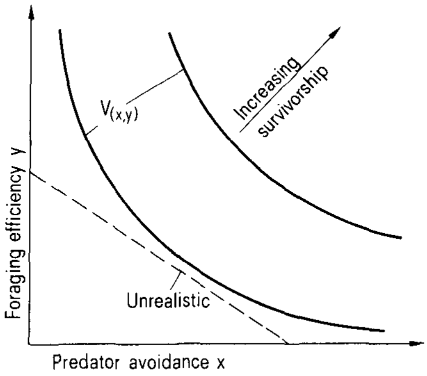

Figure 1. Value functions $V_{(x,y)}$ or indifference curves representing the optimal 'trade-off' between 2 demands in a songbird (modified from Caraco[8]). The broken line represents an unrealistic value function.

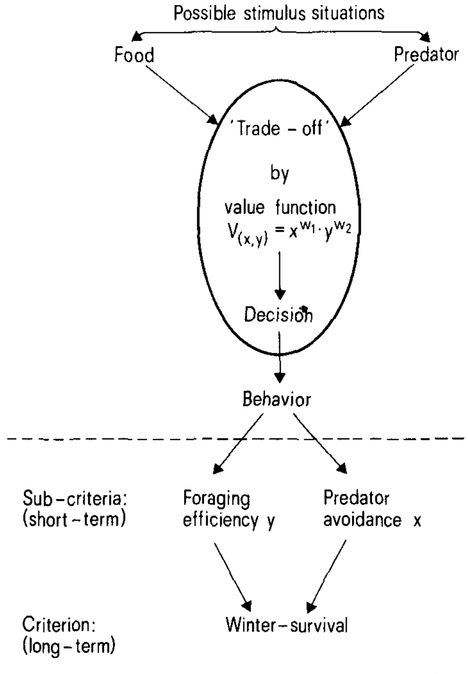

Figure 2. Flow diagram relating two possible stimulus situations or selective agents to fitness as measured by winter-survival via a decision-making process based on a value function $V_{(x,y)}$ as proposed in fig. 1. Dashed line demarcates the point in time where the behavior chosen becomes subject to selection by the agents at the top of the figure.

er, that flights of a passing trained hawk increase vigilance[10]; this is in agreement with an earlier finding in sticklebacks[40].

3. Central individuals are as vulnerable as peripheral ones. However, starlings at the periphery of a flock are more vigilant[24,32]. Furthermore, sticklebacks prefer to attack peripheral individuals of a swarm of water fleas (fig. 4)[38,39].

4. The attack rate of predators was assumed to be independent of group size. If, as is the case with cephalopod and fish predators[38,39,43-45], confusion in the predator increases with prey group size, then the formation of large groups by the prey may well be preferred. Yet, Caraco[9] discusses the opposite possibility that predation may increase with group size.

5. In the model derivation individuals are allowed only to join just one group or to stay solitary. In reality there will be groups of various sizes among which birds can choose.

Is then lack of realism fatal to the model? A model can be tested either by checking its assumptions or by testing its predictions.

Among the predictions of the time-budget model are:

A) that mean group size will vary inversely with temperature whenever foraging time requirements constrain fighting over food. This is born out by observation (fig. 5);

B) that mean group size will increase with food shortage. This is because higher food density reduces the search component of foraging. Time-constrained dominants can then show increased aggression, driving off subordinates; these in turn, are forced to feed solitarily. Caraco[9] was able to verify this prediction, too, by improving the food situation which led to a decrease in flock size. The economics of aggression seem to depend strongly on resource levels[18];

C) that when junco flocks are scared by a trained hawk, for instance, flocks become larger and (both) their members (and solitary birds) more vigilant[10]. Increased scanning no longer permits aggression to counter flocking.

Despite these successes one has to bear in mind that the model contains a decision inequality ('stay alone' vs 'join others') and is, thus, only semi-quantitative. It does not predict, therefore, at which temperature what group size should be chosen; nor does it predict at which food density aggression leads to fission of groups. The observed fit between predictions and observations means that the assumptions mentioned earlier do not harm the model even in cases where we know that they are almost certainly wrong. This lack of realism in the assumptions would probably become destructive to a more quantitative model.

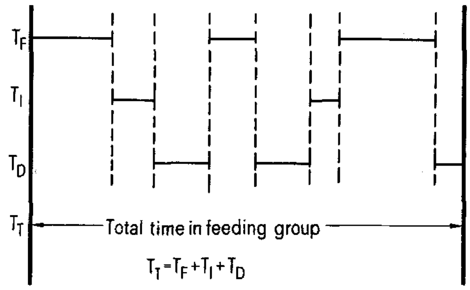

Figure 3. Total time T_T in feeding group is the sum total of foraging time T_F, interference fighting T_I, and looking out for predators T_D in a songbird (original based on conception in Caraco[8]).

Recently, modelling and experimentation have realistically taken into account stochastic fluctuation of patch profitability for foraging juncos. The latter behaved more 'risk-prone' when patches varied unpredictably and, as a consequence, the 24-h energy

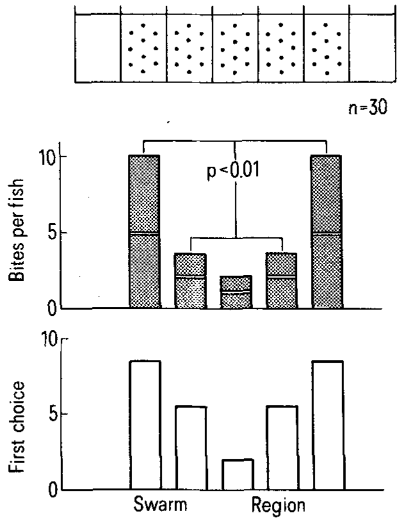

Figure 4. Distribution of attacks on live *Daphnia* in a swarm by 30 three-spined sticklebacks tested singly. Prey are evenly distributed over equal-sized compartments of a perspex cell simulating a uniformly dense prey swarm (top). First half of all bites per fish below white mark in black columns, second half of bites above (after Milinski[38]).

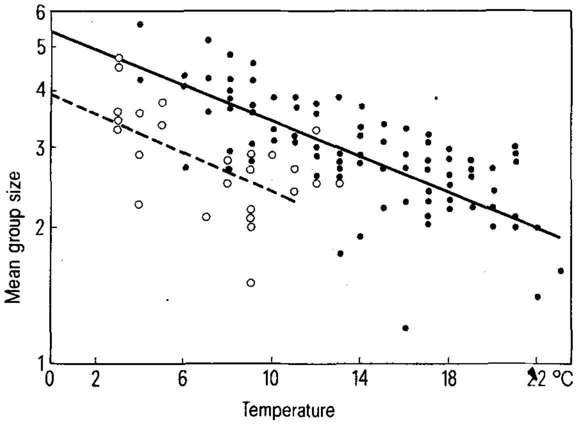

Figure 5. Mean feeding group size of yellow-eyed juncos as a function of ambient temperature. 2 scattergrams representing 2 different food situations (from Caraco[9]; Ecology *60* (1979) 618–627. Copyright © 1979. The Ecological Society of America.)

budget was negative[11] (for theoretical proof, see Stephen[57]), but there are objections to this interpretation (Regelmann 1981, personal communication).

A model with time as a variable: the Pontryagin maximum principle

While the foregoing time-energy budget analysis does not regard time as a variable, Pontryagin's maximum principle, for example, does. This more dynamic approach was pioneered by Sibly and McFarland[56] in their bioeconomic study of feeding and drinking behavior. The approach predicts the optimal trajectories of state variables and, hence, describes the behavior of the animal in time. The approach involves an assessment of the costs of a behavior pattern. Roughly speaking, it is these costs that the animal is thought to minimize[36]. In a study by Milinski and Heller[40] of optimal foraging, three-spined sticklebacks *(Gasterosteus aculeatus)* were allowed to hunt for water-fleas in a simulated swarm contained in a transparent cell. The number of bites against prey individuals was taken to be a measure of attack readiness or hunger, since prefeeding decreased the number of bites. Which prey density would a stickleback attack as a function of hunger? Theory predicts that the choice is hunger-independent, that means the fish should always maximize, but this is not the case: while starting to hunt, the fish elects to attack the densest swarm region and gradually shifts to less dense regions, as measured by a) first choice and b) number of bites in the course of time (fig. 6). To account for this discrepancy with optimal foraging theory, a model was designed in which various costs were assumed: The interaction term $\beta d(t) \cdot c^2(t)$ accounts for the fact that the fish cannot vary its capture rate $c(t)$ independently from the density chosen $d(t)$. The essential components of optimization are roughly as set out in table 3. One prediction of the model is, first, that a stickleback should start to feed in a high density region permitting a high feeding rate; it would also imply high confusion costs.

With decreasing hunger, a lower feeding rate should be achieved with less confusion at a lower prey density. This prediction is fulfilled by the experiment mentioned (fig. 6).

A more interesting prediction is that with raised costs of confusion because of a predator being present, a lower capture rate within a lower density will be optimal at the start. Thus, in the presence of a predator a hungry stickleback, which would normally attack the densest region of a swarm with a high feeding rate, has to divide its attention between prey and predator and would be expected to start with a low feeding rate and to attack a region with less confusion, i.e., a swarm region of lower density. This was in fact born out in an experiment with a kingfisher dummy serving as a predator stimulus (fig. 7): control fish not scared by the kingfisher (white

Table 3. Essential components of optimization in stickleback foraging on prey swarms (implicit in Milinski and Heller[40]). Numbers 1-4 correspond to those in table 1

1. Change of hunger; properties of prey swarm
2. Choice of optimal prey swarm density + capture rate
3. Maximization of net energy intake + predator avoidance
4. Feeding rate bounded by swimming speed; attention for overcoming confusion and detecting predators

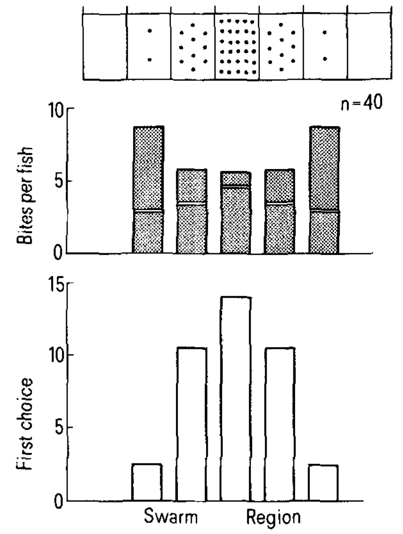

Figure 6. Distribution of attacks on a *Daphnia* prey swarm representing different densities by 40 three-spined sticklebacks tested singly. First half of all bites below white dash in black columns, second half above (from Milinski[39]).

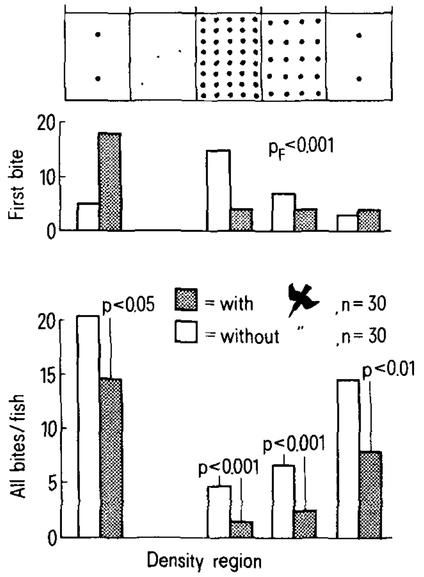

Figure 7. Distribution of attacks on different density regions of a *Daphnia* prey swarm by sticklebacks scared with a kingfisher dummy (black columns) and by control fish (white conlumns) (from Milinski and Heller[40]).

columns) first attacked the densest swarm regions and later on shifted their attack increasingly to less dense regions as was predicted by the model. This holds for 2 different measures: first choice, and all bites per fish. By contrast, fish that had been scared by the predator dummy (black columns) started to attack the least dense regions where confusion was minimal. Thereafter they continued to attack the least dense regions.

The presence of any predator, when detected, should distract the fish's attention. A decrease in visual attention affects the choice of densities (and capture rates) in the same way as does a decrease in hunger. Thus, as proposed by the model, the changed foraging behavior is an optimal one supplying both needs, namely to pay attention to a predator and with the remaining attention to maximize energy intake by attacking a less confusing swarm density.

As with time-budgeting, the Pontryagin method only allows the prediction of inequalities of, e.g., the kind: 'Choose a higher density'; it does not say exactly which density should be attacked next. For this we would need to know the precise relationship between confusion costs and density, or capture rate and density, for example.

Time scales over which to optimize

The discrepancy between the stickleback's foraging behavior and the postulate of maximization inherent in optimal foraging theory disappears when long-term maximization is considered[53]. Constrained by short-term needs other than energy intake, the fish has to sacrifice short-term maximization under certain circumstances. This brings up the important point of the time scale to be considered. The time span over which animals seem to maximize appears to range from fractions of a second over many hours in some species, to a year in others. Birds mobbing an owl approach to within a critical minimum distance when vacillating towards and away from the predator (fig. 8). This critical distance should reflect most accurately the risk a bird is willing to take; the more agile a mobber, the more closely it approaches the owl as shown for neotropical and European woodland birds. This suggests that birds optimize their chances of escape in case of attack. The species differences in critical distance implicate escape time differences of certainly less than a second. Hence, mobbers optimize chances for escape over those short intervals.

Much longer intervals are exemplified by horned lizards *(Phrynosoma cornutum)* feeding on harvester ants *(Pogonomyrmex)*[61]. On their foraging trips these lizards scorn many ants as they wander over their territory. One lizard needs about 75 ants/day, but already the loss to the colony of ca 10 ants on any one colony trail leads to the colony disappearing underground. Before eating too many ants of a colony, i.e. before the colony closes down, a lizard proceeds on its foraging trip. It does not revisit any one colony within a day. In this way it exploits its colonies parsimoniously. Horned lizards sacrifice short-term maximization to yield a long-term reward. This exploitation pattern is based on the animal's having sole access to its resource that is, it requires a territory. And a territory is what horned lizards appear to have.

Even longer intervals are taken into account by house martins. They have either 1 or 2 broods per year. Females that produce 2 broods have an annual mortality rate of over 50%, mainly due to hazards during migration. Females with just 1 brood have half the mortality (27%) and thus offset their short-term disadvantage in one summer by doubling their relative chances of reproducing the next summer[7]. Females foregoing a 2nd brood and, thus, maximizing their fitness in the long-term have a lower body weight[7]. This suggests that body weight acts as a constraint in that small females make the best of a bad job. They appear to have no true choice while heavy females would. Tree swallow *(Iridoprocne bicolor)* females whose brood-size was artificially enlarged suffered neither from weight loss nor from an increase in mortality. However, variance of nestling weight increased as a consequence of brood enlargement, suggesting parental skills differed accordingly[15] and/or females exercized parental restraint in order to forestall an increase of mortality[14]. Either way, females seem to have optimized fitness in the long-term.

In conclusion: The time scale of maximization may range from fractions of a second to more than a year if one looks at particular criteria for fitness (table 4). The time needed for the decision processes underlying this vast range may not differ proportionately: to avoid a predator may be decided as quickly as postponing another brood, but there is a dearth of information about how rapidly animals make decisions of different kinds. One thing is nevertheless

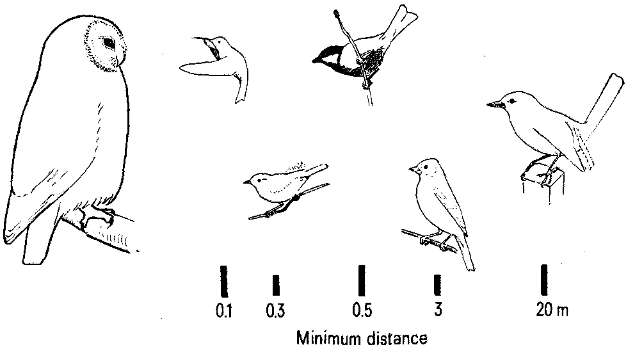

Figure 8. Minimum approach distances in various bird species endowed with different degrees of manoeuvrability while mobbing an owl. From left to right: hummingbird[1,58]; chiffchaff, willow warbler; great tit; chaffinch; European blackbird (Curio, unpublished).

Table 4. Orders of magnitude of interval over which behavior is optimized in different animal species and for different behaviors of one and the same species (see text for details)

Animal	Optimality criterion	Time scale	Source
Birds	Predator avoidance	< 1 sec	Unpublished
Three-spined stickleback	Foraging	Seconds	Milinski and Heller[40]
	Foraging + predator avoidance	Minutes	
Horned lizard	Foraging	Days	Whitford and Bryant[61]
House martin	Reproduction	≥ months	Bryant[7]

clear: While certain optimization intervals may necessitate a decision only once, for example to forego a brood, others, like a longer-term economic use of a resource, necessitate many decisions: horned lizards must decide many times during their foraging walk whether to reject an ant or not. Another unresolved problem is that the opportunity to revise a decision is similarly quite different: the opportunity for that would depend on the time preceding the act that is decided upon. If this interval is short, a decision may be irrevocable; if it is long, a decision may be checked many times against information relevant for the decision making. It would be rather difficult to know when an animal would revise a decision unless there are overt signs of behavior indicative of a decision. Intention movements would appear to be of help in detecting the making of a decision. Further, if the interval between making a decision and its execution is long, information acquired during this interval could be used to affect the final decision; if the interval is short, for example the time in which an animal has to escape from a predator, such information must be irrelevant. What then counts is information laid down before the interval over which optimization is due to occur. Work has just started to elucidate the role of time for making decisions.

Optimal diet breadth

Optimal foraging theory addresses, among other questions, how omnivorous animals ('opportunists') select their diet. Laboratory[26,59] and field work[20,27,53] has demonstrated that animals rank food sources according to their profitability; profitability is defined as an item's energy yield per unit handling time. Foragers are thought to add food items to their diet in the order of decreasing profitability as food abundance decreases (though another theory sheds doubt on this notion[37]). The success of the theory has been greatest in predicting food selection as a function of density of items. This work led to the 'always or never' rule predicting that a predator should always concentrate on the more profitable of 2 prey items once its density exceeds a certain threshold; then it should always ignore the less profitable item. However, while predators were repeatedly found to prefer the more profitable item as predicted, they also consistently took some of the other(s)[27,46]. This deviation from the rule was accounted for by the animal's appetence to maintain a nutritionally balanced diet[5,50,60]. Great tits *(Parus major)* deviated from the 'always or never' rule by taking mealworm pieces half the size of the more profitable ones when, according to prey density, they should not have done so[26]. Krebs and Davies[28] discarded the 'balanced diet' hypothesis on the grounds that both prey were bits of mealworm and, hence, nutritionally identical. However, this reasoning is only correct if the predator assesses nutritional balance via some metabolic feedback, which, in the present case, would have been qualitatively identical for both types of prey. The 'balanced diet' idea is, however, a viable explanation since diverse predators have been shown to pick up an apparently mixed diet when items appear different but are nutritionally the same[41,48]. Prey in nature that differ, e.g., in size by a ratio of 1:2 are usually nutritionally different items and the tits' decision appears to be a sound one.

When linking the optimality approach to community ecology, a test of the 'always or never' rule reveals another failure of optimal foraging theory. Theory predicts that during food shortage a predator should feed as a generalist, otherwise as a specialist. Despite the rule's verification in some tests, there have been a number of disturbing failures to predict food selection behavior:

1. A number of field studies have shown generalist foragers to become specialists during periods of food shortage, just the opposite of what the 'always or never' rule would predict[12,13]. In no single case has a satisfactory explanation been given for these discrepancies*.
2. A backswimmer *(Neoplea striola)* did not take water fleas according to their profitabilities (fig. 9), when all prey size classes were offered in equal proportions. Profitabilities had been determined by measuring prey energy content e_i calorimetrically and by measuring handling time t_i as usual. Even a correction accounting for capture success, p (left curve), does not reflect the actual prey size selection (histogram). Perhaps familiarity with the prey size distribution in

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*Recently Schluter[55] has discovered the discrepancy anew and finds that theory predicts facultative diet specialization in nature only in about ⅓ of many testable cases. It is strange that reviewers of optimal foraging theory have overlooked this discrepancy, and others, after attention had first been drawn to it in 1975.

the lake from which the backswimmers came is an explanation for the anomaly[19].

3. An unexpected complication is that intraspecific variation of prey caloric content is as marked as interspecific variation in 60 arthropod species[17], thus annihilating any ranking of items by predators in terms of energy content. Furthermore, prey size may be a misleading indicator of profitability since the handling time imposed by a bigger and, hence, seemingly more rewarding item can cause the latter to be actually less profitable. In spite of this, common shrews *(Sorex araneus)* used size as an indicator of profitability[4].

4. Time needed for correct recognition of prey, especially by invertebrate predators, may prevent foragers ranking prey according to profitability. Thus 'number maximizing' may become more important than 'energy maximizing'[22].

5. With time of passage through the gut, profitability of prey can decrease, again without any consideration of energy content[23].

6. The presence of a competitor causes common shrews *(Sorex araneus)* to behave more like generalists than theory would predict[4].

The explanation for these discrepancies may be complex and it is likely that optimal foraging theory as originally conceived is too simple to predict successfully feeding behavior in the field. I suggest a number of possibilities of potential value to a new generation of models:

1. The animal is not maximizing food intake in order a) to minimize the risk of variation of intake; b) to minimize the risk of being eaten because of reduced vigilance (p. 30), or because of becoming too heavy for a successful escape from predators[13,25]. Sub-maximal food intake also enables the skeleton to develop normally. Young birds (*Grus* spec.) used to finding highly dispersed and small food items, when raised by humans develop skeletal anomalies, suffering from crippled legs. Unconstrained feeding leads to a body weight too heavy for the leg bones, which at this age are still too weak. Food resources in the wild are probably always below what the young birds would be able to take up (Nicolai, personal communication). c) to ensure sufficient food supplies for its progeny. This may be so in skinks *(Eumeces obsoletus)* where the female does not feed as long as she cares for her babies[16]**.

Time and energy may not be the only factors that need to be minimized or maximized, respectively:

2. Nutrient content may be yet another variable[5,50,60]. There is a dearth of information on this point. A similar complication stems from our work with a Jamaican anole lizard *(Anolis lineatopus)*. Ethotypic, i.e. interindividual, variation of prey acceptance in newborn hatchlings[6] prompted us to investigate the

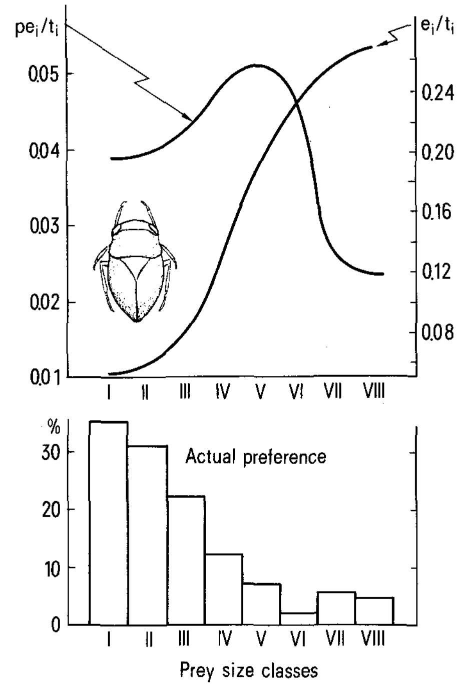

Figure 9. Prey *(Daphnia magna)* size selection by the backswimmer *Neoplea striola*, with size increasing from I to VIII (bottom). Expected size selection according to optimal foraging theory, i.e. with prey profitability (energy content/handling time = e_i/t_i) (right curve), or with prey profitability e_i/t_i weighted with hunting success rate p (left curve) being the criterion of selection (from data of 4 experiments with 10, 40, 80, and 160 prey l^{-1} in Gittelmann[19]).

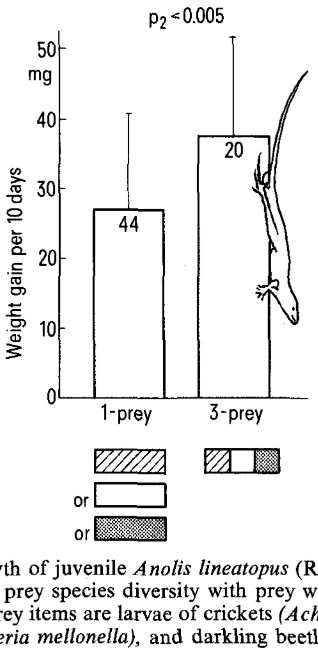

Figure 10. Growth of juvenile *Anolis lineatopus* (Rept., Iguanidae) as a function of prey species diversity with prey weight/day being dept constant. Prey items are larvae of crickets *(Acheta domesticus)*, waxmoths *(Galleria mellonella)*, and darkling beetle larvae *(Alphitobius diaperinus)*. Weight gain = mean±SD, p_2 two-tailed, Mann-Whitney U-test (from Hettrich[21]).

** Marmot females *(Marmota caligata)* with young are thought to travel farther from their dens to graze in order to ensure enough food close to their dens for their offspring[3]. Another possibility is that females do so because of greater food demands imposed by growing parental efforts.

food value of different prey items. Juveniles that are fed a mixture of crickets, waxmoth larvae and darkling beetle larvae grow more quickly than others maintained on a monotonous diet of any one of these three insects. Total weight of prey eaten was kept constant in each group (fig. 10). Hence, each prey item alone leads to reduced growth and, hence, to less fitness; apparently, prey items interact in a way still unknown. They cannot be simply ranked on a scale of profitability as defined so far (see also Rapport[54]).

3. Apart from nutrients, animals pick up remedial agents while feeding in order to fight parasites[49], a fascinating, unstudied complication of optimal foraging theory.

4. Related to the foregoing explanation 2 and 3 is the hypothesis that animals have to avoid an excess of toxins. Herbivores like monkeys[42] and granivorous birds[52] may feed on very many plant species because their capacity to detoxify any particular compound is limited - whereas a variety of toxins in small amounts will be tolerated.

The evidence from findings 2-4 and hypotheses generated therefrom force us to modify our too simple time-energy budget approach. Instead we have to consider, among other things, the subtle composition of the diet, or interaction of prey items if optimality theory is to make more realistic predictions than has been possible thus far.

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Effects of mitogens on ADCC activity and Fc receptor bearing cells

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Summary. Murine spleen cells, when activated by various mitogens (Con A, PHA, LPS, BCG) or Con-A conditioned medium show altered behavior as effector cells of antibody-mediated cell cytotoxicity (ADCC) which does not correlate with the expression of Fc-receptors (FcR) at the effector cell surface.

Antibody-mediated cell cytotoxicity (ADCC) represents one of the 4 cytotoxic immune activities, the others being a) the antibody plus complement-mediated lysis, b) the cytotoxic T cell mediated lysis, and c) lysis mediated via NK cells, or d) activated macrophages. These 4 immune activites are belived to be important for rejection of tissue grafts[3,4] and possibly of tumors[5,6].

ADCC activity is crucially dependent on antibody and a receptor linking the Fc portion of the antibody molecule to the effector cell surface. The antibody binding sites are then free to recognize tissue antigens. ADCC activity is usually measured in vitro using normal effector cells. All cells carrying Fc-receptors (FcR) are potential killer cells in ADCC and are operationally referred to as K cells. The heterogeneity of this K cell population is clearly recognized, but so far it has not been possible to attribute ADCC activities unequivocally to the various components in a mixed K cell population.

It was of interest, therefore, to stimulate spleen cells with various mitogenic principles in order to test whether a) activated cells were still effective in ADCC, b) subsets of FcR$^+$ activated cells were differentially active, and lastly, c) whether the degree of FcR$^+$ was the determining factor for K cells to be active in ADCC.

Materials and methods

Mice. C3H/HeJ, C3H/Tif and CBA/J mice were obtained from the Institut für Biologisch-Medizinische Forschung AG (Füllinsdorf, Switzerland). All experiments were done with 6-12-week-old mice.