presumably due to an error in estimating either its or rumen capacity.

The original discussion of the moose's problem (Belovsky, 1978) was more complicated than the version presented here. Two kinds of terrestrial food were distinguished, herbs and the leaves of deciduous trees. Herbs cannot be eaten as quickly as the leaves of trees, but they yield a little more energy per unit mass. Also, account was taken of the danger of overheating in the midday sun. Moose seem to have to spend part of the day on land and part in water, to control body temperature in summer.

Since three kinds of food were being distinguished it was not possible to solve the problem by drawing a two-dimensional graph like Fig. 4-2. The equivalent graph was three-dimensional, with planes instead of lines representing the constraints. Such graphs are inconvenient to draw, but linear programming problems in three (or more) dimensions can be solved by algebraic methods (see, for instance, Koo, 1977). In two-dimensional problems the solution always occurs at the intersection of two of the constraint lines. In three-dimensional problems it occurs at the intersection of three constraint planes, and in multi-dimensional problems at an intersection of the hyperplanes that represent the constraints. The standard method of solution examines the intersections systematically, avoiding any that are obviously not the optimum.

The three-dimensional analysis indicated that in the optimum diet, about 90% of the terrestrial food should be leaves of trees and about 10% should be herbs. Moose were observed to eat these foods in almost exactly these proportions.

Belovsky (1978) also considered what the optimum diet would be if the aim were not to maximize energy intake, but to minimize time spent feeding. In that case the optimum diet would include no herbs.

4.3 When to give up

The larvae of ladybirds (coccinellid beetles) feed on aphids, eating out the soft tissues and leaving the hard exoskeleton. In the
early stages feeding is quick and easy, but as the meal continues
the remaining food becomes more difficult to extract. How long
should a larva persist with one aphid before leaving it to look
for another? It will be assumed as in section 4.1 that it is advan-
tageous to make the mean rate of intake of food as large as possible.
Larvae which feed fast will probably grow and develop faster than
ones which feed slowly, and produce offspring sooner. Hence nat-
ural selection should favour behaviour which increases the rate of
intake of food.

Figure 4-3(a) shows the evidence that during a meal, the remain-
ing food becomes progressively more difficult to extract (Cook
and Cockrell, 1978). Ladybird larvae which had previously been
starved for 24 h were given an aphid each to feed on. Their meals
were interrupted after various times, and the remains of the aphids
weighed. Thus the graph for feeding on a single aphid was ob-
tained. Notice that its gradient becomes smaller (the rate of extrac-
tion of food falls) as the meal proceeds. The other graph shows
that this was not due to diminishing appetite when fresh aphids
were supplied at ten minute intervals, feeding continued at an
almost constant rate for fifty minutes.

Let a ladybird larva spend time $t$ feeding on each aphid, and let
the mass of food it extracts in this time be $m(t)$ (The letter $t$ in
parentheses indicates that $m$ is a function of $t$). Let the mean time
required to find a new aphid, after leaving a partially-eaten one,
be $T$. The mean rate of intake of food, $Q$ is given by

$$Q = \frac{m(t)}{(T + t)}$$

The optimum value of $t$ is the one which makes $Q$ a maximum,
and could be found by calculus if we had an algebraic expression
giving $m(t)$ as a function of $t$. Such an expression could be chosen
to fit the graph in Fig. 4-3(a), that shows the time course of a typical
meal on a single aphid.

Figure 4-3(b) shows a different, easier method of finding the
optimum. The curve is a graph of $m(t)$ against $t$, copied from
Fig. 4-3(a). Straight lines have been drawn from the point $(-T, 0)$
to intersect the curve at various values of $t$. The gradient of each
Figure 4.3. Graphs describing ladybird larva feeding on aphids. (a) Graphs of the dry mass of food extracted against time. Graphs for a single meal and a series of ten minute meals on successive aphids are shown. (b) A diagram based on the graph for a single meal showing how the optimum duration of the meal ($t_{opt}$) can be determined. $T$ is the time required to find an aphid. (c) A graph of feeding time $T$ against search time $T$. The points show observed values and the line shows the theoretical optimum behaviour. The points in (a) and (c) have been taken from Cook and Cockrell (1978). In (c) they are shown ± one standard error.

of these lines is $m(t)/(T+t)$ so the steepest possible line, for any given value of $T$, indicates the optimum value of $t$. This line is the one which is a tangent to the curve.
Optimum values of $t$ obtained in this way are shown in Fig. 4-3(c). These values are only rough estimates: different values would have been obtained if the smooth curve through the points in Fig. 4-3(a) had been drawn slightly differently.

Figure 4-3(c) also shows the mean feeding times $t$ actually used by ladybird larvae. Between 2 and 32 aphids were distributed evenly on a tray, 0.5 m square. A ladybird larva was put on the tray and watched continuously for 4 h. Any aphid it ate was replaced immediately. The time spent feeding on each aphid and the time spent searching for the next one were recorded. Hence mean values of $t$ and $T$ were obtained. The more aphids there were on the tray, the shorter the searching time $T$ and also the time $t$ spent feeding on each aphid. The observed values of $t$ are close to the graph of theoretical optimum values in Fig. 4-3(c). The ladybird larvae behaved approximately as the theory suggested they should.

A similar analysis has been applied to the mating of dungflies, Sarcophaga (Parker & Stuart, 1976). This is another situation in which persistence brings diminishing returns. Females arriving at cowpats to lay eggs are intercepted by males who copulate with them, although most of the females have sperm from previous matings in their spermathecae and could lay fertile eggs without further copulation. The longer the male prolongs copulation, the more of the sperm from previous matings are displaced and the larger the proportion of the offspring that are fathered by him. This proportion increases at a diminishing rate, just as the rate of feeding of a ladybird larva diminishes in the course of a meal. To maximize his number of offspring a male should copulate for a particular optimum time, and then go in search of another mate. It was estimated from field observations, using a graph like Fig 4-3(b) that the optimum duration for copulation in the particular circumstances was 41 minutes. The observed mean duration was only a little different: it was 36 minutes.

The theories for the ladybird larvae and dungflies are particular cases of the Marginal Value Theorem (Charnov, 1976b). This theorem refers to situations in which food or some other resource is patchily distributed, and exploitation of a patch gives diminish-
ing returns. In the case of the ladybird larvae, the patches were individual aphids and the resource was their food content. In the case of the dungflies, the patches were individual females and the resource was unfertilized eggs. The theorem also assumes that when one patch is abandoned, appreciable time is needed to find or travel to the next. The theorem states that the rate of benefit is maximized by exploiting each patch until the rate of benefit from it falls to the maximum mean rate that can be sustained over a long period.

The theorem has also been applied to animals searching for hidden food. Cowie (1977) studied great tits (Parus major) looking for mealworms hidden in small jars of sawdust. The tits found the first few mealworms in each jar faster than they could find the remainder: the fewer the mealworms that remained, the longer on average it took to find each one. The tits moved on from each jar to the next at about the optimal times. The theorem could also be applied to natural patches of hidden food. For a bird feeding on caterpillars, each plant on which caterpillars might be found would be a separate patch.

The theorem applies only if patches are searched at random. If the prey are stationary and the predator searches each patch systematically, never going over the same ground twice, the number of prey removed has no effect on the rate of finding the remainder and the theorem does not apply.

4.4 Ideal free ducks

Imagine two people feeding the ducks in a pond. One, on the north bank, throws them bread at a rate (pieces per minute) \( r_N \). The other, on the south, throws bread at a rate \( r_S \). The ducks divide into two groups, \( n_N \) of them going to the north and \( n_S \) to the south. The ducks in the north group get bread at an average rate \( r_N/n_N \) and those in the south group at a rate \( r_S/n_S \). If \( r_N/n_N < r_S/n_S \), a duck in the north group can hope to improve its rate of feeding by moving to the south, and vice versa. Therefore, if each duck is trying to maximize its rate of feeding we should expect them