Optimal Activity Times and Habitat Choice of Moose

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Summary. A set of concepts was presented which could be used to model an animal's activity cycle and habitat choice as an optimization process. The model was applied to moose (*Alces alces*) summer activity and its predictions were consistent with observed feeding times and habitat selections. The optimization model had a goal of maximizing daily feeding time at the least possible energetic cost. This goal was consistent with a foraging strategy that maximized the intake of some nutritional component, i.e. energy, protein, etc. The optimization problem, however, was bounded. Three constraints appeared to limit the goal: body temperature must be maintained within set upper and lower limits, thermal equilibrium must be maintained over an extended period so the activity cycle strategy can be repeated and sufficient time must be spent ruminating.

Naturalists have long been aware that animals demonstrate daily activity cycles; this paper attempts to demonstrate that these cycles and associated hourly changes in habitat use result from an optimization process, which balances the goals of maximizing feeding time and minimizing risks. Risks are posed to animals by predators and the inability to maintain internal homeostasis (i.e. thermal balance, water turnover, etc.). The moose (*Alces alces*) is an ideal test case for several reasons. First, moose, as herbivores, have activity cycles which are not tied to prey activity cycles, since plants are sessile. Second, as large animals, moose are not capable of burrowing or using microhabitats to avoid the ambient environment, and are relatively predator-free. Thus risks are restricted to breakdowns in internal homeostasis.

Optimization models for determining daily feeding time are inseparably tied to foraging strategy theory (Schoener 1971; Pyke et al. 1977). An animal has two alternatives in determining daily feeding time. First, if the animal is maximizing its intake of some nutritional component (synonymous with an energy-maximizing feeding strategy), it should attempt to maximize daily feeding time. This strategy provides an animal with greater food supplies, since items of lower quality can profitably be consumed (Schoener 1969), and more food can be consumed each day. Nevertheless, an animal can not feed all day, since its digestive organ can only hold so much food and the environment presents many deleterious factors (predation, excessive heat gains and losses, dessication, etc.).

Second, an animal might minimize its daily feeding time, while still attaining nutritional requirements. This is synonymous with a time-minimizing feeding strategy. While feeding-time-maximization increases resources for reproduction and times of scarcity, time-minimization provides more time for non-feeding activities: i.e. reproduction and grooming, and minimizes exposure to deleterious factors in the environment.

If an animal was a time-minimizer, it would feed until its nutritional requirements were satisfied and only at times that posed the least risk. After feeding, the animal would retire to habitats that posed the least risk. On the other hand, a feeding-time-maximizer would balance the benefits of feeding in each period against the risks, assuming that the digestive organ was not full. Furthermore, while not feeding, the animal would perform behaviors in habitats which not only minimized risks but allowed a return to feeding as soon and for as long as possible.

Moose at Isle Royale, Michigan, were faced with the feeding-time-maximization problem since they were known to be energy maximizers in their feeding (Belovsky 1978). Furthermore, it appeared that the risk while feeding was a breakdown of thermal homeostasis; feeding was associated with cooler and less sunny periods of the day and the amount of time spent feeding on a summer day was highly correlated with daily average temperature (Belovsky and Jordan 1978). This was not to imply that air temperature was the determinant of feeding in itself, rather it was an easily measured thermal parameter which was seasonally correlated in the field with other, perhaps more important but more difficult to measure, parameters: i.e. solar radiation (see Appendix). Dessication was not thought to be an alternative explanation since moose ingested 28.7 l/day of water in food (Belovsky 1978) and environmental water was abundant.

The thermal imbalances experienced by moose performing different behaviors in various habitats at different times of the day had to be quantified. These behavior-habitat-time choices and their resulting thermal imbalances were incorporated in an optimization model which maximized daily feeding time at the least possible energetic cost and within tolerances to thermal imbalances. If two alternative sets of behavior-habitat-time choices gave the same daily feeding time, but at different energetic costs, the least costly would be selected (Belovsky 1978). The optimization technique employed was dynamic programming (Bellman and Dreyfus 1962). The solution provided a prediction of a moose's choice of behavior and habitat at each hour of an average summer day, given the potential choices set forth in the model. These could be compared to the observed habitat-behavior choices observed in the field.

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Methods and Model

Methods

The summer (June-September) behavior of moose was studied at Isle Royale National Park, Michigan, from 1972 to 1974. These investigations provided information on a moose's hourly choice of behaviors and habitats through direct observation (Belovsky and Jordan 1978) and radio-telemetry. Direct observation provided data on times of the day and habitats that moose used while feeding, along with other feeding parameters, and were presented elsewhere with a habitat description (Belovsky and Jordan 1978).

Of 8 moose radio-collared, 5 did not provide data because their radios malfunctioned or they left the study site. The 3 successfully radio-collared moose were used to determine distances traversed hourly, average habitat utilization and hourly-habitat utilization. The hourly-distances were based upon the line joining locations obtained initially and an hour later, as such they represented a minimum distance traversed. By locating a cow moose at each hour of the day over three different days and plotting these locations on a habitat map, the number of observations in each habitat was determined as well as their regularity with time of day. Air temperature measurements were made simultaneously with all direct and radio-telemetered observations.

The environment was sampled randomly for bed remnants, which appeared as depressed vegetation. This was done by walking transects for a fixed distance and direction from a starting point chosen using random numbers and a map grid. Each bed was classified by habitat and orientation, whether the long axis of the depressed vegetation, length of moose body, was parallel or perpendicular to the sun's path. A perpendicular orientation maximizes the solar radiation striking a moose, while a parallel attitude minimizes solar radiation.

Thermal imbalances experienced by an average adult moose for hourly behavior-habitat choices during an average summer day were computed using a simple thermodynamic model of heat flow between an animal and its environment (Porter and Gates 1969):

$$HS = M + Q_{abs} - \gamma \varepsilon T_r^4 - h_c(T_r - T_a) - E_{ex} - E_{sw} \pm C \qquad (1),$$

where HS is heat stored by the animal's body (Wm^{-2}), M is the metabolic heat produced by the animal (Wm^{-2}), Q_{abs} is the solar radiation absorbed by the animal (Wm^{-2}), γ is the Stefan-Boltzman constant ($Wm^{-2}/°K^4$), ε is the emissivity of the animal's surface, T_r is the animal's surface (fur) temperature (°K), h_c is the convection coefficient ($Wm^{-2}/°K$), T_a is the ambient air temperature (°K), E_{ex} is the heat lost through respiratory evaporation (Wm^{-2}), E_{sw} is heat lost through sweating (Wm^{-2}), and C is conductive heat loss (Wm^{-2}). An average summer day was a hypothetical 24 hour period in which thermal parameters for each given hour were an average for that hour over the summer. An average adult moose had the average weight of an adult at Isle Royale, 358 kg, and an energy metabolism which was an average of adult male and female metabolisms (Belovsky 1978).

The National Park Service at Isle Royale collected daily summer thermal measurements: maximum-minimum air temperature, relative humidity and wind speed. In addition, measurements of solar radiation, soil temperature, water temperature, vegetation temperature, moose surface temperature, and moose convective, conductive and evaporative heat losses were made and these values appear in the Appendix. In many instances, these data represented crude estimates, but it was felt that their accuracy was sufficient for use in an optimization model.

Only observed moose behaviors and available habitats were used to compute HS values. Moose were observed during the summer either active-feeding or bedded; moose were never observed standing without feeding. Moose also chose the orientation of their body to the sun's path: parallel or perpendicular. While moose were feeding, there did not appear any way for them to consistently orient their bodies while moving from plant to plant. Rather at times they were perpendicular and at others, parallel, providing an averaged orientation.

The environment was arbitrarily divided into four habitat types which appeared important to moose. Beaver ponds were sites for aquatic feeding and were never used for bedding. Conifer forest had a canopy dominated by conifer trees (> 50%) and was used only as a bedding site in summer, since food plants were rare. Deciduous forest had a canopy dominated by deciduous trees (≥ 50%) and open areas had less than 20% canopy cover. Open areas provided the majority of moose-food, with well-developed shrub layers which had high nutritional quality due to the absence of shading. Because open areas were relatively small and distributed throughout the deciduous habitat, a moose experienced both habitats in equal proportion while terrestrial feeding in a coarse-grained manner. Consequently, 8 behavior-habitat choices were observed (feeding-open-deciduous, feeding-pond, bedded-parallel-open, bedded-perpendicular-open, bedded-perpendicular-deciduous, bedded-parallel-deciduous, bedded-parallel-conifer, bedded-perpendicular-conifer), providing 192 hourly behavior-habitat choices during an average summer day, if moose "view" their day in discrete hourly periods.

The Model

The goal was maximization of daily feeding time at the least possible energetic cost, since moose were known to be energy maximizers in their feeding (Belovsky 1978). The limitation of "least possible energetic cost" emerged from contingency models of feeding behavior (Schoener 1974), which predict that an animal should feed in a time period only if the net energy gained by feeding is positive. A corollary is that if an animal is presented with N feeding periods that have positive net energy values for feeding, but the animal can only feed in X periods due to risk factors or digestive capacity (N greater than X), then the N minus X periods which have the lowest positive net energy values should be dropped. This follows from the notion that the net energy available to an animal is positively related to its fitness. This approach has been extended by Huey and Slatkin (1976) to theoretically determine when a lizard should move from one micro-habitat to another for passive thermoregulation.

Moose, as herbivores, have constant energetic costs for search and handling within a given environment and net energy available from feeding in any hour should be positive because gross energy intake is a large constant (Belovsky 1978). Therefore, energy expenditure for thermoregulation should determine which hours have greater positive net energy values. Moose HS values deviating from 0 (thermoneutrality) were assumed to require greater energy expenditure for shivering, panting, changes in blood flow, etc., to maintain a constant body temperature or reduce changes and Q_{10} effects on metabolism (Gordon et al. 1968; Schmidt-Nielsen 1975; Whittow 1971). Because all feeding energy values were constants except thermoregulatory costs, relative energy costs for thermoregulation were sufficient for the comparison of hourly behav-
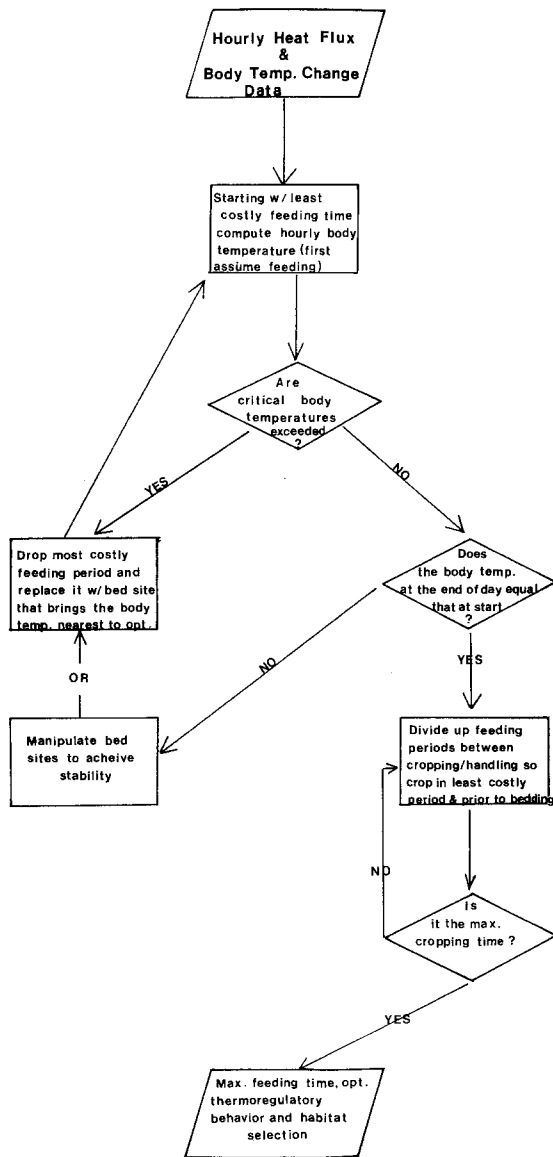
Fig. 1. The flow chart represents the optimization model used to predict a moose's maximum daily feeding time at the least energetic cost on the basis of the constraints presented in the text

ior-habitat choices, and a metabolic index was developed for this purpose.

Several large ungulate metabolism studies (Blaxter 1962; Weiner 1977; Blaxter and Wainman 1961; Brockway and Maloiy 1968) indicated that metabolism increased 2.6 times faster (s.d.= 0.4) with negative HS values than with positive, assuming a linear relationship between HS and a metabolism increase (observed metabolism – minimum recorded metabolism). This observation appeared reasonable (linear regression: average $r^2 = 0.95 \pm 0.02$). Furthermore, Silver et al. (1971) indicated that large ungulates might possess a linear plot of metabolism versus environmental temperature rather than the conventional curvilinear plot. The metabolic index, based on this information, was:

Metabolic Index $= 2.6|HS|$, if $HS < 0$,

and

Metabolic Index $= |HS|$, if $HS \geq 0$. $\qquad$ (2)

Constraint – Limits to Body Temperature. An animal's body temperature cannot vary beyond lethal upper and lower values. If the animal, however, followed this course, a predator attack or any other unexpected increase in activity when the animal was at its upper body temperature limit would result in death since activity increases body temperature. On the other hand, a storm when the animal was at its lower limit could be lethal. Therefore, it seems likely that an animal will set its upper and lower body temperature limits to provide a 'dead band' or 'margin for error' between normal acceptable limits and the lethal level (Heath 1964; DeWitt 1967).

The easiest way of determining the 'dead band' limits was to permit moose to demonstrate them, when provided with a free choice of thermal environments and behaviors. Knorre (1959) found that Siberian moose in summer allowed their body temperatures to vary from 38.4 to 38.8° C, a 0.4° C variation, when permitted to choose between shaded conditions (bedded in a barn) and open (feeding in a pen). This constraint can be written:

$$0.4°\text{C} \geqq \sum_{i=1}^{n} |HS_i/57.4 \text{ Wm}^{-2}/°\text{C}| \qquad (3),$$

where n is any time period between 1 and 24 h later, where all interim periods are included, 57.4 Wm^{-2} is the heat required to change an average adult moose's body temperature 1° C, and HS_i is the HS value chosen at hour i.

Constraint – Steady Periodic Fluctuation of Body Temperature. The short-term steady state or 'climate space' analysis developed by Porter and Gates (1969) and applied successfully by them and others to determine feasible behavior-habitat choices for small animals with short time constants (Morhardt and Gates 1974; Morhardt 1975; Porter et al. 1973, 1975) cannot be applied to moose because of their large body masses which provide long time constants for the heat flow model [Eq. (1)]. This, however, does not negate the importance of a long-term 'steady state' or 'steady periodicity' for moose heat flow. If an animal is to develop a useful strategy for the selection of behavior-habitats, it must be able to repeat the strategy on average, or, sooner or later, the animal will reach a point where any decision might violate its physiological body-temperature limits and result in feeding-time-minimization. This is further complicated when daily variations in climatic conditions are considered, since they require the animal to have sufficient behavior-habitat flexibility to compensate. This constraint, assuming a 24-h periodicity, can be written as:

$$0 = \sum_{i=1}^{24} HS_i$$

Constraint – Digestive Organ Capacity and Food Processing Time. A moose cannot continue to feed if its digestive organ, the rumen, is full or it must regurgitate food for rumination. The digestive organ capacity constraint was presented elsewhere (Belovsky 1978) and was written for the present model as:

32,900 g-wet wt/day $\geqq 62.2 \ T_1 + 400 \ T_a$, $\qquad$ (5)

where 32,900 g-wet wt/day is the rumen capacity, T_1 is terrestrial feeding time (min) and T_a is aquatic feeding time. If a moose must drop feeding times because the rumen is full, aquatic times should be deleted since aquatic feeding provides less gross energy intake than does terrestrial feeding (Belovsky 1978).

To properly digest food, a ruminant must spend time regurgitating the rumen contents and masticating them (Blaxter 1962). A moose was assumed to crop food up to the maximum observed period, 2.1 h ($\bar{x}=0.9\pm0.6$, $N=7$) and then to ruminate for a period which satisfied the average observed feeding-to-ruminating ratio, 1/1.5 (observed ruminating time: $\bar{x}=1.3$ h ±0.8, $N=7$) (Belovsky and Jordan 1978).

Solving the Model. There were 24 h time periods, each of which had 8 potential behavior-habitat combinations, providing 8^{24} potential daily combinations of moose behavior-habitat choices. One combination (or perhaps several equivalent) had to be found which satisfied the constraints and maximized daily feeding time at the least possible energetic cost. The solution was found using an iterative computer program, which reduced the number of iterations on the basis of the optimality theories developed in dynamic programming (Bellman and Dreyfus 1962).

In simplified terms, the program operated by following these steps:

1) The feeding option (terrestrial or aquatic) at each hour which had the lowest metabolic index was chosen and these were ranked according to their metabolic indices (1-lowest to 24-highest).

2) Starting with the moose feeding in all 24 h periods, it was determined whether or not the 'steady periodic' [Eq.(3)] and body temperature [Eq.(4)] constraints were violated.

3) If these two constraints were violated, the hourly feeding option with the *highest* metabolic index was replaced with a bedded-behavior-habitat choice which tended to reverse the most recent changes in body temperature at the least possible energetic cost without violating the constraints.

4) This process was continued (return to step 2, except the moose now feeds for only 23 h periods, 22, 21, ...), dropping
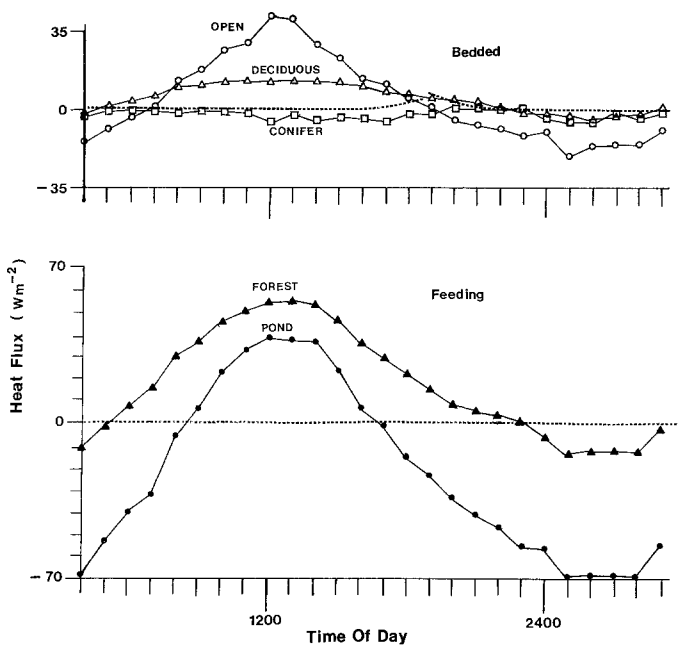

Fig. 2. These graphs present an average adult moose's hourly *HS* values (Wm^{-2}) for an average summer day. The *HS* values in the upper figure are for moose bedded in open, deciduous and conifer habitats with their bodies oriented perpendicular to the sun's path during daylight hours. The lower graph presents the *HS* values for moose feeding in a beaver pond or forest. It is assumed that their bodies alternate between parallel and perpendicular orientation thus producing an average orientation to the sun's path during daylight
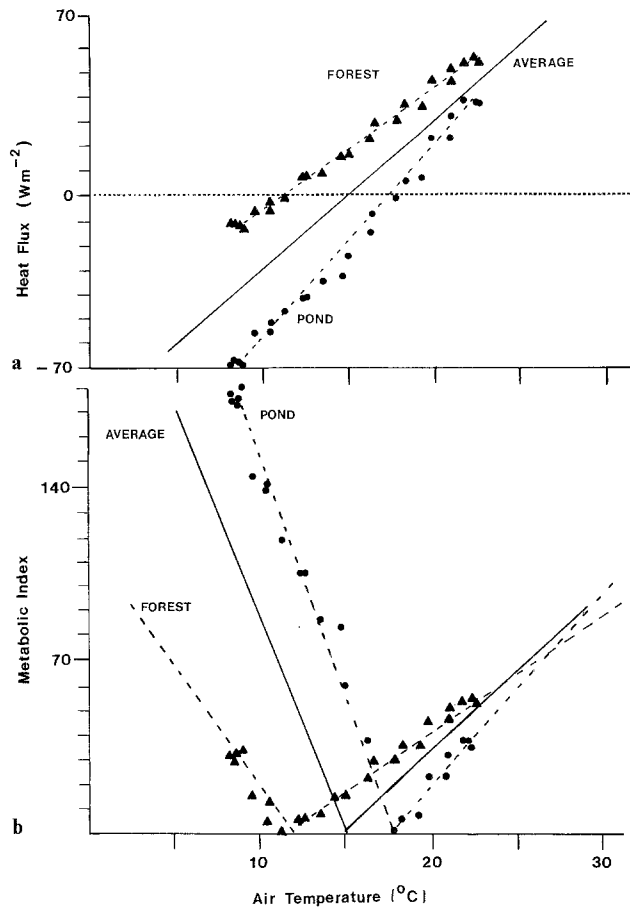

Fig. 3. a Presents a plot of a moose's *HS* value (Wm^{-2}) against the corresponding air temperature (°C) on a given day which was not significantly different from average and for which all necessary thermal parameters were simultaneously measured. The *HS* values correspond to a moose feeding on land and in a pond; the solid line represents an average of these two feeding behaviors. b Presents a plot of a moose's metabolic index, as computed from the *HS* values above, versus the observed air temperature. The solid line presents the average index for feeding on land and in a pond

the most costly feeding period and replacing it with a bedded behavior-habitat choice until the 'steady periodic' [Eq.(3)] and body temperature [Eq.(4)] constraints were satisfied.

5) After the 'steady periodic' and body temperature constraints were satisfied, the digestive organ capacity and food processing constraints were applied.

a) Violations of the digestive organ capacity constraint were eliminated by replacing the *highest* metabolic index aquatic feeding period with the *least* costly bedded option for the hour.

b) Violations of the ruminating constraint were handled by having the moose ruminate rather than crop for the necessary time period, such that the least amount of potential feeding time was spent ruminating and rumination occurred in feeding times with the *highest* metabolic index. One manner of accomplishing this was to have cropping always occurring just prior to a bedded period so rumination could occur while the moose was bedded.

6) The 'steady periodic' and body temperature constraints were re-examined at this point for violations. Any violations at this point were usually small and were corrected by making variations in the bedded behavior options previously chosen.

The solution requires many iterations, for moose a minimum of 30 iterations were required. The least costly feeding option
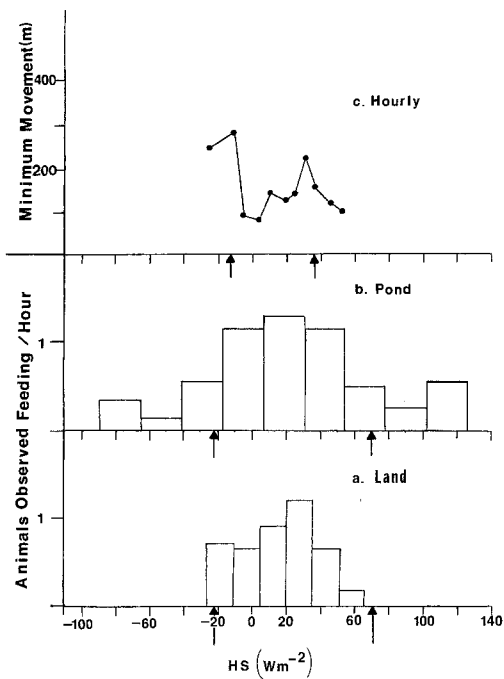
Fig. 4a–c. The observed distribution of moose feeding on land (a), feeding in water (b) and hourly movement in meters (c) plotted against the HS value for that activity at the time of the observation. The HS values were obtained by using the observed air temperature and the air temperature-HS relationship plotted in Fig. 3, where movement HS values come from an average of terrestrial and aquatic feeding values (Fig. 3). The feeding-on-land plot is based upon 48 observations, feeding-in-water plot on 65 observations and the movement data on 69 measurements. At least 5 h were spent watching for moose feeding at each interval of HS values plotted. The arrows in the graphs represent the HS values where the moose's metabolic index equals 70 for terrestrial and aquatic feeding and 35 for the movement plot

was terrestrial feeding between 2100 and 2200; this was the feeding time that was never dropped and from which all constraint calculations were started.

Results and Discussion

Figure 2 presents the hourly HS values for 5 of 8 behavior-habitat combinations during an average summer day. Figure 3 illustrates the close correlation between air temperature and the simultaneously computed HS values for feeding moose (terrestrial: $r^2 = 0.92$, $N=24$; aquatic: $r^2 = 0.86$, $N=24$). Also, presented in Fig. 3 is the relationship between metabolic index and air temperature. These plots were based upon thermal parameters that were collected simultaneously over a 24-h period.

Figures 4a and b present the observed feeding per hour of observation and Fig. 4c the mean distance travelled per hour by moose at different HS values. The HS ranges used in each histogram class encompassed the observed average hourly change. All HS values were computed using the air temperature-HS correlations in Fig. 3 and air temperatures measured during the observational period.

Peaks of hourly feeding on land and water (Fig. 4a and b) occurred at similar HS values, 20 and 22 Wm^{-2}. This is somewhat surprising, since zero HS values (thermoneutrality) are considered better, but HS values in themselves might not be all important because they also have a cumulative effect. The feeding distribu-
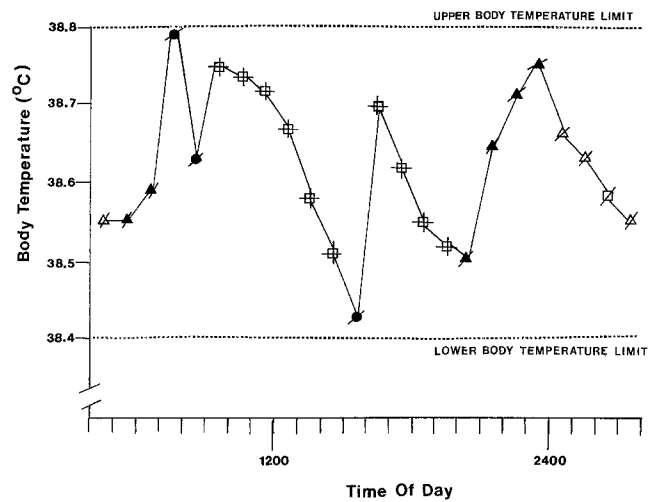

Fig. 5. The solution to the optimization model is presented in this graph. Prior to the imposition of rumen capacity and rumination time constraints, a moose has 9 h in which to feed. The solid symbols represent times suitable for feeding, while open symbols represent bedded times. The deciduous habitat is represented by a $\triangle$, the conifer by a $\square$, and a beaver pond by a $\circ$. X's represent a parallel body orientation to the sun's path (none predicted), +'s a perpendicular orientation and /' s an average between the parallel and perpendicular (the effect of orientation becomes unimportant). The manner in which a moose's body temperature changes as a result of its predicted behavior-habitat choice at each hour is presented and compared with the observed minimum and maximum body temperature limits observed for captive moose given a free-choice of habitat and activity (Knorre, 1959)

tions were skewed towards positive HS values. The skewness might have emerged because positive HS values had lower metabolic indices per Wm^{-2} deviation from zero than did negative values; an index of 70 and less encompassed 100% of terrestrial feeding and 80% of aquatic observations.

An alternative explanation for peak feeding and a skewness towards positive HS values was that moose 'keyed' their feeding to dawn and dusk, so light aided in the visual search for food, even though thermal conditions were slightly less advantageous. However, this was unlikely since moose have notoriously poor vision (Peterson 1955) and from observation, moose seemed to rely upon smell and taste to locate foods; e.g., aquatic feeding was done with the eyes closed. Furthermore, over the summer, HS values at peak feeding occurred any time from 4–5 h before or after sunset or sunrise depending upon the date and weather conditions.

Hourly movement (Fig. 4c), synonymous with feeding periods, increased to a maximum as HS values either increased or decreased from zero and then movement decreased again. As HS approached zero, moose fed intensively, reducing movement; however, as HS departed from zero and metabolism increased, moose shuttled between habitats to increase feeding time by using different habitats and behaviors for thermoregulation. Finally, as HS continued to depart from zero and metabolism increased, moose remained bedded (sought shade or cover) for longer periods to avoid excessive HS values. Furthermore, the asymetry of HS versus behavior, as discussed above, was also apparent in the movement plots (peak movement at -10 and 24 Wm^{-2}) and could be accounted for by metabolic indices of 35.

Figure 5 presents the solution to the optimization model at each hour of an average summer day, prior to the imposition of digestive capacity and rumination constraints. There were 9 h
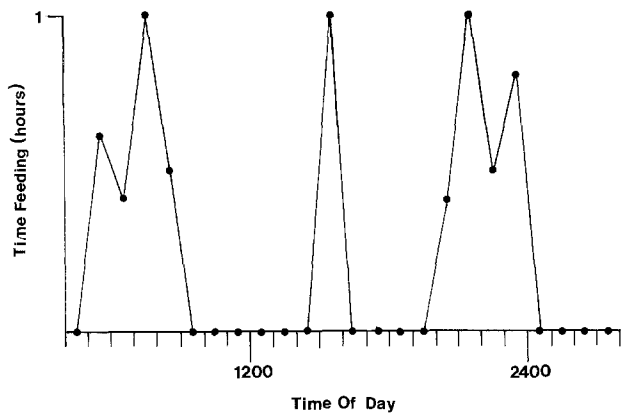
Fig. 6. This plot presents the predicted daily activity cycle for an average moose in summer. The fraction of each hour a moose is predicted to feed is plotted against the time of day
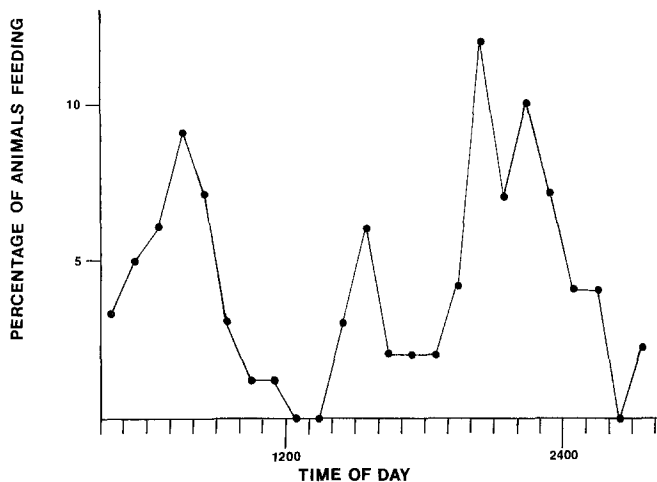

Fig. 7. A plot of the observed moose summer activity at Isle Royale National Park, Michigan. The plot is based upon 194 observations of feeding moose and presents the percentage of all animals observed feeding (194) that were observed at a given hour (Belovsky and Jordan, 1978)

suitable for moose feeding-related activities (cropping and ruminating): 3 h in water and 6 on land. After rumination (Fig. 6), there would be 150 min in ponds and 256 min on land for cropping. The fraction of each hour of an average summer day spent cropping compared very well with the observed cropping peaks and their duration, comparison of Fig. 6 and 7 (0500-0900, 1500-1600 and 2000-2400).

Moose were predicted to have less aquatic cropping time because the night, dawn and dusk provided on average thermal conditions which led to excessive heat losses due to the high conductivity of water; and during the warmer midday period, despite the high conductivity of water, excessive heat gain resulted from too much solar radiation due to the openness of the ponds. Therefore, only very limited periods of the day were acceptable for aquatic cropping and provided metabolic indices less than those for terrestrial feeding at the same hour.

The average adult moose must drop some cropping times because of the digestive organ constraint. Belovsky (1978) demonstrated, using an energy-maximizing feeding model, that an average Isle Royale adult moose should drop 107 min of available

aquatic cropping time, but no terrestrial cropping time. Because of higher metabolic indices, aquatic cropping at 0700-0800 and 1500-1600 should be reduced to satisfy the digestive organ constraint, but the amount of reduction during each hour could not be estimated since both hours have virtually identical metabolic indices for aquatic feeding. Both periods, however, had less aquatic cropping than expected from the model without considering the digestive organ constraint.

A goodness of fit test between the model's predicted cropping times (Fig. 6) and observed times (Fig. 7) demonstrated no statistical difference ($X^2 = 2.74$, $p \leq 0.10$, d.f. = 2: for three time classes 0500-0900, 1500-1600 and 2000-2400, 159 cropping observations). The test was only done for periods in which the model predicted cropping since the presence of a small amount of cropping (18%) in periods not predicted resulted in a X^2 value of ∞.

Table 1 presents observed and the model's predicted habitat utilizations, along with the abundances of each habitat in the study area, based upon a point sampling of the environment. The open habitat was combined with the deciduous forest since open areas were small patches in the forest beyond the resolution of the radio-telemetry-map system used to collect the data. Consequently, moose were found to have chosen habitats in a non-random manner ($X^2 = 17.24$, $p < 0.005$) which was not different from the model's predictions ($X^2 = 0.06$, $p < 0.05$).

Observed and predicted bed habitats (Table 2) and orientations (Table 3) were important aspects of thermoregulation and feeding-time-maximization in the model). The observed bed habitats did

Table 1. A comparison of the observed abundance of various habitats at Isle Royale National Park with the observed and predicted habitat utilization by moose in summer (number of observations)

Habitat	Abundance	Utilization by moose in summer	
		Observed	Predicted
Conifer	15	29	10
Deciduous	61	30	11
Pond	3	9	3

Table 2. Moose habitat selection for bedding sites compared with the predicted bedding site from the model and the abundance of sites in the environment (number of observations)

Bedding site	Abundance	Utilization of bedding sites	
		Observed	Predicted
Conifer	15	11	11
Deciduous	61	1	4
Open	4	0	0

Table 3. A comparison of the observed orientation of moose beds in relation to the sun's path (perpendicular vs. parallel) with the orientation predicted by the model (number of observations)

Orientation	Observed	Predicted
Perpendicular	27	12.5
Parallel	6	2.5

not appear to have been chosen randomly ($X^2 = 57.39$, $p < 0.05$) and were not statistically different from the predicted bed habitats ($X^2 = 1.40$, $p < 0.50$). The model predicted that all daytime beds should be perpendicular to the sun's path to reduce the moose's surface area exposed to direct solar radiation. This was important, even though no beds were predicted in the open, since most forest areas had a sufficiently open canopy to allow body orientation to influence the solar radiation striking a moose. Nocturnal beds, however, should not be influenced by orientation and should, therefore, be randomly oriented between the parallel and perpendicular. Observed and predicted bed orientations were not statistically different ($X^2 = 0.03$, $p < 0.85$).

43 of 72 hourly habitat observations from radio-collared moose agreed with the model's hourly predictions; this amount of random agreement was highly unlikely (binomial probability: 1/3 because of three potential habitat choices, $p < 0.001$). Furthermore, a chi-squared contingency test indicated that the model's hourly predictions were not statistically different from the hourly moose observations ($X^2 = 17.67$, d.f. $= 23$, $p < 0.75$). Of the three days on which moose were tracked hourly, one day was not statistically different from the average (20 of 24 habitat choices agreed), one day was almost different (part of day was cloudy and rainy: 16 of 24 habitat choices agreed with the model's predictions), and the third day was statistically different from the average at each hour (cloudy, rainy and cold: 7 habitat choices agreed with the model's predictions).

Several simpler decision-making models were constructed for comparative results. One model attempted to minimize hourly body temperature changes, a second minimized the hourly metabolic index and a third allowed moose to shuttle between feeding and bedding at each hour to minimize body temperature changes. All three provided a moose with less feeding time than required to crop sufficient food for energy requirements.

There was no way to explain how moose might make a complicated set of decisions which were consistent with the model. One decision-making method was ruled out: moose could not base decisions on whether or not thermal conditions at any one hour satisfied the constraints (i.e., is it 'too hot or cold'), since this could exclude one or more future feeding periods with a lower energetic cost and, at day's end, the maximum amount of feeding time might not be attained.

An alternative, similar to the 'too hot or cold' mechanism, could provide behavior similar to that predicted by the model: if moose anticipated future hourly-thermal conditions based upon present conditions, they could 'decide' whether it might be better to presently feed or wait for some future period. This is plausible because hourly-thermal parameters have a daily pattern (see Appendix), such that given conditions at time X, there is a large probability that at hour $X + N$, where N is less than 24 h, thermal conditions can be approximated. Moose could accomplish this using a set of maximum-minimum thermal conditions as limits for acceptable feeding which varied from day to day with changing thermal conditions and could be either 'learned' or physiologically set.

Conclusion

Modifying the 'steady-state' thermodynamic equations (Porter and Gates 1969) to transient equations for an animal's heat flux, and establishing a likely goal and set of constraints on behavior, a model of optimal thermoregulatory behavior was developed for moose. The goal was maximization of a moose's daily feeding time at the least possible energetic cost. The constraints were a 'steady periodic' fluctuation in body temperature, upper and lower body temperature limits, and rumination and digestive organ capacity limits on feeding. The model's solution was consistent with a moose's observed summer behavior, on average. The model's predictions did not present what a moose *should* do, given free-choice, but what it *should* do given the observed behavior flexibility, as potential but unobserved behaviors were not included in the model.

Standing without feeding was a likely behavioral alternative, but was never observed; because, when heat gain posed a problem, conductive heat losses while bedded exceeded the increased convection while feeding. Furthermore, when heat loss posed a problem, conduction while bedded reduced losses, while standing increased convective losses. Standing increased convective heat loss because more body surface was exposed to wind.

If moose followed the model's decision criteria, fitness would be increased because feeding-time maximization at the least possible energetic cost would increase food supply by reducing minimum-required food quality and increasing potential daily food consumption, and would provide greater net energy per unit of feeding time.

The generality of these results for other animals depends upon the importance of predation, interference competition, variability in the thermal environment and/or food processing constraints. As these conditions change, an animal may find it more and more difficult to maximize feeding time. Nevertheless, the thermoregulatory criteria employed in the model should apply to periods chosen for feeding, after all other limits are satisfied. Therefore, the model should apply in varying degrees to most animals.

Appendix: Data Used in Computing HS

The hourly observed *air, soil, vegetation* and *water temperatures* and *vapor pressure deficits* could be predicted using the equations:

$$V_i = V_{min} + (V_{max} - V_{min}) \cos{}^1/_2 \pi (1 - t_{min}/10),$$

for the period 0400–1400, and:

$$V_i = V_{max} - (V_{max} - V_{min}) \cos{}^1/_2 \pi (1 - t_{max}/14),$$

for the period 1400–0300, where V was the value of concern at time i, V_{max} was the daily maximum value, V_{min} was the daily minimum value and t was the time of day with the maximum (1400) and minimum (0400) values. The hourly solid and vegetation temperatures (T_{v-g}) were measured with a surface temperature probe. 96% of observed variation in hourly values was explained by the equations over a 10 day period. Hourly values for an average summer day were computed using the equations and the maximum-minimum values in Table A.

Long and *shortwave radiation* were not measured at the Isle Royale weather station; consequently, a simple net radiometer was constructed using a flat-black aluminum cylinder (12 cm-dia., 16 cm-length) with a known emissivity (0.97–3 M paint). The cyclinder was positioned parallel to the sun's path and shielded from the wind. Total long and short-

Table A. Thermal parameters used in calculating the conditions on an average summer day at Isle Royale

Air Temperature (T_a):

max.	22.6°C ± 3.1	over 600 days (1970–1974)
min.	8.3°C ± 3.2	over 600 days (1970–1974)

Water Temperature (T_w):

max.	16.0°C ± 1.7	over 10 days
min.	11.0°C ± 2.1	over 10 days

Average soil and vegetation surface temperature (T_{v-g}):
Open:

max.	20.2°C ± 2.3	over 10 days
min.	16.2°C ± 2.7	over 10 days

Deciduous:

max.	19.2°C ± 2.2	over 10 days
min.	17.2°C ± 2.9	over 10 days

Conifer:

max.	17.4°C ± 1.9	over 10 days
min.	15.4°C ± 2.6	over 10 days

Vapor Pressure Deficit (*VPD*):

max.	12.5 mm Hg ± 0.3	over 10 days
min.	15.4 mm Hg ± 0.2	over 10 days

Total Long and Shortwave Radiation (Q: Wm^{-2}):*

$Q_{open} = 6.7 \times 10^{-26} T_a^{11.3}$	($r = 0.88$, $N = 72$, $p \leq 0.001$)
$Q_{deciduous} = 2.7 \times 10^{-10} T_a^{5.0}$	($r = 0.84$, $N = 72$, $p \leq 0.001$)
$Q_{conifer} = 4.1 \times 10^{-6} T_a^{3.3}$	($r = 0.79$, $N = 72$, $p \leq 0.001$)

  * T_a in °K

c:

open – 1.00
deciduous – 1.19
conifer – 1.28

Wind Velocity (V_z):

weather station, 6 m above ground	1.9 ms^{-1} ± 1.0 over 600 days
open, 1.6 m above ground, mean moose height	1.9 ms^{-1}
deciduous and conifer, 1.6 m above ground	0.7 ms^{-1}

wave radiation striking the cylinder, assuming thermodynamic equilibrium, was computed as:

$$Q = \varepsilon\gamma(BB)^4 + h_c(BB - T_a),$$

where Q was net long and shortwave radiation (Wm^{-2}), γ was the Stefan-Boltzman constant, ε was the emissivity (0.97), BB was the cylinder's temperature (°K), h_c was the free convection coefficient (0–2.4 Wm^{-2}: Monteith, 1973), and T_a was the air temperature (°K). BB was the cylinder's surface temperature measured as the air temperature within the cylinder. Q was measured at each hour over 3 days in open, deciduous and conifer habitats, and correlated with air temperature (regressions in Table A).

Knowing longwave radiation, Q was separated into its shortwave component:

$$TS = 1/a(Q - \gamma\varepsilon c(0.5 T_{v-g} + 0.5 T_a)^4),$$

where TS was shortwave radiation (Wm^{-2}), a was the shortwave absorptivity of the painted surface (0.8–3 M paint), and c was a multiple determined experimentally when shortwave radiation was not present to account for the vegetation's 'insulating' effect (values in Table A). TS was allocated between direct and diffuse sources:

$$S = \frac{TS}{(0.24)(0.9) + (0.5)(0.1)}$$

and:

$$s = 0.1 S,$$

where S was direct shortwave radiation (Wm^{-2}), s was diffuse shortwave radiation (Wm^{-2}), 0.24 was the cylinder's solar profile (Monteith 1973), 0.9 was the fraction of TS which was direct (Morhardt and Gates 1974), 0.1 was the fraction of TS which was diffuse (Morhardt and Gates 1974), and 0.5 was the fraction of surface area exposed to diffuse shortwave radiation.

The radiation values for an average summer day were computed using average hourly air temperatures and the T_a versus Q regressions (Table A). This technique estimated shortwave radiation values within 10% of values measured with a pyranograph and gave total radiation values comparable with the average total radiation over 16 summer days in similar habitats (Lull and Reigner 1967).

Radiation absorbed by a moose (Q_{abs}: Wm^{-2}) was calculated as (Porter and Gates 1969):

$$Q_{abs} = azS + 0.5(as + ar(S + s) + \varepsilon\gamma c(0.5 T_a + 0.5 T_{v-g}))^4,$$

where a was the absorptivity of a moose's surface for shortwave radiation and was assumed to be 0.74, the same as a brown cow (Blaxter 1962; Porter and Gates 1969; Riemerschmid and Elder 1945), z was the fraction of a moose's surface area exposed to direct shortwave radiation: 0.27 when parallel to the sun's path and 0.10 when perpendicular (average adult moose's dimensions and Monteith, 1973), and r was the reflectivity of the environment to shortwave radiation, 0.2 (soil, vegetation and average for water: Monteith 1973).

The moose's *surface temperature*, T_r (°K), was measured by inserting thermal probes just under the fur tips at six locations and averaging. This was done by immobilizing moose with succinyl-choline chloride. Although this was not an error-free measure since fur is a porous media, making it partly transparent to infra-red radiation, the measure was no worse than those obtained using a radiometer because this instrument is susceptible to the same problem in addition to the problems of the instrument's angle to the fur surface and its field of view (Cena and Clark 1973; W. Porter pers. comm.). Nevertheless, T_r was approximated and was found to be related to radiation absorbed by a moose (Q_{abs}):

$$T_r = 32.6(Q_{abs})^{0.25} - 120.5,$$

($r = 0.91$, $N = 7$, $p < 0.001$). The regression provided moose T_r values similar to those measured for other mammals with a radiometer under identical thermal conditions (Gates 1972; Finch 1972a, b; Morhardt and Gates 1974).

Moose *metabolic heat production* (M: Wm^2) was approximated as:

$$M = 3.6 \text{ b } W^{0.75}/54.9 \text{ m}^2$$

where W was the moose's body mass (358 kg for an average adult), $3.6 b$ was a constant dependent upon activity (Kleiber 1961), where b was 1.5 for resting and 2.1 for feeding (Moen 1973: based upon deer and sheep), and 5.9 m^2 was the moose surface area based upon Moen's (1973) surface-to-body mass relationship for deer.

A moose's *convection coefficient* (h_c) was computed using Mitchell's (1976) characteristic dimension equation (body mass of 358 kg):

$$h_c = 7.86 V_z^{0.60},$$

where V_z was wind speed at height z above the ground. V_z values appear in Table A for an average summer day, as measured at 6 m above the ground in the open by the Isle Royale weather station and estimated for other heights and habitats using Seller's (1965) height-velocity equations.

A moose's *conductive heat loss* (C: Wm^{-2}) was dependent upon the relationship:

$$C = fk(T_r - T_*)/d,$$

where k was the conduction coefficient (Schmidt-Nielsen, 1975: 2.5 Wm^{-2} (°K/cm)$^{-1}$ for air while bedded and 58.7 Wm^{-2} (°K/cm)$^{-1}$ for water), d was the distance between the moose and the other conducting medium (0.5 cm of air while bedded against the soil-vegetation and 3 cm of water while in a pond, as determined with hide samples), T_* was the

temperature of the conducting medium (°K), and f was the fraction of the moose's surface in contact with the conducting medium (0.2 while bedded and 0.2–0.35 while in a pond, as estimated by observing moose.

A moose's *evaporative heat loss* was primarily a function of respiratory water loss since moose, as cervids, do not normally sweat (Irving 1964). Using binoculars at distances of 3–5 m to measure a moose's respiration rate (breaths/min) and simultaneously recording air temperature as an estimate of thermal conditions, a function relating respiration rate to air temperature was found ($r^2 = 0.89$, $N = 15$, $p < 0.001$). Using this function, as well as an estimate of a moose's tidal volume based upon Schmidt-Nielsen's (1975) body mass-tidal volume regression and the assumption that a moose's body temperature is an average of 38.6° C (Knorre 1959), the respiratory evaporative heat loss (E_{ex}: Wm^{-2}) was estimated to be:

$$E_{ex} = VPD(0.28)e^{0.07} T_a,$$

where *VPD* was the vapor pressure deficit (mm Hg).

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