

## **A cost-benefit analysis of behavioural sequences organization in laboratory mice**

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To test the hypothesis that the actual organization of diurnal and nocturnal behavioural sequences observed in C3H mice tend to maximize a classical functional criterion - the net energy gain - artificial behavioural sequences were defined by reorganization of the acts of actual ones, through application of three Monte-Carlo-type processes (ALT, SEQ and RND). ALT sequences correspond to a random choice of rest/activity bouts, and SEQ sequences to a random reorganization of acts in each activity bout. RND sequences correspond to a random choice of rest/activity bouts together with a random choice of acts in each activity bout. The net energy gain associated with each of these artificial behavioural sequences was derived from a computation of the corresponding energy inputs - by means of a dynamic feeding model - and energy outputs - on the basis of the energy cost of each constituting acts. This net gain was then compared with the net gain corresponding to the actual behavioural sequence of the animal. The results of RND and ALT sequences substantiate the maximization hypothesis, while those of SEQ sequences reveal individual differences. This suggest the existence of two independent behavioural strategies - choice of rest/activity alternations and choice of acts during an activity bout - as they can lead to antagonist effects on the functional criterion.

KEY WORDS: behavioural sequences, cost-benefit, feeding model, mouse, ultradian rhythm.

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## INTRODUCTION

Once it has been established - by means of appropriate descriptive and causal analyses - that the behavioural sequences of a given animal do not result from mere background noise and that its overall organization is similar for other individuals of the same species, one may attempt to ascertain whether it could optimize a variable related with the animal's fitness (SIBLY & MCFARLAND 1976, MCFARLAND 1982, ROITBLAT 1982). Such an endeavour entails defining a criterion for evaluating the fitness of a particular sequence, as well as using a common currency for assessing the respective contributions to this criterion of the various acts which constitute the given sequence (MCFARLAND & SIBLY 1975, MCCLEERY 1978, MCNAMARA & HOUSTON 1986, CLARK 1991). It can then be determined whether or not the observed behavioural organization corresponds to a higher value of that criterion than those derived from other possible organizations. In general, this procedure - because it technically cannot incorporate all other possible organizations - constitutes only a partial verification of the criterion optimization hypothesis. Its aim is accordingly to test the coherency of this hypothesis rather than to establish a formal proof of its validity. It is such a procedure, based upon the behavioural sequences of C3H mice, that has been applied here. Thus, the major objective of this work has been to test whether the actual organizations of behavioural sequences in mice entailed higher values of a functional criterion - the net energy gain - than the random organizations of artificial sequences.

## MATERIAL AND METHOD

### *Experimental procedure*

Eighteen C3H male (Iffa-Credo, Les Oncins, France), 4 and 6 weeks old, were isolated in individual transparent 23 x 8 x 8 cm polystyrene cages containing water and food (AO3R pellets, UAR, Villemoison-sur-Orge, France) ad libitum, together with a cotton ball for nest building. The cages were in an enclosure lighted by fluorescent white tubes (100 lux) for the "day" situation (L) or red tubes (10 lux) for the "night" situation (D). The enclosure's temperature and humidity were maintained at between 19 and 21 °C and 60 and 70%, respectively. Two weeks prior to the observations, 9 individuals (SM1 to SM9) were placed in LD 12:12 from 7 a.m. to 7 p.m., and 9 others (SMA to SMI) in DL 12:12, from 7 a.m. to 7 p.m.. For 4 days, a cage was placed within a transparent 52 x 125 x 90 cm PVC enclosure and the behavioural sequence of the corresponding animal was recorded on videotapes during 11 hr 30 min. Off-line analysis of such records made it possible to carry out the chronological succession of 6 general acts (rest, sniffing, locomotion, feeding, drinking, nest building) and of 4 grooming categories (3 in the nest, 1 out of the nest) with a sampling rate of 1 minute, in the day situation for mice SM1 to SM9 and in the night situation for mice SMA to SMI. Each act's duration was then estimated by dividing 60 sec by the number of acts observed during each minute.

The behavioural sequences of the C3H mouse, which have been described in previous works, display, as shown in Fig.1, an ultradian rhythm of rest/activity alternations combined with a circadian one (GUILLOT 1988). Moreover, each activity bout has a typical behavioural organization, generally made up of a sequence that begins by grooming in the nest, followed by alternations of locomotion, feeding, drinking, grooming out of the nest, and ending with nest building and grooming in the nest (GUILLOT 1988, HAZOUT et al. 1989, MEYER & GUILLOT 1990, GUILLOT 1991).

### *Functional criterion*

The issue is to determine which functional criterion could be maximized by such an organization. The conditions in which the experiment reported here took place did not allow the

computation of a global criterion of fitness directly bound to the mouse's reproductive success. Therefore the present analysis centered upon a related criterion, the net energy gain associated with the behavioural sequence considered. This actually constitutes a classical choice (LENDREM 1986), for this criterion has a strong bearing upon the animal's reproductive and survival potential. Lastly, this choice is coherent in view of the results of a complementary study showing that theoretical sequences of rest and activity alternations, extracted by dynamic programming and optimizing this criterion, exhibit a pattern similar to the actual sequences (GUILLOT 1991, GUILLOT & MEYER 1995).

Thus, as the functional criterion is an energetic variable, any behavioural sequence under further consideration will be translated into a succession of metabolic costs associated with the ongoing acts, in order to manage a common currency that allows comparisons.

### *Artificial behavioural sequences*

To ascertain whether the net energy gain corresponding to the actual behavioural sequence displayed by the individual is higher than the gain attached to any other possible behavioural organization, artificial behavioural sequences that entail different metabolic expenditures over time have been elaborated. However, in order to maintain the corresponding differences within plausible biological limits, such artificial sequences have been generated through Monte-Carlo reorganizations of energy expenditures corresponding to actual behavioral sequences. Then, under three conditions of random choice, 100 artificial sequences were generated from each of the 9 diurnal and the 9 nocturnal actual sequences.

RND sequences were obtained from a random reorganization of rest/activity bouts of each actual sequence, together with a random reorganization of acts within each activity bout. Likewise, ALT sequences were obtained from a random reorganization of rest/activity bouts of each actual sequence, without changing the order of acts in the activity bouts. Finally, SEQ sequences were obtained from a random reorganization of acts within each activity bout of each actual sequence, without changing the order of the rest/activity alternations.

The net energy gain values of the RND, ALT and SEQ artificial sequences have been computed as explained below.

### *Computation of the net energy gains*

The net energy gain of a behavioural sequence is the difference between the total energy inputs and the total energy outputs associated with the sequence.

The estimation of energy outputs associated with each behavioural sequence relied upon a previous work that involved mice of the same age and observed under the same conditions as the individuals in this experiment (MEYER & GUILLOT 1986) and allowed the calculation of the metabolic costs of the different acts considered. These costs, recapitulated in Table 1, were used to calculate the energy expenditures of the behavioural sequences studied here. These values - expressed in J/g/s - multiplied by the duration in seconds of the corresponding act and by the animal's instantaneous computed weight, then summed from act to act, yielded the total energy output associated with each behavioural sequence considered.

The energy input associated with a given behavioural sequence is estimated from the amount of the animal's food intake. However, if such inputs associated with the actual sequences are known, this is not the case when the artificial sequences are concerned. It is thus necessary to estimate what the energy inputs of an animal would be if it has organized its energy expenditures differently, because the onset and the termination of its meals rely upon the pattern of such costs. This estimation has been made possible by the application of a dynamic feeding behaviour model (BOOTH 1978), which has been adapted and validated with respect to the mouse. Essentially, this model links food intake to the instantaneous value of energy flow entering the lean tissues: if this flow falls beneath a given threshold, a food intake is triggered; if it exceeds this threshold, food intake stops. From a sequence of metabolic expenditures, given as an input, the model correctly predicts the initiation and the termination of the mouse's food intakes. It therefore yields the time distribution of the meals and the total quantities of food consumed (GUILLOT & MEYER 1987, GUILLOT 1988). Thus, the estimation of energy inputs associated with each artificial behavioural sequence relied upon the

translation of the sequences into sequences of metabolic expenditures, and upon the simulation of the meals that such costs would have triggered. The corresponding total energy input has been computed by multiplying the amount of the food consumed by its assimilable energy value.

Table 1.

*Energy costs of mouse acts (Grooming 2 = grooming out of the nest, Grooming 3 = grooming in the nest at the end of an activity bout, Grooming 4 = grooming in the nest during rest.)*

Acts	Costs(J/g/s)
Locomotion	0.0280
Drinking	0.0239
Feeding	0.0204
Sniffing	0.0178
Grooming 1	0.0159
Grooming 2	0.0136
Nest building	0.0130
Grooming 3	0.0115
Grooming 4	0.0092
Rest	0.0086

For the sake of comparability, the energy input has been computed in the same way for actual sequences as well, once it has been verified that the computed values were very close to the observed ones.

## RESULTS

Table 2 gives the net gain values corresponding to the actual sequences and the average values corresponding to the 100 sequences, randomized under each of the 3 conditions. For each mouse, the average net gain value of the artificial sequences of a given condition has been compared to the observed value. Table 3 shows the results of the comparison, by means of a standard t-test, for the RND, ALT et SEQ sequences corresponding to all mice, in day and night situations.

Table 2.

Net gain values (*J*) associated with observed sequences (*OBS*) and average values of the corresponding 100 artificial sequences in *RND*, *ALT* and *SEQ* sequences.

Mice	Day	OBS	RND	ALT	SEQ
SM1		4986.0	2535.17	2946.19	4763.61
SM2		5686.35	3387.51	2425.78	6010.13
SM3		1387.63	-208.29	-355.30	1123.75
SM4		1052.11	-432.46	-808.49	827.68
SM5		13264.10	10879.12	11319.82	12766.09
SM6		22.36	-1515.04	-1610.64	177.23
SM7		-2858.32	-4024.50	-4074.37	-2761.47
SM8		-530.06	-2478.19	-2710.85	-237.13
SM9		687.86	464.10	193.57	1652.65
	Night				
SMA		35846.30	32508.49	32635.98	35604.40
SMB		36102.87	34245.40	33896.41	34462.97
SMC		46092.11	46360.84	44451.46	46958.29
SMD		38714.03	38091.29	37187.66	38958.56
SME		26335.88	24495.13	23735.21	26843.71
SMF		15452.66	14929.37	14293.51	16213.59
SMG		34528.01	33348.58	32697.30	35231.09
SMH		32245.52	30445.82	30200.33	32396.25
SMI		28693.15	28270.59	27322.44	29465.28

Table 3.

Comparisons (*t*-test) of the average values of *RND*, *ALT* and *SEQ* sequences and the *OBS* values. If  $t > 0$ , then observed value > average value; if  $t < 0$ , then observed value < average value;

\* = not significant.  $ALT > OBS$ ,  $SEQ > OBS$  = number of artificial sequences (out of 100) the net gain values of which are higher than the actual one.

		RND	ALT	ALT > OBS	SEQ	SEQ > OBS
Day	SM1	14.97	12.80	6	4.06	21
	SM2	13.13	18.30	0	-13.30	92
	SM3	18.57	18.33	0	7.81	22
	SM4	12.45	15.40	2	6.18	31
	SM5	15.31	11.58	12	7.83	19
	SM6	12.91	12.73	11	-5.13	66
	SM7	12.12	13.14	9	-4.55	66
	SM8	15.50	18.12	1	-16.53	96
	SM9	* 1.81	4.33	34	-17.94	98
Night	SMA	12.78	13.73	2	5.98	34
	SMB	7.84	8.03	25	18.11	
	SMC	* -0.78	4.8	41	-14.47	94
	SMD	3.10	7.16	34	-2.45	56
	SME	10.79	14.92	1	-20.53	99
	SMF	4.54	10.57	0	-33.90	100
	SMG	6.47	10.34	11	-9.99	87
	SMH	9.89	11.42	8	-2.57	63
	SMI	3.26	11.05	30	-22.30	96

### *RND* sequences

The observed net gain values are significantly greater than the average net gain of the *RND* artificial sequences in both day and night situations - two exceptions apart, the results of which are not statistically significant (*SM9* and *SMC*) - thus suggesting that the overall organization of mice's behavioural sequences might contribute to increase their net energy gain.

The results obtained with *ALT* and *SEQ* sequences help to specify the respective role of the rest/activity alternations and of the detailed organization of activity bouts in such a maximization.

### *ALT* sequences

The observed net gain values are all significantly greater than the average net gain of the *ALT* artificial sequences, in both day and night situations, thus suggesting that the particular alternation of rest and activity bouts exhibited by each mouse contributes to the maximization of its net energy gain.

Table 4.

*ALT sequences. Comparison (Wilcoxon test) between the net gain values (J) associated with sequences with 1 or 2 activity bouts (Group A) and sequences with 4 or 5 activity bouts (Group B) in each day/night situation.*

	Group	n	Means (J)	Means of ranks
	<i>Day</i>			
A		10	2624.70	5.50
B		10	5865.20	15.50
		Z = -3.7418	p ≤ 0.0002	
	<i>Night</i>			
A		10	22632.02	6.00
B		10	25270.86	15.00
		Z = -3.3639	p ≤ 0.0008	

In order to clarify this effect, the sequences randomly chosen under ALT condition that resulted in the highest and the lowest net gains were singled out. It appeared that the sequences yielding low values of the criterion display a smaller total number of activity bouts - due to the merging of several activity bouts - than the sequences with high values. This point is illustrated in Fig.2 for the case of one particular mouse in each day/night situation. It is also checked statistically on 10 sequences exhibiting 1 or 2 activity bouts (Group A) and 10 sequences exhibiting 4 or 5 activity bouts (Group B) randomly selected among the 100 artificial ALT sequences relative to one particular mouse in each day/night situation (Table 4). It is therefore possible that one of the solutions available to the mouse for increasing its net energy gain is to perform - over a given lapse of time - a large number of brief activity bouts rather than a small number of longer ones.

Fig.3, which shows the simulation details of the onset and the duration of meals corresponding to a low energy gain sequence (Fig.3 A) and a high energy gain sequence (Fig.3 B), explains the results obtained. Indeed it appears that, in line with the logic of the feeding model which has been used, the animal is prompted to feed whenever its behavior entails high energy expenditures (METAB). The size of the corresponding meal is thus linked with the delay separating the energy flow (FLO) entering the lean tissues from the threshold determining the beginning and end of feeding. For a given energy expenditure, if FLO is already near the threshold value, it will decrease beneath this value and will remain there longer than if it were further separated from this value when the energy expenditure occurs. Now, what allows FLO to decrease are the rest bouts of the animal. Consequently, the same energy expenditure brings about larger meals if it takes place after a rest bout than during a long activity bout. The net energy gain is therefore higher when the animal's activity is dispersed than when it is lumped.

### *SEQ sequences*

The statistical tests for the SEQ artificial sequences are all significant, but are characterized by individual variations, as the actual organization of acts within the activity bouts leads 6 mice to get a higher value of the criterion and leads 12 animals to get a lower net energy gain value than those of the reorganized SEQ sequences - this last result being in contradiction with the hypothesis of the criterion maximization.

In order to ascertain what organization of observed acts corresponds to a lower or a higher value of the criterion, the random SEQ sequences giving rise to the lowest and the highest net benefits were sought out. In this case, differences appear in the distribution of acts generally situated at the beginning and at the end of an activity bout, i.e., acts involving low energy costs, like grooming or nest building. In the random sequences, such acts may be located at any moment within the activity bout, thus creating larger numbers of alternations of low and high energy expenditures. Each activity bout then begins and ends with high energy cost acts, inducing great differences of energy expenditures during the shift between rest and activity. These points are illustrated in Fig.4 for the case of one particular mouse in each day/night situation. It is also checked statistically on 20 sequences randomly selected among the 100 artificial SEQ sequences corresponding to one particular mouse in each day/night situation. These sequences are separated into 10 sequences - where acts with

low energy costs are at the beginning and/or the end of each activity bout ( Group A) - and 10 sequences - where acts with low energy costs are distributed within each activity bout (Group B) (Table 5). Sequences of group B exhibit significantly higher net gains than sequences of group A.

Table 5.

*SEQ sequences. Comparison (Wilcoxon test) between the net gain values (J) associated with sequences where low energetic cost acts are lumped at the beginning and/or the end of each activity bout (Group A) and to sequences where low energetic cost acts are dispersed within each activity bout (Group B).*

	Group	n	Means (J)	Means of ranks
	<i>Day</i>			
A		10	5443.32	6.20
B		10	5864.87	14.80
			Z = -3.2127	p ≤ 0.0013
	<i>Night</i>			
A		10	25640.70	5.50
B		10	26603.98	15.50
			Z = -3.7418	p ≤ 0.0002

The simulations by the feeding model can explain that, for both ALT and SEQ conditions, a sequence where low energy cost acts (rest for ALT sequences; grooming in the nest, nest building for SEQ sequences) are distributed within costly acts (activity bout for ALT sequences; locomotion, feeding, drinking for SEQ sequences) leads to a higher net energy gain than a sequence where low energy cost acts are lumped before and/or after costly acts.

## DISCUSSION

The results obtained by random modifications of actual behavioural sequences under ALT conditions do not contradict the hypothesis whereby C3H mice attempt to maximize their net energy gain over the day and over the night, thus suggesting that mice actually optimize this criterion over a nycthemeral period. These results also confirm those obtained elsewhere, showing that theoretical sequences of rest and activity alternations extracted by dynamic programming, and optimizing this criterion, exhibit a pattern similar to the actual sequences (GUILLOT 1991, GUILLOT & MEYER 1995). Thus, for these mice, ultradian alternations of rest and activity may be an efficient behavioural strategy to maximize their net energy gain.

It should however be emphasized that the results described herein were obtained by use of one particular feeding model and then relied on mechanisms triggering starts and stops of food intake specific to this model. Nevertheless, the fact that the model and its mechanisms have been validated both on the rat (BOOTH 1978, CLIFTON et al. 1984) and on the mouse (GUILLOT & MEYER 1987, GUILLOT 1988), makes a convincing case for the conclusion suggested here. They also are in line with the results of various authors demonstrating that feeding behaviours in the rat rely upon similar energy optimization mechanisms (KAGEL et al. 1980, COLLIER & ROVEE-COLLIER 1981, JENSEN et al. 1983, JOHNSON & COLLIER 1989, COLLIER & JOHNSON 1990, KOTLER & MITCHELL 1995, MORATO et al. 1995) acting over a nycthemeral period (BAUMAN 1992, JOHNSON & COLLIER 1994). Such conclusions are also comforted by the fact that the results obtained by descriptive and causal analyses of observed sequences in mice - in which the feeding model used here was not involved - can be explained in the evolutionary perspective of this work. In particular, the ultradian rest/activity rhythm, brought to light by spectral analysis (GUILLOT 1988), seems to be performed by various mouse strains, both wild and domesticated (BAUMGARDNER et al. 1980). It also has been shown that it could be coded in the mouse genome (BEAU 1988), being thus amenable to an evolutive process.

SEQ sequences show, in contrast with an absolute optimization which could be attained by selecting both an optimal rest/activity alternation and an optimal sequence of acts, that some of the individuals temper and some others reinforce the first choice by the second. Thus, in performing a

given sequence of acts within the activity bouts, C3H mice display another behavioural strategy of energy control. This strategy seems to have a lower effect on the net gain than the first one, considering the small average deviations of SEQ sequences, and the similarity between RND and ALT results. Yet it could explain the non-significant results corresponding to SM9 and SMC mice in RND sequences, as the deviations of their ALT and SEQ sequences are antagonist.

Most of the animals (5 out of 9 in day condition, 7 out of 9 in night condition) seem to adopt an organization of their activity bouts that decrease - rather than increase - the value of the net energy gain. As demonstrated in Table 5, this effect is obtained by lumping low energy cost acts at the beginning and at the end of an activity bout. Such behavioural rules - or melodies - have been evidenced in the sequences of these C3H mice (GUILLOT 1988, HAZOUT et al. 1989, MEYER & GUILLOT 1990) but also in the behavioural sequences of other Muridae (KAVANAU 1963, MCNAB & MORRISON 1963, BAUMGARDNER et al. 1980). It could thus have a functional role for many rodents. However, as this behavioural strategy leads to a sub-optimization of the criterion, it could be related to constraints of non-energetic nature. First, independently of their energy cost, the nature of each act - not considered in this work, because it focused upon mere energy - compels evident choices of behavioural succession, e.g. when the animal has to perform locomotion in order to drink after eating. Second, because mice were isolated during the observations, their behavioural successions were not constrained by possible social effects, a factor that is not evaluable in terms of energy (SMITH et al. 1994). Finally, ecological constraints (MCNAMARA & HOUSTON 1992) could explain why the two behavioural strategies can be antagonist. Indeed, while being required to leave its nest several times in order to maximize the net energy gain over a nycthemeral period, the animal could have to limit the number of nest entries and nest exits during each activity bout, in order to minimize a risk of predation. Consequently, the acts performed in the nest - acts of low energy costs - are also limited during each activity bout. This constraint bounds alternations of high and low energy cost acts, which is the condition of an increase of the net energy gain.

Results of the SEQ sequences are also characterized by individual differences. They can be linked to the fact that animals have different initial states before being observed - rearing conditions before the arrival in the laboratory, behavioral sequences performed before the observation, effects of learning - states that may lead to different reactivities towards the various non-energetic constraints evocated above.

## CONCLUSION

This work strengthens the hypothesis, already suggested in a previous paper (GUILLOT & MEYER 1995), that C3H mice maximize their net energy gain in achieving an ultradian alternation of rest and activity bouts over a nycthemeral period. It also suggests the existence of another behavioural strategy, concerning the organization of acts within the activity bouts. This strategy seems to be independent of the first one, in that it could lead to conflicting results. Further experiments might be designed to complete the validation of the net energy gain optimization hypothesis, to determine the nature of other constraints and to precise the function of the second behavioral strategy. In particular, such experiments might involve a modification of the energy costs entailed by specific acts exhibited by the mouse (KANAREK & COLLIER 1979, JOHNSON & COLLIER 1994). Another direction of future research is to ascertain what nervous architectures might account for decision-making concerning the succession of energy costs, by calling solely on the sensory information known to be accessible to the animal. These architectures might be discovered by means of an evolving process, like genetic programming (KOZA 1992), which simulates mechanisms of natural selection. In line with the so-called *animat approach* (MEYER & GUILLOT 1994, MEYER 1995, MAES et al. 1996), or the *dynamic system approach* (AGRE 1995, BEER 1995) these architectures would interact with realistic environments and would make it possible to study how the corresponding interactions could generate the two different behavioural strategies that have been evidenced herein.

## REFERENCES

- AGRE P.E. 1995. Computational research on interaction and agency. *Artificial Intelligence* 72: 1-52.
- BAUMGARDNER D.J., WARD S.E. & DEWSBURY D.A. 1980. Diurnal patterning of eight activities in 14 species of muroid rodents. *Animal Learning and Behavior* 812: 322-330.
- BAUMAN R.A. 1992. The effects of wheel running, a light/dark cycle, and the instrumental cost of food on the intake of food in a closed economy. *Physiology & Behavior* 52: 1077-1083.
- BEAU J. 1988. Mise en évidence de corrélats polygéniques des caractéristiques du rythme de l'activité chez un mammifère: étude de deux lignées de souris consanguines C57BL/6By et BALB/cBY. *Compte-Rendus de l'Académie des Sciences, Paris* (III) 307: 37-40.
- BEER R.D. 1995. Computational and dynamical languages for autonomous agents, pp. 121-147. In: Port R.F. & van Gelder T., Edits. *Mind as motion. Cambridge: The MIT Press.*
- BOOTH D.A. 1978. Prediction of feeding behavior from energy flows in the rat, pp. 227-278. In: Booth D.A., Edit. *Hunger models: computable theory of feeding control. London: Academic Press.*
- CLARK C.W. 1991. Modeling behavioral adaptations. *Behavioral and Brain Sciences* 14: 85-117.
- CLIFTON P.J., POPPLEWELL D.A. & BURTON M.J. 1984. Feeding rate and meal patterns in the laboratory rat. *Physiology & Behavior* 32: 369-374.
- COLLIER G.H. & ROVEE-COLLIER C.K. 1981. A comparative analysis of optimal foraging behavior: laboratory simulations, pp. 39-76. In: Kamil A.C. & Sargent T.D., Edits. *Foraging behaviour: ecological, ethological and physiological approaches. New York: Garland Press.*
- COLLIER G.H. & JOHNSON D.F. 1990. The time window of feeding. *Physiology & Behavior* 48: 771.
- GUILLOT A. 1988. Contribution à l'étude des séquences comportementales de la souris: approches causale, descriptive et fonctionnelle. *Diplôme de Doctorat de l'Université Paris 7, Spécialité Biomathématiques.*
- GUILLOT A. 1991. Le comportement de la souris Mus computatrix. *Habilitation à Diriger des Recherches en Psychophysologie, Université Paris X.*
- GUILLOT A. & MEYER J.A. 1987. A test of the Booth energy flow model (Mark 3) on feeding patterns of mice. *Appetite* 8: 67-78.
- GUILLOT A. & MEYER J.A. 1995. A functional analysis of ultradian activity in laboratory mice. *Ethology Ecology & Evolution* 7: 205-219.
- HAZOUT S., GUILLOT A. & MEYER J.A. 1989. Extraction of melodies in behavioral sequences. *Behavioural Processes* 20: 61-7.
- JENSEN G.B., COLLIER G.H. & MEDVIN M.B. 1983. A cost benefit analysis of nocturnal feeding in the rat. *Physiology & Behavior* 31: 555-559.
- JOHNSON D.F. & COLLIER G.H. 1989. Patch choice and meal size of foraging rats as a function of the profitability of the food. *Animal Behaviour* 38: 285-297.
- JOHNSON D.F. & COLLIER G.H. 1994. Meal patterns of rats encountering variable food procurement cost. *Animal Behaviour* 47: 1279-1287.
- KAGEL J.H., BATTALIO R.C., GREEN L. & RACHLIN H. 1980. Consumer demand theory applied to choice behavior of rats, pp. 101-141. In: Staddon J.E., Edit. *Limits to action. The allocation of individual behaviour. London: Academic Press.*
- KANAREK R.B. & COLLIER G.H. 1979. Patterns of eating as a function of the cost of the meal. *Physiology & Behavior* 23: 141-145.
- KAVANAU J.L. 1963. Continuous automatic monitoring of the activities of small captive animals. *Ecology* 44: 95-110.
- KOTLER B.P. & MITCHELL W.A. 1995. The effect of costly information in diet choice. *Evolutionary Ecology* 9: 18-29.
- KOZA J.R. 1992. Genetic programming: on the programming of computers by means of natural selection. *Cambridge: The MIT Press.*
- LENDREM D. 1986. Modelling in behavioural ecology: an introductory text. *Portland: Timber Press.*
- MCCLEERY R.H. 1978. Optimal behaviour sequences and decision making, pp. 377-410. In: Krebs J.R. & Davies N.B., Edits. *Behavioural ecology: an evolutionary approach. Oxford: Blackwell Scientific Publications.*
- MCFARLAND D.J. 1982. Functional ontogeny. *London: Pitman.*

- McFARLAND D.J. & SIBLY R.M. 1975. The behavioural final common path. *Philosophical Transactions of the Royal Society of London* 270: 265-293.
- MCNAB B.K. & MORRISON P. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecological Monographs* 33: 63-82.
- MCNAMARA J.M. & HOUSTON A.I. 1986. The common currency for behavioural decisions. *American Naturalist* 127: 358-378.
- MCNAMARA J.M. & HOUSTON A.I. 1992. Risk-sensitive foraging: a review of the theory. *Bulletin of Mathematical Biology* 54: 355-378.
- MAES P., MATARIC, M., MEYER, J.A., POLLACK, J. & WILSON, S.W., Edits. 1996. From animals to animats 4. Proceedings of the Fourth International Conference on Simulation of Adaptive Behavior. *Cambridge: The MIT Press*.
- MEYER J.A. 1995. The animat approach to cognitive science, pp. 27-44. In: Roitblat H.L. & Meyer J.A., Edits. Comparative approach to cognitive science. *Cambridge: The MIT Press*.
- MEYER J.A. & GUILLOT A. 1986. The energetic cost of various behaviors in the laboratory mouse. *Comparative Biochemistry and Physiology* 83 (3): 533-538.
- MEYER J.A. & GUILLOT A. 1990. Rule induction from examples for expert systems in mouse behavior. *Behavioural Processes* 22: 197-212.
- MEYER J.A. & GUILLOT A. 1994. From SAB90 to SAB94: four years of animat research, pp. 2-11. In: Cliff D. et al., Edits. From animals to animats 3. Proceedings of the Third International Conference on Simulation of Adaptive Behavior. *Cambridge: The MIT Press*.
- MORATO S., JOHNSON D.F. & COLLIER G.H. 1995. Feeding patterns of rats when food-access cost is alternately low and high. *Physiology & Behavior* 57: 21-26.
- ROITBLAT H.L. 1982. Decision making, evolution and cognition, pp. 108-116. In: Schmidt H.D. & Tembrock G., Edits. Evolution and determination of animal and human behaviour. *Berlin: VEB Deutscher Verlag der Wissenschaften*.
- SIBLY R.M. & MCFARLAND D.J. 1976. On the fitness of behaviour sequences. *American Naturalist* 110: 610-617.
- SMITH J., HURST J.L. & BARNARD C.J. 1994. Comparing behaviour in wild and laboratory strains of the house mouse: levels of comparison and functional inference. *Behavioural Processes* 32: 79-86.

## FIGURE CAPTIONS

Fig. 1.- Graphic representation of the actual behavioural sequences of two mice, observed during 11hr 30 min (A, day; B, night). Ten acts are plotted and ranked from 1 to 10 on the Y-axis according to the amount of their energy costs (MEYER & GUILLOT 1986) (Rest = 1, Grooming 4 = 2, Grooming 3 = 3, Nest building = 4, Grooming 2 = 5, Grooming 1 = 6, Sniffing = 7, Feeding = 8, Drinking = 9, Locomotion = 10).

Fig. 2.- ALT sequences. Artificial behavioural sequences corresponding to mice of Fig. 1, associated with the lowest (A, day; C, night) and the highest net energy gains (B, day; D, night).

Fig. 3.- ALT diurnal sequences. Dynamic relationships between energy expenditures (METAB), the net flow entering the lean tissues (FLO) and simulated meals (SIM) when energy expenditures are lumped (A, low net gain) or dispersed (B, high net gain). The FLO threshold that trigger and stop a meal is set to -0.21 J/sec.

Fig. 4.- SEQ sequences. Artificial behavioural sequences corresponding to mice of Fig. 1, associated with the lowest (A, day; C, night) and the highest net energy gains (B, day; D, night).