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| Author(s) | KUKIHARA,Reiji; MATSUKAWA,Masaki; Martin, G. Lockley |
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# The paleoecosystem reconstruction using energy flow of the late dinosaur age based on tracks from the Late Cretaceous Laramie Formation, Colorado Plateau, North America

Reiji KUKIHARA*, Masaki MATSUKAWA** and Martin G. LOCKLEY***

*Department of Environmental Sciences*

## Abstract

This paper presents an attempt to reconstruct the paleoecosystem of the late Cretaceous Laramie Formation as a forerunner to know variation of earth past ecosystems and environments. Ecosystems are controlled by energy flow so they can be reconstructed by using energy flow. The sun energy is converted to carbohydrates by plants and they move to from primary consumers to higher level consumers and at last they are emitted in the air as heat. There are three kinds of transform efficiencies, consumption, assimilation and production efficiencies that can be decided by types of animals when energy moves to next trophic level. Moved energy is distributed to each animal species of the trophic level accordingly ratios of numbers and energy intake of each species. Number of animals can be estimated by dividing distributed energy by each energy intake. Energy intake of animals including dinosaurs can be calculated from weights, metabolic types and activity levels. Ratios of numbers of dinosaurs depend on track fossil numbers. Fossil tracks are superior to body fossils for this ecosystem reconstruction model because fossil tracks have large occurrence, uniform preservation, and in-situ ability. The reconstruction results of the Laramie paleoecosystems showed that the Laramie paleoecosystem is characterized by the dominance of large herbivorous dinosaurs and high secondary productivity by them. And predator / prey biomass ratios indicated that it is impossible to decide dinosaur's metabolic types by them. This work provides a basic way of comparing different paleoecosystems and it could be the keystone to know transitions of paleoenvironments and paleoecosystems.

Key words: fossil ichno-assemblages, Paleoecosytem, Laramie Formation, late Cretaceous, dinosaur track

*Department of Environmental Sciences, Tokyo Gakugei University, 4-1-1 Nukuikita-machi, Koganei-shi, Tokyo 184-8501, Japan*

## 1. Introduction

For some time since environmental words such as ecology and ecosystem have been widely known. They have generated much interest in environments in terms of ecologic dynamics. But it is difficult to understand environments and ecologies. Their changes may be small components of big variations in the earth environment or exceptional abnormal variations caused

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  * Keio Gijyuku Yochisha (Shibuya, Tokyo 150-0013, Japan)
 ** Department of Environmental Sciences, Tokyo Gakugei University (4-1-1 Nukui-kita-machi, Koganei-shi, Tokyo 184-8501, Japan)
*** Dinosaur Track Museum, CB 172, University of Colorado at Denver, PO Box 173364, Denver, Colorado 80217-3364, USA

by human activities. Generally environmental variations accompany too much time for human comprehension. It is necessary to know how past environments changed in order to grasp current environmental variations. If we can understand the previous tide of environmental variations, we may be able to know not only current variations but also future ones.

As ecosystems are significantly influenced by environmental phenomena, we can know environmental variations from them. The term *ecosystem* is used to denote the biological community together with the abiotic environment in which it is set, and they are strongly linked to each other by fluxes of energy and of matter (Begon et al., 1996). So it is important to understand energy flow in order to understanding ecosystems.

There have been some attempts to reconstruct paleoecosystems. For example, Jacobs and Murry (1980) dealt with vertebrate community of the Late Triassic Chinle Group of the southwestern United States and Anderson et al. (1997) examined Late Triassic paleoecosystems of southern Africa. But both of them only showed fauna and flora based on fossils. Bakker (1972) tried to reconstruct Late Cretaceous dinosaur communities by using energy flow to prove endothermic dinosaurs. Farlow (1976) estimated dinosaur metabolism from present endothermic and ectothermic animals and tried to reconstruct large dinosaur community aiming at trophic dynamics of the Late Cretaceous Oldman Formation. Foster (2003) also conducted a paleoecological study of the Morrison Formation. Paul (1988) estimated predatory dinosaur populations by energy flow and used it to infer evidence of endothermic dinosaurs. There were, however, some problems such as biases of fossil preservations, many assumptions in reconstruction processes, lack of detailed examination of food webs and plant environments in their methods. Thus, those studies are not sufficient in reliability though their methods suggest ways of approaching the trophic dynamics of ancient vertebrate communities.

Matsukawa et al. (2001, 2006) made a new reconstruction model of paleoecosystem by using food –web and energy-flow which cleared problems indicated above and evaluated it, and applied its model to the Early Cretaceous terrestrial ecosystem in East Asia. Kukihara et al. (2004) revised formulas of energy intake which can logically adjust to each type of animals according to their metabolic rates and activity levels. Then, they applied the formulas to current Serengeti ecosystem. Their result showed that the reconstructed animal census correspond with real census in permissible range. There are several researches which applied this reconstruction model to various paleoecosystems (Matsukawa et al., 2008; Shibata et al. 2007). In this paper, the paleoecosystem reconstruction model by Matsukawa et al. (2006) was used for the Cretaceous Laramie Formation in the Colorado Plateau region which is rich in plant fossils and dinosaur tracks and result was discussed.

## 2. Reconstruction model of paleoecolosystem

### 2. 1. Outline of reconstruction model

Trophic dynamics of ecosystems consist of the flow of matter such as carbon and nitrogen and energy flow. Although matter keeps cycling semipermanently in the ecosystem, energy is finally emitted in the air as heat and never reform to trophic dynamics. So energy flow can be considered as a key factor of ecosystems, including the food web structure, because of its one-way property. The food web structure can be modeled generally by energy flow (Heal and Maclean, 1975). They estimated secondary productivity by making an ecosystem reconstruction model that is controlled by energy flow and they attempted validation by comparing estimated data with confirmed data of 10 tundra, grassland, and forest ecosystems. There is good agreement in their results. Because their model is given specified values for components that control energy flow to various environments and animals, it can reduce many assumptions for ecosystem reconstructing processes. Thus in this paper, we use an ecosystem reconstruction model that can estimate animal numbers at each trophic level based on the Heal and Maclean model. Although their model includes the Herbivore system and the Saprovore system, this model takes only the Herbivore system because it is very difficult to estimate the ancient Saprovore system from fossil records.

Since only plants can convert the energy from the Sun into carbohydrates that can be used by other living things, ecosystems are controlled by Net Primary Productivity (NPP) of plants. So it is indispensable to know NPP of each ecosystem to reconstruct them. This is determined by the types of vegetations. Three transform efficiencies, consumption efficiency, assimilation efficiency, and production efficiency are used in the NPP using process by primary consumer and in further high trophic level (Begon et al., 1996). These efficiencies vary by types of environments, food habits and metabolism type of animals, and so on. Energy quantities that go to the next trophic levels can be calculated by multiplying NPP or distributed energy by these efficiencies. This energy is distributed to each animal species

of one trophic level according to ratios of numbers and energy intake of each species. For example, assuming that there are two kinds of animals, A and B, in one trophic level which has energy of quantity E and their numbers are a and b and individual energy intake are X and Y respectively, then energy which is distributed to A (Ea) can be calculated by the formula:

$$Ea=(a \times X/(a \times X + b \times Y)) \times E$$

Numbers and ratio of yielded fossils are used instead of living animals and numbers ratios in paleoecosystem reconstructions. We use fossil tracks in this paper. Fossil tracks are superior to bone fossils because there are less influences of animal type such as body size and taphonomy as long as they are in the same site than bones. These features can solve one of problems of previous studies. Each species numbers can be estimated by dividing distributed energy by each individual energy intake.

## 2. 2. Energy intake and metabolic rates of animals

Energy intake is required energy amount for animal living and is one of the most important factors for this paleoecosystem reconstruction model using energy as the limiting factor. Farlow (1976) made formulas for energy intake of endothermic herbivores, endothermic carnivores, ectothermic herbivores and ectothermic herbivores based on dada that are taken from the literature on caged and free-living animals. Those formulas are credible because they are derived from actual data. Those actual data, however, is based on current animals thus Farlow's formulas can not be always applied to extinct animals in case they had different metabolic rates from current animals. Therefore Kukihara et al. (2004) made new formulas of energy intake which can logically adjust to each type of animals according to their metabolic rates and activity levels.

It is necessary to know metabolic types and rates to estimates numbers of animals. Standard Metabolic Rate (SMR) is metabolic rate of inactive animals and defined by the minimum level of oxygen consumption required to sustain life at a standard temperature and pressure. SMR of mammals can be calculated from animal weights by the Fowler (1978)'s formula:

$$SMR (kcal / day) = 70 \times W^{0.75}$$

W is body weight in kg. This formula is effective for all mammals from small mice to big elephants (Fowler, 1978). The SMR formula of birds except for Passeriformes is:

$$SMR (kcal / day) = 78.3 \times W^{0.723}$$

And one of Passeriformes is:

$$SMR (kcal / day) = 129.0 \times W^{0.724}$$

SMR of reptiles is 10 – 20 % that of mammals that are the same size and body temperature (Fowler, 1978). More energy besides SMR is necessary due to heat keeping, various activities, growth, nursing, etc. This additional energy plus SMR is called Activity Metabolic Rate (AMR). AMR can be as twice or three times SMR. In this study, it is set that SMR of ectotherms is 15 % of endothermic animals and AMR is double of SMR for all types of current animals. AMR of dinosaurs is discussed in the later section. Animals must ingest more energy than actual requirement since animals can not assimilate all consumed energy. Values of the assimilation efficiency of animals are 0.5 for herbivores and 0.8 for carnivores respectively. Thus formulas of energy intake can be made by multiplying AMR by reciprocal of assimilation efficiency. For example, the energy intake formula of herbivore endotherms is:

$$Ed (kcal / day) = 2 \times (70 \times W^{0.75}) \times (1 / 0.5) \quad (Ed: energy intake for a day)$$

2 of this formula means AMR =$2 \times$ SMR. Thus this number can be used as activity level variables.

These formulas were compared to Farlow's formulas to evaluate if they are reliable (Kukihara et al., 2004). Farlow's formulas were made by plotting data of actual animal weight and energy intake on a logarithm graph and drawing approximated line (Farlow, 1976). Thus Kukihara et al. (2004) plotted new formulas on logarithm graphs with Farlow's formula and found they almost accord in respective animal type (Kukihara et al., 2004). This means that new formulas are reliable.

## 2. 3. Verification of the model from the Serengeti ecosystem

Kukihara et al. (2004) applied this reconstruction model to the current Serengeti ecosystem and compared to a couple of actual census data (Houston, 1979; Snerson, 1986). Both comparison results showed that assumed values exceed actual data about three times in the primary consumer and about eight times in the secondary consumer. There are two reasons for the error of the primary consumer. One is the difference of NPP and the other is influence from other limiting factors such as water, human activities and tastes of habitat. For example, there are many farmlands facing to the Park border of northwestern and southwestern parts and local people hunt around there which means animals should be driven away. In tall grasslands, as ruminants are handicapped in digestion of stringy tall grass in comparison with non-ruminants because ruminants need much time for ruminating stringy

grass (Koizumi et al., 2000), they can not approach new areas before stringy tall grass are consumed by non-ruminants such as zebra. So their numbers should be restricted.

There is still an overestimated error of about 2.7 times for secondary consumers even if the error for primary consumers was corrected. Maybe there are two types of reasons for this. One is same reasons as herbivores and the other is characteristic or strong for carnivores. As an example of former, one of main carnivorous mammals in the Serengeti, hyenas (*Hyaena hyaena*) have to have a large territory for each group, known as a *clan* (Kruuk, 1972). So they need a larger area than the model predicts. As an example of the latter, generally, comparing vertebrate carnivores with vertebrate herbivores, populations of carnivores are very much smaller than those of herbivores. Thus, once vertebrate carnivores reduce their population, it is harder for them to recover than herbivores. These causes may keep populations of vertebrate carnivores lower than estimated.

Although these factors are difficult to modify by specific estimates and can be considered difficult to verify from the fossil record, it errors can be kept to within an order of magnitude of the confirmed data, one can say that the reliability of this reconstruction model is enough to reconstruct paleoecosystem at least provisionally. But it is necessary to remember that there are such errors when we discuss results of this reconstruction model.

## 3. Paleoecosystem reconstruction in the Laramie Formation

### 3. 1. Geological setting

The Upper Maastrichtian (Upper Cretaceous) Laramie Formation is a nonmarine deposit distributed in the Denver Basin of northern Colorado (Fig. 1). The Formation consists of alternating beds of sandstone, kaolinitic claystone and siltstone and in the study area is vertical to slightly overturned because of the west dipping Golden reverse fault (Lockley and Hunt, 1995a). The sedimentary environment is considered to be a mosaic of coastal plain, fluvial and floodplain environments developed during the regression of the Western interior seaway in middle to late Maastrichtian time (Kauffman, 1977). Weimer (1976) reconstructed the paleogeography of the Laramie Formation as a mosaic of delta plain environments with fine-grained flood plain, swamps and levee deposits splayed by channels trending East-West (Weimer, 1976). The Formation is known for abundant plant fossils (Knowlton 1922) and various dinosaur tracks (Lockley and Hunt, 1995a,b). Dinosaur tracks are known from several localities in the Golden-Leyden-Mashall area west and northwest of Denver (Fig. 1) and the sites are called the Parfet Clay Pit (PCP), Colorado School of Mines Clay Pits (CSM), Leyden Gulch and Marshall Area. Most of tracks are known from PCP and CSM (Fig. 2, Table 1).
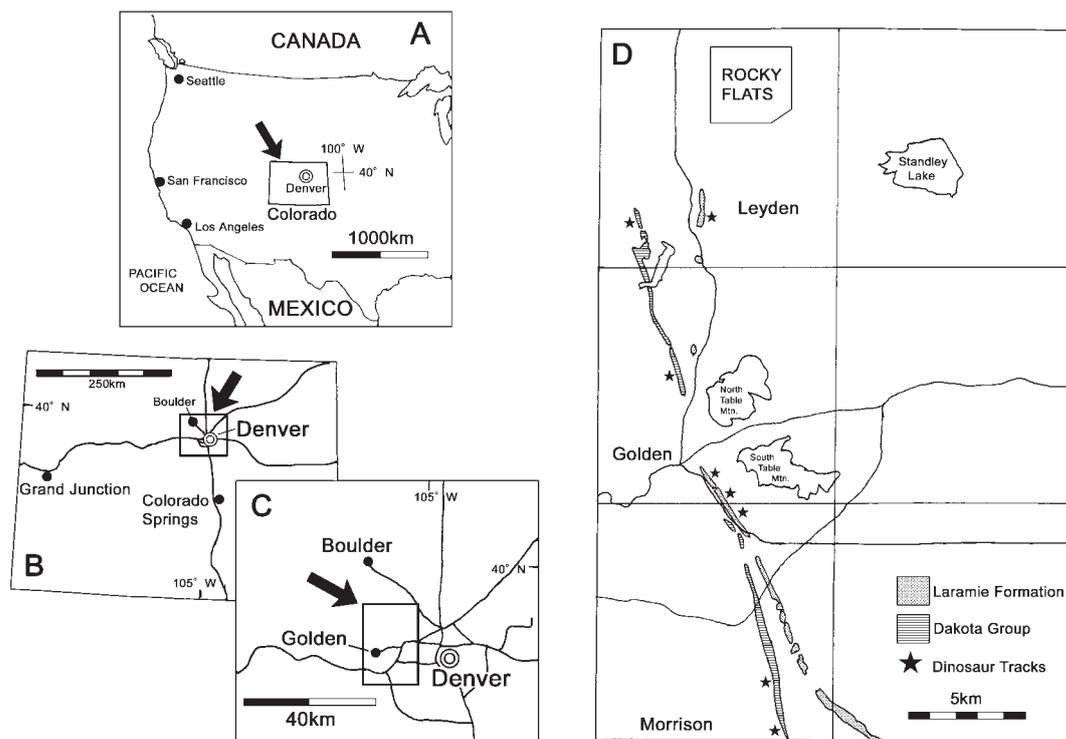


Figure 1. A, B and C: Index maps of tracksites. D: Locality map of tracksites of the Laramie Formation and the Dakota Group between Leyden and Golden, Colorado. D redrawn from Lockley and Hunt (1995a).

## COLORADO SCHOOL OF MINES SECTION

## PARFET CLAY PITS SECTION



★CSM upper

RED CLAY MARKER

★ CSM lower

★PCP 6

★PCP 5

★PCP 4b
★PCP 4a
★PCP 3
★PCP 2
★PCP 1

★PCP 4l

50m

★PCPsouth upper
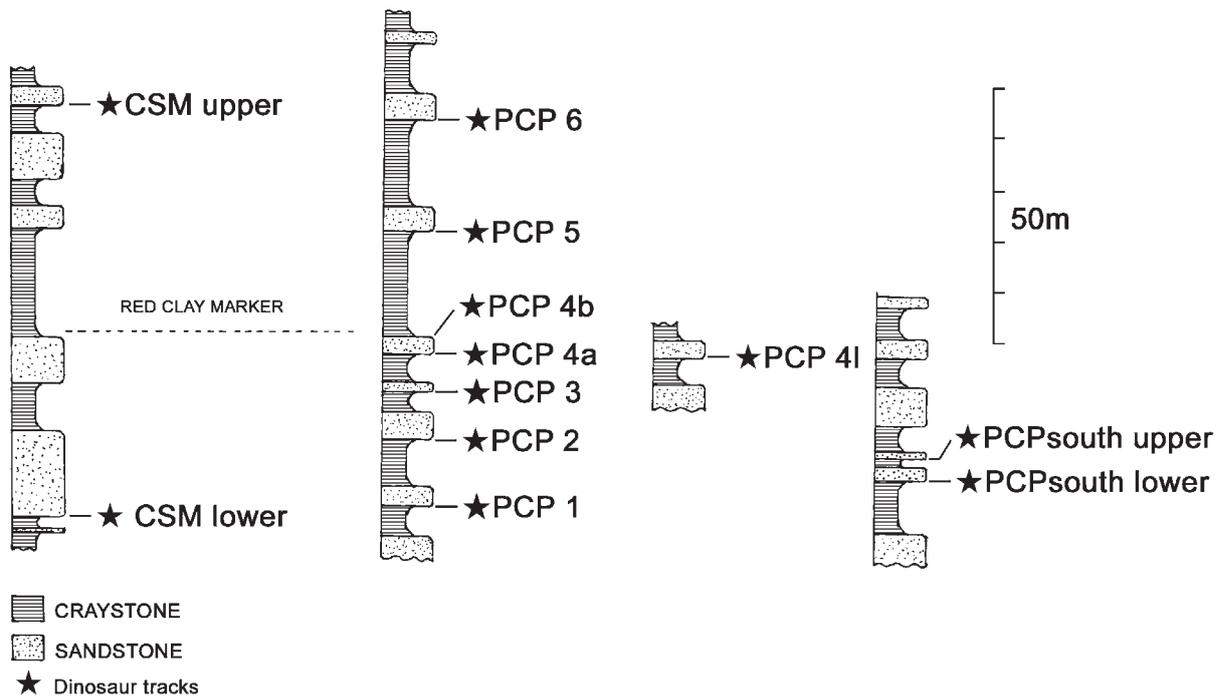★PCPsouth lower

⊟ CRAYSTONE

⊡ SANDSTONE

★ Dinosaur tracks

Figure 2. Stratigraphic sections of the lower part of the Laramie Formation at the Colorado School of Mines and Parfet Clay Pits area with occurrences of dinosaur tracks at each stratigraphic level. Redrawn from Lockley and Hunt (1995a).

Table 1. Summary of vertebrate track and trackway types at different localities and stratigraphic levels in the Laramie Formation: CSM, Colorado School of Mines: PCP, Parfet Clay Pits.

| | Taxa | *Ceratopsipes goldenensis* | HADROSAURIDS | THEROPODS | | | | | | | indet. biped | others |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | A | B | C | D | E | F | G | | |
| Site/Level | PCP 1 | 1 | | | | | | | | | 1(Hadrosaurids?) | |
| | PCP 2 | 2 | | | | | | | | | 2(large Theropods?) | |
| | PCP 3 | 1 | | | | | | | | | | |
| | PCP 4a | 6 | | | | | | | | | | |
| | PCP 4b | | | | | | | 1 | 1 | | 1(Hadrosaurids?) | lizard |
| | PCP 4l | 1 | | | | | | | | | | |
| | PCP 5 | 5 | | | 6 | 3 | 1 | | | 1 | | |
| | PCP 6 | | | 7 | | | | | | | | champsosaur |
| | PCP south(lower) | 3 | | | | | | | | | | |
| | PCP south(upper) | 1 | | | | | | | | | | |
| | CSM lower | 8 | 3 | | | | | | | | 1(Theropods?) | |
| | CSM upper | 1 | | | | | | | | | 1(Hadrosaurids?) | |
| | Leyden | | 1 | | | | | | | | | |
| | Subtotals | 29 | 4 | | | | 20 | | | | 6 | |
| | Total of all dinosaur tracks and trackways | | | | | | 59 | | | | | |

### 3. 2. Fauna and flora

Animal fossils of the Laramie Formation are trace fossils. They consist mainly of dinosaur tracks, 29 ceratopid tracks (*Ceratopsipes goldenensis*), 4 Hadrosaurid tracks, 20 various sized theropod tracks and 6 unknown tracks (Lockley and Hunt, 1995a) (Figs. 3, 4, 5, Table 1). *Ceratopsipes goldenensis* may be attributed to *Triceratops* and the biggest theropod track, morphotype G may be attributed

*Tyrannosaurus* (Lockley and Hunt 1995b). There are also tracks of *Champsosaurs* (*Champsosaurichnus parfeti*, Lockley and Hunt, 1995a) and lizards (Lockley, personal communication, 2002). Since it can be considered that the habitat of *Champsosaurs* as under water, their effect on terrestrial ecosystems should be relatively small. The existence of lizards shows that there are herbivorous and carnivorous invertebrate, such as insects and spiders, as their

diets. Plant fossils of the Laramie Formation mainly consist of ferns, gymnosperms, monocots, and dicots (Knowlton, 1922). The most dominant arboreal group is the dicots and they dominate 71 % of all species numbers (Fig. 6). They include walnuts (*Juglans*), willows (*Salix*), beech (*Quercus*) etc, and most of them were deciduous trees. The herbaceous group consists mostly of ferns and monocots. It could be considered that the climatic zone of these fossils was temperate because there were coexistences of deciduous trees such as beech and subtropical trees such as palms (*Sabalites*) and cycads (*Cycadeoidea*). Those plants should have grown ranged nearby and accumulated near where they were found since most plant fossils represent good preservation, (c.f. Okubo, 1998). The paleoenvironment of the Laramie Formation could be interpreted to be temperate forest and grassland consisting of dicot trees, ferns and monocot herbs distributed in the coastal and fluvial floodplain. This grassland is not poaceous because Poaceae appeared for the first time in Eocene (McNaughton, 1991).

### 3. 3. Energy intake of dinosaur

It is necessary to estimate dinosaur's body weight to calculate energy intake. There are two types of methods for estimating weights of dinosaurs. The first method is using volumes of scale models of dinosaurs (Colbert, 1962, Alexander, 1985). The second method is using circumferences of limb bones (Anderson et al., 1985). Because there are model maker's biases in using scale models, the second method could be considered to be reliable. For example, Colbert (1962) estimated the weight of *Brachiosaurus brancai* at 87.0 t by the first method and Alexander (1989) estimated it at 46.6 t by the same method. This error is caused by volumetric difference is scale models and it is hard to confirm which is correct. The problem of the second method is that its results always produce some errors (Alexander, 1989). However, it is more objective than the first method because the second one does not include human biases. Thus specimens in the Royal Tyrrell Museum, Canada were used for the second method to estimate dinosaur's body weight (Table 2). Since dinosaur trackmakers of the Laramie Formation are not known except for theropod G and *Ceratopsipes goldenensis*, body weights of theropods A-F were assumed by their size. First, it is assumed that the cube of track length is relative to weight then a cube equation that passes (0, 0) and (37, 1724.49) from data on *Albertsaurus libratus* ($y = 0.034x^3$; $x$ = track length, $y$ = weight) was
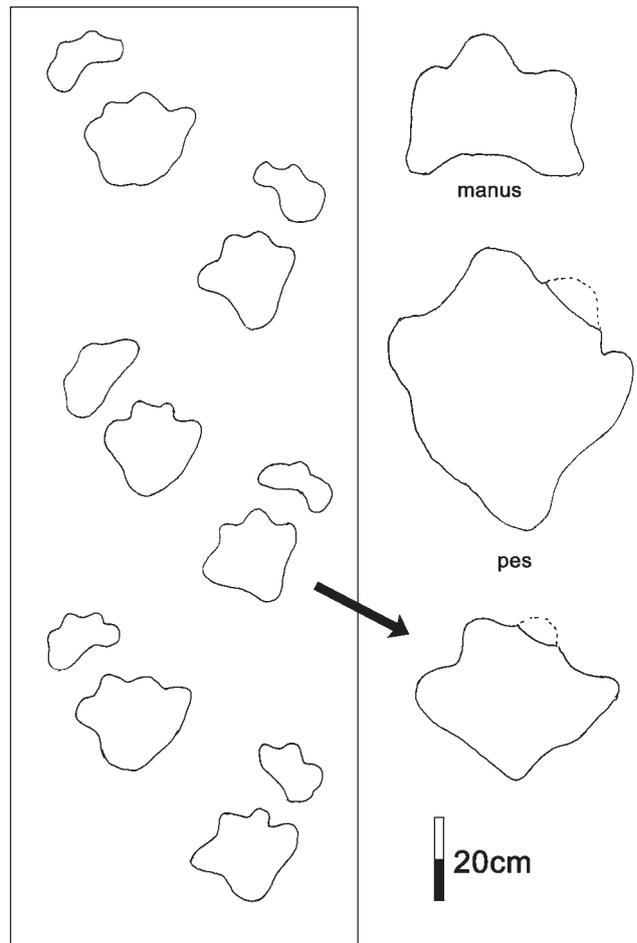


Figure 3. Tracks and a trackway of *Ceratopsipes goldenensis*. Redrawn from Lockley and Hunt (1995a).
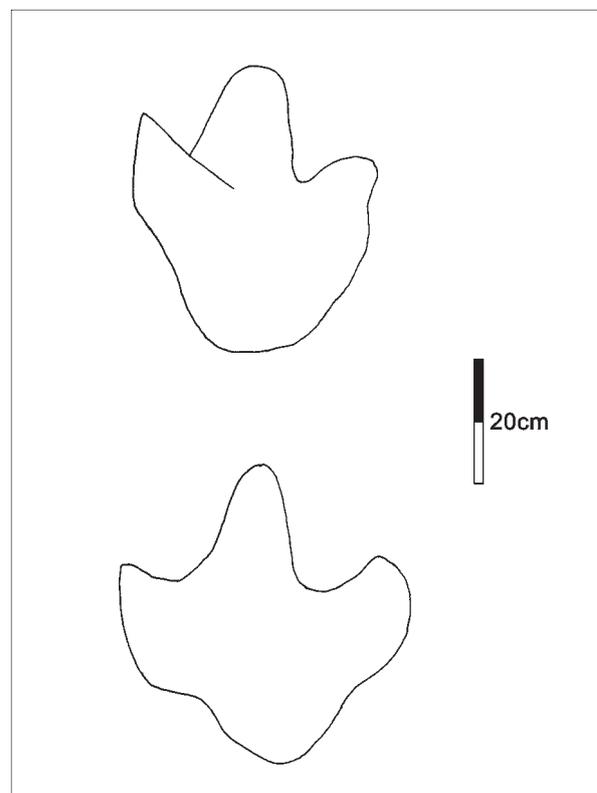


Figure 4. Ornithopod tracks from the Laramie Formation. Redrawn from Lockley and Hunt(1995a).
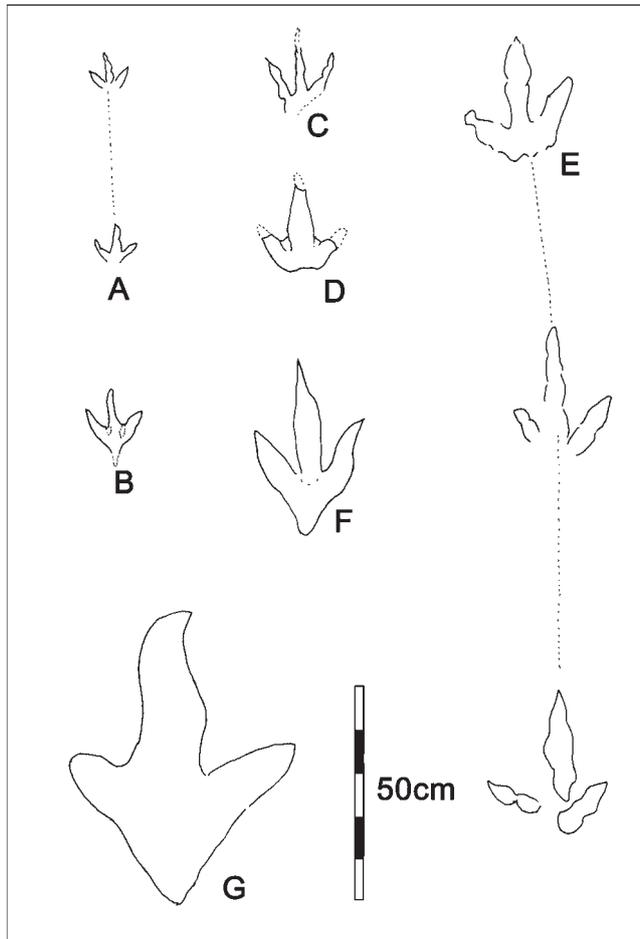
Figure 5. Various theropod tracks of the Laramie Formation. Morphotype G may be attributed to *Tyrannosaurus*. Redrawn from Lockley and Hunt (1995a).
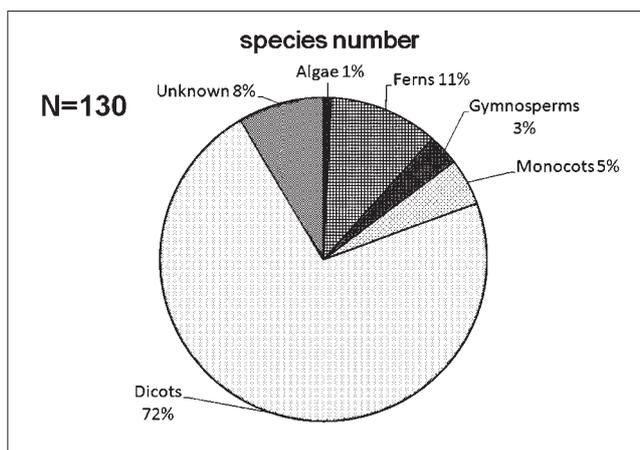


Figure 6. The species structure of the Laramie plants. Data cited from Knowlton (1922).

made and estimated weight of each theropod were calculated (Table 3). An average body weight of four species of large ornithopod was used for the Laramie ornithopod trackmaker (Table 2).

It is easier to estimate diets of dinosaurs than weights.

Theropods are carnivores and ceratopsids and ornithopods are herbivores in the Laramie Formation (Table 3). Energy intake of dinosaurs probably varied greatly depending on whether their metabolisms were endothermic or ectothermic. For over 30 years paleontologists have argued about it (e.g. Bakker, 1986), but it has not yet been solved. Reid (1997) suggested that dinosaurs have more efficient circulation than any modern reptile possesses because of hemodynamics and fast growth to large size. He also suggested dinosaur aerobic activity on the grounds of the evidence of air sacs in saurischians. Reid's dinosaur image reveals animals that have low SMR close to ectotherms and higher activity levels close to endotherms. Though it can not be claimed conclusively, it seems to be reasonable and fit current evidence. So the term "ectotermic dinosaurs" is used for dinosaurs whose SMR are at an ectothermic level but whose activity level is the same as endotherms in this paper. There are some reports about feathered small theropods (e.g. Xu et al., 1999) and small theropods that sat on eggs i.e. *Oviraptor* (Norell et al., 1995). Especially, this sitting on eggs activity is peculiar to endothermic animals because it needs a high SMR. So, the possibility of endothermic small theropods is strong. Therefore, we reconstruct the Laramie paleoecosystem in three models; the model A is that both theropods and herbivorous dinosaurs are ectothermic, the model B is that theropods are endothermic and herbivorous dinosaurs are ectothermic and the model C is that both of theropods and herbivorous dinosaurs are endotherms. Small theropods whose weights are 100 kg or less are assumed to be endothermic in every case. The case that ectothermic theropods and endothermic ornithopods was not considered because there is little possibility in a such case.

Table 4 shows various models of formulas for energy intake of dinosaurs. A value of 1.15 for ectothermic dinosaurs means that ectothermic dinosaurs have ectothermic SMR and endothermic activity level. Formulas for endothermic dinosaurs are the same as birds because dinosaurs could be considered more closely related to birds than mammals.

### 3. 4. The food web of the Laramie paleoecosystem

The food web of the Laramie Formation which is estimated from trace fossils principally consists of various carnivorous theropods and two kinds of herbivorous dinosaurs. As mentioned above, traces of lizards indicates existence of carnivorous and herbivorous invertebrates. They could have

Table 2. Estimated weights of dinosaurs based on specimens of the Royal tyrrel museum. Every size data are average of left and right.

| Dinosaurs | specimen number | humerus(cm) | | femur(cm) | | hand size L × W(cm) | foot size L × W(cm) | estimated weight(kg) |
|---|---|---|---|---|---|---|---|---|
| | | Length | Circumference | Length | Circumference | | | |
| *Gryposaurus notabilis* | TMP 80.22.01 | 60 | 26 | 105 | 44 | 10 × 15 | 32 × 40 | 4,914 |
| *Parasaurolophus walkeri* | TMP 78.32.01 | 53 | 26 | 103 | 42 | 8 × 11 | 35 × 41 | 4,540 |
| *Lambeosaurus lambei* | TMP 82.38.01 | 57 | 20 | 116 | 39 | unkown | 45 × 49 | 3,081 |
| *Prosaurolophus maximus* | TMP 84.00.09 | 56 | 22.5 | 105 | 39.5 | unkown | 42 × 37 | 3,528 |
| mean of Hadrosaurids | — | — | — | — | — | — | — | 4,016 |
| *Triceratops horridus* | TMP 82.06.01 | 76.5 | 50 | 105 | 47.5 | 35 × 65 | 40 × 64 | 12,141 |
| *Albertsaurus libratus* | TMP 80.4.02 | — | — | 78 | 30 | — | 37 × 31 | 1,724 |

Table 3. Estimated weights and presumed diets of Laramie animals. The weight data of theropod G cited from Anderson et al. (1985).

| Taxa | estimated weight (kg) | Presumed diets |
|---|---|---|
| Theropod A | 26 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod B | 75 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod C | 233 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod D | 918 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod E | 918 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod F | 1,458 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Theropod G | 4,500 | Herbivorous dinosaurs, lizards, carnivorous invertebrates and herbivorous invertebrates |
| Ceratpsid | 12,000 | Aboveground plants |
| Hadrosaurids | 4,015 | Aboveground plants |
| Lizards | — | Carnivorous invertebrates and herbivorous invertebrates |
| Carnivorous insects | — | Herbivorous invertebrates |
| Herbivorous insects | — | Aboveground plants |

Table 4. Formulas for energy intake of dinosaurs.

| Animal type | unit | Formula |
|---|---|---|
| Ectothermic herbivorous dinosaurs | kcal/day | $Ed = 1.15 \times (78.3 \times W^{0.723}) \times (1/0.5)$ |
| Endothermic herbivorous dinosaurs | kcal/day | $Ed = 2 \times (78.3 \times W^{0.723}) \times (1/0.5)$ |
| Ectothermic theropods | kcal/day | $Ed = 1.15 \times (78.3 \times W^{0.723}) \times (1/0.8)$ |
| Endothermic theropods | kcal/day | $Ed = 2 \times (78.3 \times W^{0.723}) \times (1/0.8)$ |

been food not only for lizards but also for small theropods (but not for large theropods such as *Tyrannosaurus*). But although adult large theropods may not have eaten invertebrates, there is the possibility that juveniles ate them. In this reconstruction model, as biomass of animals including juveniles are converted into numbers of adults, there is no problem including invertebrates as foods for large theropods. Therefore, the food web of the Laramie can be considered to have vertebrate herbivores and invertebrate herbivores routes from NPP to theropods (Fig. 7).

## 3. 5. Application of the model

NPP of the Laramie paleoecosystem is caluculated by assuming vegetation to be temperate grassland and temperate deciduous forest and area to be 10,000 km² (with a Temperate grassland : Temperate deciduous forest ratio of 1:1). Energy intake of each animal was calculated using the above formulas. Then the reconstruction model was applied to the Laramie paleoecosystem based on the Serengeti ecosystem model (Table 5, 6).
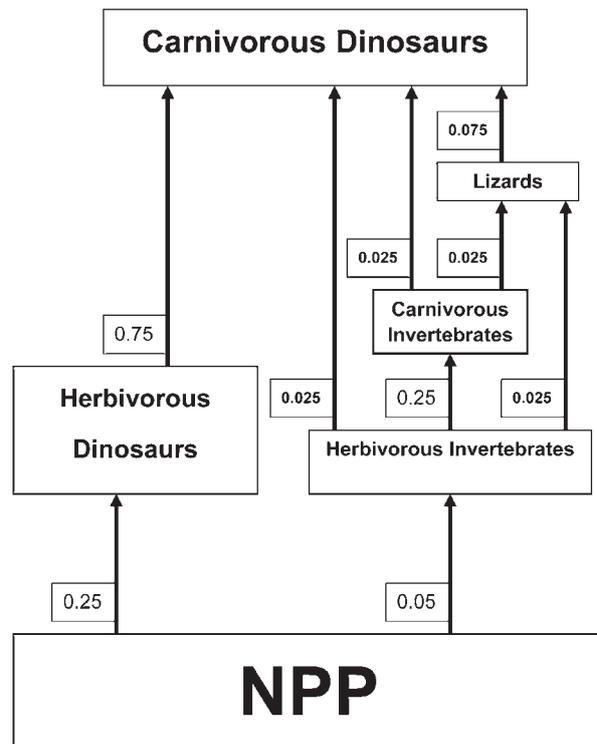


Figure 7. The food web of the Laramie terrestrial paleoecosystem. Numbers show consumption efficiencies.

## Table 5. Fixed and calculated values for the reconstruction of the Laramie paleoecosystem.

| | | unit | quantity | ground | memo |
|---|---|---|---|---|---|
| Area | Temperate grassland | ㎡ | 5,000,000,000 | Convenience value | |
| | Temperate deciduous forest | ㎡ | 5,000,000,000 | Convenience value | |
| | Sum of assumed area | ㎡ | 10,000,000,000 | Convenience value | |
| NPP | NPP of temperate grasslamd | g/㎡/y | 600 | Whittaker, 1970 | |
| | NPP of temperate deciduous forest | g/㎡/y | 1,200 | Whittaker, 1970 | |
| | Energy transformation efficiency of | kcal/g | 4.25 | Whittaker, 1970 | |
| | NPP of assumed area | kcal/y | 38,250,000,000,000 | | |
| Invertebrate herbivores | Consumption efficiency | raio | 0.05 | Begon et al., 1999 | At every ecosystems |
| | Consumption | kcal/y | 1,912,500,000,000 | | |
| | Assimilation efficiency | raio | 0.40 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.40 | Begon et al., 1999 | |
| | Productivity | kcal/y | 306,000,000,000 | | |
| Invertebrate carnivores | Consumption efficiency | raio | 0.25 | Begon et al., 1999 | |
| | Consumption | kcal/y | 76,500,000,000 | | |
| | Assimilation efficiency | raio | 0.80 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.30 | Begon et al., 1999 | |
| | Productivity | kcal/y | 18,360,000,000 | | |
| Lizards | Consumption efficiency | ratio | 0.025 | | share with carnivorous dinosaurs |
| | Consumption | kcal/y | 8,109,000,000 | | |
| | Assimilation efficiency | raio | 0.80 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.10 | Begon et al., 1999 | |
| | Secondary productivity | kcal/y | 648,720,000 | | |
| Herbivorous Dinosaurs | Common — Consumption efficiency at grassland | raio | 0.25 | Begon et al., 1999 | |
| | Consumption efficiency at forest | raio | 0.05 | Begon et al., 1999 | |
| | Consumption of herbivorous dinosaurs | kcal/y | 4,462,500,000,000 | | |
| | Ectothermic — Assimilation efficiency | raio | 0.50 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.10 | Begon et al., 1999 | |
| | Productivity | kcal/y | 223,125,000,000 | | |
| | Endothermic — Assimilation efficiency | raio | 0.50 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.02 | Begon et al., 1999 | |
| | Productivity | kcal/y | 44,625,000,000 | | |
| Carnivorous dinosaurs | Common — Consumption efficiency for invertebrates | raio | 0.025 | Begon et al., 1999 | share with lizards |
| | Consumption for invertebrates | kcal/y | 8,109,000,000 | | |
| | Consumption efficiency for vertebrates | raio | 0.75 | Begon et al., 1999 | |
| | Consumption for lizards | kcal/y | 486,540,000 | | |
| | Consumption for ectothermic | kcal/y | 167,343,750,000 | | |
| | Consumption for endothermic herbivord | kcal/y | 33,468,750,000 | | |
| | Ectothermic — Small theropods (endotherm) — Assimilation efficiency | raio | 0.80 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.02 | Begon et al., 1999 | |
| | Energy distribution | ratio | 0.256 | Table 9 | |
| | Productivity | kcal/y | 720,647,332 | | |
| | Ectothermic — Large theropods — Assimilation efficiency | raio | 0.80 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.10 | Begon et al., 1999 | |
| | Energy distribution | ratio | 0.744 | Table 9 | |
| | Productivity | kcal/y | 10,471,906,541 | | |
| | Total — Productivity | kcal/y | 11,192,553,873 | | |
| | Endothermic — Assimilation efficiency | raio | 0.80 | Begon et al., 1999 | |
| | Production efficiency | raio | 0.02 | Begon et al., 1999 | |
| | Productivity for ectothermic | kcal/y | 2,815,028,640 | | |
| | Productivity for endothermic | kcal/y | 673,028,640 | | |

## Table 6. Track census, weights, total biomass of track census, required energy of individuals per year, required energy of total individual numbers of species per year, energy distribution for each species, estimated individual numbers, total biomass of estimated data in 1 ㎞, population density of dinosaur taxa in 1 ㎞, revised estimated individual numbers, total biomass of revised estimated data in 1 ㎞, revised population density of dinosaur taxa in 1 ㎞ in the Laramie paleoecosystem. Data cited from Lockley and Hunt, 1995a.

| Feeding habitat | Taxa | Numbers | Estimated weights (kg) | Required energy per year of an individual animal(kcal/year) | Required energy per year of total number of speceis(kcal/year) | Ratio of required energy of each species | Energy distribution for each species(kcal) | Estimated individual number | Population density of estimated vertebrate taxa in 1 ㎞ | Total biomass (kg/㎞) | memo |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A herbivores | Ceratopsipes goldenensis | 29 | 12,000 | 58,483,116 | 1,696,010,362 | 94.1% | 4,200,000,803,497 | 71,816 | 7.2 | 86,179 | |
| | Hadrosaurid | 4 | 4,015 | 26,500,076 | 106,000,303 | 5.9% | 262,499,196,503 | 9,906 | 1.0 | 3,977 | |
| total | — | 33 | — | — | — | — | — | 81,721 | 8.2 | 90,156 | |
| A carnivores | Theropod A (endotherm) | 7 | 26 | 763,325 | 5,343,278 | 9.1% | 16,006,393,806 | 20,969 | 2.1 | 56 | |
| | Theropod B (endotherm) | 6 | 75 | 1,615,835 | 9,695,010 | 16.5% | 29,042,502,919 | 17,974 | 1.8 | 134 | |
| | Theropod C | 3 | 233 | 2,116,110 | 6,348,331 | 10.8% | 19,017,145,094 | 8,987 | 0.9 | 210 | |
| | Theropod D | 1 | 918 | 5,698,988 | 5,698,988 | 9.7% | 17,071,964,788 | 2,996 | 0.3 | 275 | |
| | Theropod E | 1 | 918 | 5,698,988 | 5,698,988 | 9.7% | 17,071,964,788 | 2,996 | 0.3 | 275 | |
| | Theropod F | 1 | 1,458 | 7,961,691 | 7,961,691 | 13.6% | 23,850,148,805 | 2,996 | 0.3 | 437 | |
| | Theropod G (Tyrannosaurus) | 1 | 4,500 | 17,986,022 | 17,986,022 | 30.6% | 53,879,169,801 | 2,996 | 0.3 | 1,348 | Anderson et al. 1985 |
| total | — | 20 | — | — | — | — | — | 59,912 | 6.0 | 2,734 | |
| B herbivores | Ceratopsipes goldenensis | 29 | 12,000 | 58,483,116 | 1,696,010,362 | 94.1% | 4,200,000,803,497 | 71,816 | 7.2 | 86,179 | |
| | Hadrosaurid | 4 | 4,015 | 26,500,076 | 106,000,303 | 5.9% | 262,499,196,503 | 9,906 | 1.0 | 3,977 | |
| total | — | 33 | — | — | — | — | — | 81,721 | 8.2 | 90,156 | |
| B carnivores | Theropod A (endotherm) | 7 | 26 | 763,325 | 5,343,278 | 5.9% | 10,327,521,269 | 13,530 | 1.4 | 36 | |
| | Theropod B (endotherm) | 6 | 75 | 1,615,835 | 9,695,010 | 10.7% | 18,738,578,486 | 11,597 | 1.2 | 87 | |
| | Theropod C | 3 | 233 | 3,680,192 | 11,040,575 | 12.1% | 20,355,772,370 | 5,531 | 0.6 | 129 | |
| | Theropod D | 1 | 918 | 9,911,283 | 9,911,283 | 10.9% | 19,156,592,546 | 1,933 | 0.2 | 177 | |
| | Theropod E | 1 | 918 | 9,911,283 | 9,911,283 | 10.9% | 19,156,592,546 | 1,933 | 0.2 | 177 | |
| | Theropod F | 1 | 1,458 | 13,846,419 | 13,846,419 | 15.2% | 26,762,448,757 | 1,933 | 0.2 | 282 | |
| | Theropod G (Tyrannosaurus) | 1 | 4,500 | 31,280,039 | 31,280,039 | 34.4% | 60,458,260,980 | 1,933 | 0.2 | 870 | Anderson et al. 1985 |
| total | — | 20 | — | — | — | — | — | 38,389 | 3.8 | 1,758 | |
| C herbivores | Ceratopsipes goldenensis | 29 | 12,000 | 101,709,767 | 2,949,583,238 | 94.1% | 4,200,000,803,497 | 41,294 | 4.1 | 49,553 | |
| | Hadrosaurid | 4 | 4,015 | 46,087,088 | 184,348,353 | 5.9% | 262,499,196,503 | 5,696 | 0.6 | 2,287 | |
| total | — | 33 | — | — | — | — | — | 46,990 | 4.7 | 51,840 | |
| C carnivores | Theropod A (endotherm) | 7 | 26 | 763,325 | 5,343,278 | 5.9% | 2,469,146,316 | 3,235 | 0.3 | 9 | |
| | Theropod B (endotherm) | 6 | 75 | 1,615,835 | 9,695,010 | 10.7% | 4,480,096,513 | 2,773 | 0.3 | 21 | |
| | Theropod C | 3 | 233 | 3,680,192 | 11,040,575 | 12.1% | 5,101,886,627 | 1,386 | 0.1 | 32 | |
| | Theropod D | 1 | 918 | 9,911,283 | 9,911,283 | 10.9% | 4,580,037,036 | 462 | 0.05 | 42 | |
| | Theropod E | 1 | 918 | 9,911,283 | 9,911,283 | 10.9% | 4,580,037,036 | 462 | 0.05 | 42 | |
| | Theropod F | 1 | 1,458 | 13,846,419 | 13,846,419 | 15.2% | 6,398,476,461 | 462 | 0.05 | 67 | |
| | Theropod G (Tyrannosaurus) | 1 | 4,500 | 31,280,039 | 31,280,039 | 34.4% | 14,454,610,012 | 462 | 0.05 | 208 | Anderson et al. 1985 |
| total | — | 20 | — | — | — | — | — | 9,242 | 0.9 | 422 | |

## 4. Discussion

### 4. 1. Features of the Laramie paleoecosystem

Estimating both numbers and biomass of the Laramie dinosaurs in three patterns shows that the dinosaur community consists predominantly of herbivorous dinosaurs and a minority of theropods that depended on herbivores (Fig. 8, 9; Table 7). Comparing track data with estimated data for each models at population (Fig. 8), model A and B generally correspond with track data. The comparison of biomass gives similar estimated (Fig. 9). These results may suggest that model A and B are similar to the real metabolic pattern of dinosaurs. But it can not be concluded now because there is no clear criterion to decide whether differences between track data and estimated data are significant or not. It is necessary to collect a lot of data from various sites and reconstruct paleoecosystems for establishing such a clear criterion.

Comparing estimated data from the Laramie with estimated data from the Serengeti, for the population density of herbivorous vertebrates in the Serengeti is 217 / km², the Laramie has 8.2, 8.2 and 4.7 / km² for model A, B, and C respectively. But as the primary consumption of the Serengeti is 7,741,797 kcal / km²/y compared with the Laramie at 4,462,500 kcal / km²/y, it is necessary to modify this difference for comparison. Assuming the primary consumption of the Serengeti to be the same as the Laramie, the population density of the Laramie is about 127.7/ km². Even after the modification, the Serengeti exceeds considerably the Laramie in the population density. Of course there must be more in the Laramie because all individuals were converted into adults for this model. But as the estimated Serengeti had the same assumptions, it can not be the reason. The biggest reason for this difference may be differences of animal weights. For the largest animal of the Serengeti is the elephant (1,725 t), in the Laramie, even smaller ornithopods weigh about 4 t on average and large ceratopsids weigh 12 t! In the case of ceratopsids, 12 t may not be their average weight because probably estimated weight was caluculated from the largest class specimen. In other examples, Colbert (1962) estimated it at 9.4 t and Alexander (1985) estimated it at 6.1 t and these estimates still surpass elephants. It is worth noting that though elephants are not dominant in the Serengeti, ceratopsids are dominant at the Laramie. Most of tracks of ornithipods and ceratopsids are attributed to adults or semi-adults (Lockley and Hunt 1995a). Although there is a possibility that young herbivorous dinosaurs could not leave tracks because of their light weights,

as there are many tracks of small theropods in the Laramie it could be considered that there were very few young herbivorous dinosaurs. Besides, as ornithopods are interpreted to prefer moist, flood plains and coastal plain (Lockley, 1991), the population bias between ornithopods and ceratopsids probably reflects their actual ratio, not habitat preferences. So the Laramie paleoecosystem can be interpreted as being characterized by very large adult herbivorous dinosaurs especially ceratopsids that are larger than current herbivorous mammals.

On the other hand in the comparison of biomass / km², data from the Laramie exceeds the Serengeti 2 - 3 times (Table 7) while the primary consumption of the Serengeti exceed, the Laramie by about 1.7 times as noted above. Thus, it means that herbivorous dinosaurs in the Laramie could produce energy more efficient by than today's herbivorous mammals by about 3.4～5.1 times. This is probably because metabolic rates of dinosaurs are considered to be lower than mammals in models A and B and the metabolic rate per weight decreases in proportion to increasing weight (Fig. 10). This estimated characteristic of the Laramie paleosystem is supported by the size and low metabolic rate (except for model C) of animals. If model C is correct the Serengeti ecosystem also should be characterized by large herbivores such as elephants and giraffes, but it is dominated by smaller ungulates such as wildebeests. It may imply that it is necessary to get another energy source to cause their metabolic rates to grow large bodies. If the SMR of dinosaurs was lower than mammals, they would have been be able to get other energy for growing, but if their SMR were equal to mammals their body size should have remained at the same level as mammals. Therefore, characters of the Laramie paleoecosystem may suggest that there is little possibility of complete mammal like endothermic dinosaurs. In other words, dinosaurs were large because their SMR was ectothermic.

### 4. 2. Predator / prey biomass ratios and dinosaurs metabolisms

Bakker (1972, 1974, 1980) claimed at that ectothermic predators eat only a seventh to a tenth as much as endothermic ones of similar sizes, and thought that the metabolic rates of extinct animals can be measured by predator / prey biomass. He surveyed a wide array of fossil communities and compared predator / prey biomass ratios of modern mammals, fossil mammals, dinosaurs, thecodonts, therapsids, and early reptiles (Bakker, 1980). His data showed that ratios
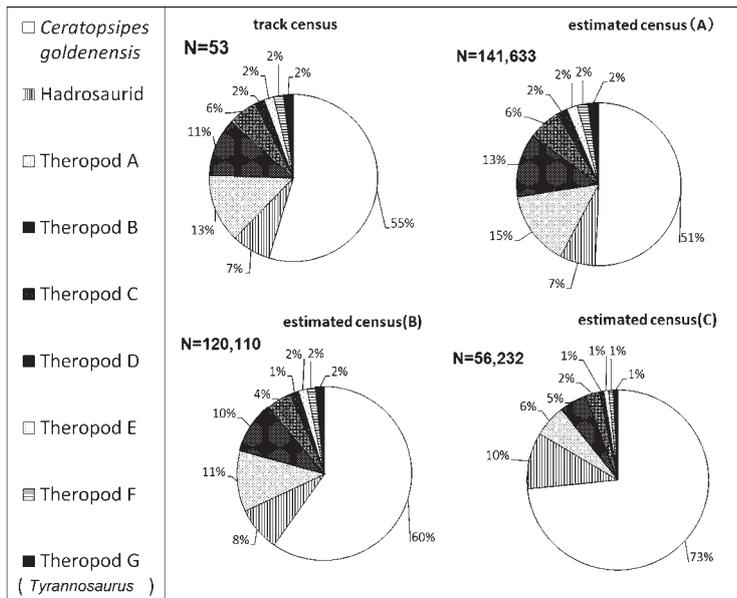
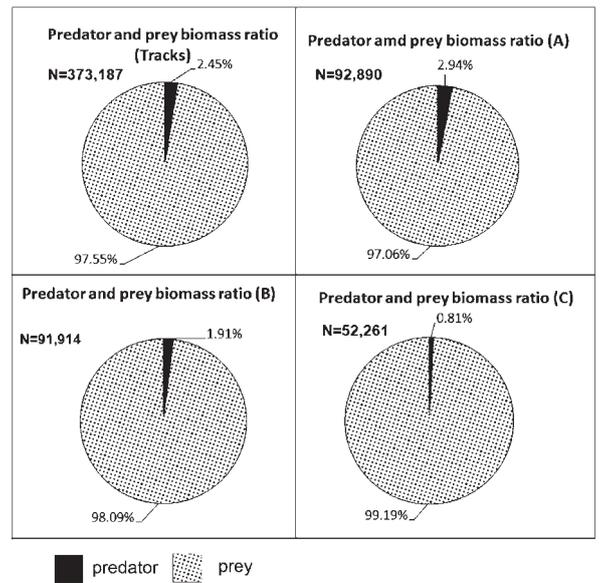Figure 8. Confirmed track census and estimated census of each metabolic pattern.



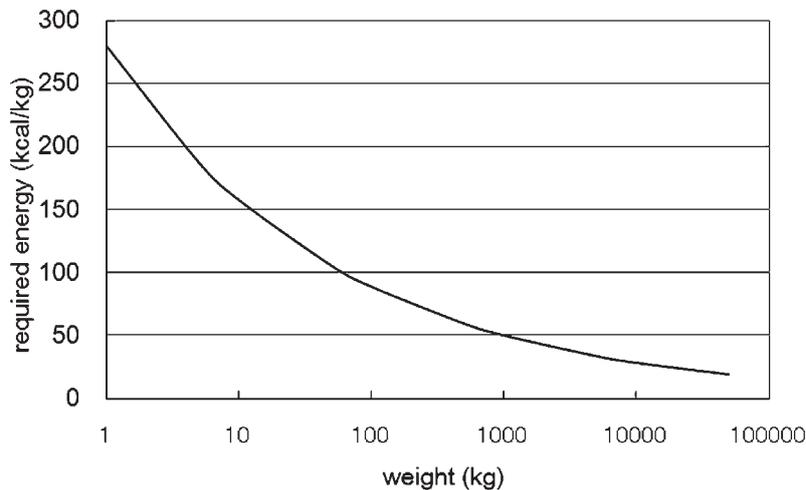Figure 9. Predator and prey biomass ratio of tracks and each metabolic pattern.



Figure 10. Weight vs. required energy per kilogram in herbivorous endotherms. Required energy per kilograms decreases as weight increases.

| Locality | | Biomass (kg/km$^2$) | | Predator biomass/ prey biomass |
|---|---|---|---|---|
| | | Carnivore | Herbivore | |
| Serengeti (Houston) | confirmed | 44 | 9,386 | 0.47% |
| | estimated | 308 | 25,926 | 1.19% |
| Serengeti (Snerson) | confirmed | 44 | 9,886 | 0.45% |
| | estimated | 346 | 27,213 | 1.27% |
| Laramie | A | 2,734 | 90,156 | 3.03% |
| | B | 1,758 | 90,156 | 1.95% |
| | C | 422 | 51,840 | 0.81% |
| Locality | | Biomass (kg) | | Predator biomass/ prey biomass |
| | | Carnivore | Herbivore | |
| Laramie | Track | 9,127 | 364,060 | 2.51% |

Table 7. Predator/prey biomass ratios of the Serengeti ecosystem and the Laramie paleoecosystem of each metabolic patterns.

of dinosaurs clustered around a scant 5 %, the same as fossil mammals as compared with ratios of about 25 – 65 % for early reptiles. He also showed that ectothermic spider - insect communities have predator/prey ratios of 40 % or more and concluded that dinosaurs are endothermic. Farlow (1980)

questioned Bakker's method by suggesting that there are a lot of complicating factors such as biases of preservation and correction for fossils (Corrected fossils are not represent natural presences because correctors do not always all fossils equally.), predator and prey productivity / biomass (P / B)

ratios, the quantitative composition of predator diets, the possibility of competition with predators other than those considered, predation by one carnivore species on another and cannibalism. But this paleoecosystem reconstruction model can reduce these factors considerably. To begin with biases of preservation and correction for fossils, as noted above, preservation of fossil bones are affected by various factors. For example, Paul (1988) said that predatory dinosaur had bones that were denser than those of herbivorous dinosaurs of equal size, and this probably made theropod bones more resistant to rot, and more likely to be incorporated into the fossil record than those of other dinosaurs. But as we mentioned (2.1), this problem can be solved by using fossil tracks as materials. Besides, relative large numbers of tracks also reduce such biases. Though one dinosaur can leave only one set of bones, it can leave a lot of tracks. Prey productivity / biomass (P / B) ratios can be solved by giving specific numbers based on Heal and Maclean (1975). Matsukawa et al. (2006) showed predator / prey weight ratio is 0.4 % from the Early Cretaceous Choir ecosystem in Mongolia. This is less than 4 % estimated by Bakker (1986). So, they concluded that predator / prey weigt ratios cannot infer dinosaur metabolism as either endothermic or ectothermic. This conclusion supported Farlow's (1980) discussion of dinosaur metabolism based on predator / prey ratio by Bakker (1980). The problem of the quantitative composition of predator diets is relatively small in the Laramie paleoecosystem because there are only two kinds of large vertebrate herbivores which can be considered to be prey, and they are dominated by ceratopids. Although we can not know whether the possibility of competition with predators other than those considered is strong or not, estimated numbers take into account such effects because track number ratios presumably reflect results of competition. The possibilities of predation by one carnivore species on another and cannibalism can effectively be ignored because the population density of herbivorous dinosaurs is at least about 3.6 times that of theropods. Although Kruuk (1972) reported fights between lions and hyenas, they just scramble for prey. They do not eat competitors and seldom kill each other. Even if lions kill hyenas, they rarely eat the loser. Likewise, theropods probably did not have to attack another theropods, that might counterattack, because they had enough herbivorous prey. Of course there is still some possibility such as problems but they can be ignored in this simplified model. Therefore, this model can reduce most of Farlow's complicating factors, we compared estimated predator / prey

biomass ratio from the Laramie paleoecosystem (Table 7). Estimated results all fall below 5 %, the fixed criterion for endothermic dinosaurs. Moreover, these percentages will decrease because this model uses only energy as a restricting factor as the Serengeti. Therefore Bakker's method is insufficient to prove endothermic dinosaurs.

The problem of Bakker's method was using ectothermic spider – insect communities as a criterion for an ectothermic community. Although they are ectothermic, there may be big problems to use them as a model for vertebrates because they are invertebrates that have small bodies, with different life history strategies and quite different genealogy from vertebrates. High predator / prey biomass ratio values for thecodonts, therapsids, and early reptiles may be caused by complicating factors as indicated by Farlow (1980).

The big differences in predator / prey biomass ratios among different taxonomic ecosystems reflect fundamental differences in life histories and life history strategies. It is necessary to examine ecosystems carefully to exclude other factors such as differences in life histories before using predator/prey biomass ratios as grounds for inferring endothermic dinosaurs. Thus this result shows that it is very difficult to use simple predator / prey ratio comparisons from bone fossils as the evidence of endothermic dinosaurs.

## 5. Conclusions

(1) Comparing the track census ratio with three metabolic models of reconstructed census ratios for the Late Cretaceous Laramie paleoecosystem in Colorado, north America, model of ectothermic herbivorous and carnivorous dinosaurs and endothermic carnivorous and ectothermic carnivorous dinosaurs showed similar values to the track data.

(2) The Laramie paleoecosystem is characterized by the dominance of large herbivorous vertebrates and thus high secondary productivity.

(3) Comparing predator / prey biomass ratios for three types of metabolic rates reveals that there is no significant difference among them. This supports Matsukawa et al.'s (2006) discussion of dinosaur metabolism based on predator / prey ratio by Bakker (1980). Therefore Bakker's (1980) hypotheses that one can decide metabolic type of dinosaurs by predator/prey biomass ratios and infer dinosaurs as endotherms are rejected.

(4) Uncertain factors of the reconstruction model can be reduced by using fossil tracks as a proxy for ratios of living

animals because of their uniform preservation and *in situ* occurrence.

## Acknowledgements

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# 北米コロラド高原の後期白亜紀ララミー層の陸上生態系
## ：食物網とエネルギー流解析に基づいて

柊原　礼士・松川　正樹・マーティン・ロックレー

環境科学分野

**要　　旨**

　本論文は地球の過去の生態系と環境の変化を知る先駆けとして，白亜紀後期のララミー層の古生態系の復元を試みたものである。生態系はエネルギー流によってコントロールされているため，それを用いることによって生態系を復元することが可能である。太陽エネルギーは植物によって炭水化物に固定され，一次消費者を経て高次の消費者へと移動し，最終的には熱として放出される。エネルギーが次の栄養レベルに移動するとき，それは動物種によって異なる値を持つ，消費効率・同化効率・生産効率の３つの変換効率に制御される。移動したエネルギーはその栄養レベルに属する動物達にそれらの存在数と所要エネルギー量の比率に応じて分配される。この分配されたエネルギー量を各動物種の一個体分の所要エネルギー量で割ることで，動物の存在数が推定される。恐竜を含む動物の所要エネルギー量はその体重，代謝型，そして活動レベルを元に計算することができる。恐竜の場合，存在数の比率は化石を元に決められる。足跡の化石はその豊富な産出数，保存率の一貫性，そして原位置性において，この生態系復元モデルにおいて体化石と比較して優れた材料である。ララミー古生態系の復元結果は，そこが大型の草食恐竜の優占とそれらによる高い二次生産量に特徴付けられることを示していた。そして，捕食者と被食者の生物量の比率は，そのデータを元に恐竜の代謝型を決定することは不可能であることを示唆した。本研究は異なる複数の古生態系を比較するための基本的な方法を提供し，そしてそれは古環境と古生態系の変遷を知る手がかりとなるであろう。

キーワード：化石足跡群集，古生態系，ララミー層，白亜紀後期，恐竜足跡