# Terrestrial ecosystems in the early age of dinosaurs based on food-web and energy-flow models applied to data from western North America

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食物網とエネルギー流モデルに基づいた恐竜時代初期の陸域古生態系
－北米西部を例として－

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Paleoecosystems in the early "age of dinosaurs" in the Colorado Plateau region were reconstructed based on food-web and energy-flow modeling. Two track sites were investigated for the paleoecosytem reconstruction. Footprints of dinosaurs such as primitive sauropods, prosauropods, and theropods occur from the Upper Triassic Chinle Group at the Peacock Canyon track site, New Mexico. This track site also yields tracks of armored aetosaurs, therapsids, small lizards, and other fossils. This site is suitable for considering the ecosystem where dinosaurs hadn't dominated yet. Footprints of abundant carnivorous dinosaurs, primitive crocodilians, small lizards and other terrestrial vertebrates from the mainly Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, Utah are shedding light on an ecosystem where dinosaurs began to dominate. We tried to infer the energy-flow patterns of paleoecosystems based on three categories of transfer efficiency and food-web modeling. As a result, energy-flow in paleoecosystems can be represented, and possible energy dynamics and population size for animals in each trophic level can be estimated and quantified in the study area. The results are evaluated by comparison with those of other reconstructed paleoecosystems and modern ecosystems. It is inferred that differences in energy-flow and population size between ecosystems are caused by differences in the types of ecosystem, the structures of the food-web, and the metabolic rates of animals. The energy-flow and estimated population size suggest that a highly diverse reptile fauna in the Late Triassic changed to a low diversity fauna dominated by dinosaurs. Ecological pyramids based on productivities at each trophic level show that the ecological niche for herbivorous vertebrates was essentially empty in the Early Jurassic ecosystem. Thus, low diversity indices and the lack of herbivorous vertebrates indicate that there was a physically (and chemically) stressed ecosystem in the Early Jurassic.

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コロラド高原に露出する三畳紀後期－ジュラ紀前期の陸成層を研究対象とし，エネルギー流モデルに基づいて古生態系を定量的に復元した。三畳系上部の Chinle Group が露出するニューメキシコ州 Peacock Canyon の足跡産地は，原始的な竜脚類，古竜脚類，獣脚類の恐竜足跡化石に加え，アエトサウルス類，獣弓類，小型のトカゲなどの多様な爬虫類の足跡化石を産出する。従って，この足跡産地は恐竜がまだ優勢でない時代における古生態系を考察するために適している。主としてジュラ系下部の Moenave Foramtion が露出するユタ州 St. George の足跡産地は，獣脚類の足跡化石を豊富に産出し，原始的なワニ類やその他の陸上動物の足跡化石も産出する。2000 年に発見されたこの足跡産地から得られる情報によって，恐竜が卓越し始めた時代の古生態系の特徴が明らかになってきている。この研究では，古生態系復元の場所として，これら２つの足跡化石産地を検討対象とした。この研究で用いたモデルでは，食物網と３つの変換効率（消費効率，同化効率，生産効率）を考慮して，古生態系中のエネルギー流パターンが推測されている。結果として，各栄養段階，および各分類群におけるエネルギーの流入量が見積もられ，存在可能な動植物の量や個体群密度が定量的に推定された。推定されたエネルギー量や動物の個体群密度は，復元されたほかの古生態系や現世の生態系との比較により評価される。各生態系間のエネルギー量や個体群密度は，生態系の生産力，食物網構造，動物の代謝量に依存して変化すると解釈できる。推定されたエネルギー流パターンと個体群密度に基づくと，三畳紀後期の多様な爬虫類で特徴付けられる動物相は，ジュラ紀前期には恐竜が優占する多様性の低い動物社会へ変遷したことが示された。各栄養段階の生産力に基づき作成されたジュラ紀前期の生態的ピラミッドからは，草食脊椎動物の生態的地位が空白であったことが解釈される。ジュラ紀前期の生物多様性の低下と，草食脊椎動物の生態的地位の欠如は，当時の生態系が物理的・化学的に圧力を受けていた可能性を示す。

## INTRODUCTION

Ecosystem and environment existing on the Earth's surface today have changed any number of times and have evolved past to present as a result of various factors. Therefore, to reconstruct the paleoenvironment and paleoecosystem, and to understand the formative process and the primary dynamic factors are a prerequisite for understanding the earth at present and in the future.

The term "ecosystem" means the combined system of animal assemblages and non-animate environments surrounding them. Both are strongly related to each other though the flow of energy and matter. Although matter can be recycled in the ecosystem repeatedly, energy is eventually converted into heat and released into the air. All systems are simultaneously open and closed with both input and output. Since Lindeman (1942) tried to quantify the concept of food-chain and food-web considering the transfer efficiency between the each trophic level, the concept was improved and developed by Begon et al. (1996), Heal and MacLean (1975), Odum (1983), Whittaker (1975) and others.

It has been thought that determining the energy -flow through ancient ecosystems is virtually beyond the reach of paleoecology (Raup and Stan-

ley, 1978). Therefore, most studies of paleoecosystem reconstruction were based on the descriptions of fossil species and assemblages (e. g. Anderson et al., 1997; Murry, 1986). An early study which attempted to reconstruct a paleoecosystem (Bakker, 1972) tried to reconstruct Late Cretaceous dinosaur communities inferring energy-flow in order to prove endothermy in dinosaurs. Farlow (1976) and Paul (1988) also tried to reconstruct Mesozoic dinosaur assemblages based on energy-flow and biomass. These studies were somewhat incomplete because they dealt with only the taxa selected by the researchers, and many assumptions were required for the analyses. Matsukawa et al. (2006), who studied Early Cretaceous ecosystem in East Asia, reconstructed food-web structures and ecological pyramids based on all fossil taxa occurring in the selected strata, taking the problems of Bakker (1972), Farlow (1976) and Paul (1988) into consideration, and described paleoecosystems from a viewpoint of energy-flow. The reconstruction process of Matsukawa et al. (2006) which can quantify inferred energy-flow and population size of animals in each trophic level is novel.

The purpose of this paper is to reconstruct paleoecosystems in the Late Triassic to Early Jurassic by food-web and energy-flow models based on data

from the Chinle Group and Moenave Formation exposed in the Colorado Plateau region. The Late Triassic to Early Jurassic was when continental drift began separating Pangea and strongly seasonal environments with dry condition were dominant worldwide. At the same time, dinosaurs appeared, and began to dominate the terrestrial vertebrate faunas. Therefore, it is important to reconstruct paleoecosystems of the Late Triassic to Early Jurassic (the early age of dinosaurs) in order to not only reveal the evolution of animal assemblages including those dominated by dinosaurs, and the interaction between animals and environments but also to understand the transition of ecosystems through time. In this paper, we describe the structures of two paleoecosystems in the early age of dinosaurs, and discuss the transitions of faunas and ecosystems from a viewpoint of energy-flow. The reconstruction process is largely based on Matsukawa *et al.* (2006) with some modifications.

## GEOLOGICAL SETTING AND AREAS INVESTIGATED

Many dinosaur and other vertebrate tracks and skeletal remains have been reported from the Chinle and Glen Canyon Groups, Colorado Plateau region, North America.

The Upper Triassic Chinle Group is distributed across the southern, eastern and northern Colorado Plateau region and includes the units formerly referred to the Dockum Group. The group is composed of terrestrial deposits and yields many kinds of plant and animal fossils including dinosaurs and other reptiles (Lockley, 1991; Lockley and Hunt, 1995; Murry, 1986). The Late Triassic was generally a time of seasonal precipitation, called "the megamonsoon" in western North America (Dubiel *et al.*, 1991). The Late Triassic deposits of the western states were divided into many different formations and members. However, all these units can be considered part of the Chinle Group (Lucas, 1993).

Our research group investigated the Peacock Canyon tracksite at the Cimarron area, northeast-

ern New Mexico (Fig. 1A, B). The varicolored calcareous mudstones and sandstones of this tracksite can be interpreted as floodplain and channel deposits respectively (Fig. 1C). The site yields various kinds of vertebrate tracks. The site is assigned to the upper part of the Chinle Group, or Rock Point Sequence (Lucas, 1993).

The Lower Jurassic (partly Upper Triassic) Glen Canyon group is distributed across the Colorado Plateau region, North America and divided into four formations, the Wingate, and Moenave (which are partly equivalent depending on the locality), the Kayenta and Navajo formations in ascending order. The Glen Canyon Group mainly consists of desert deposits, or eolian, dune sandstones (especially the Wingate and Navajo) and elsewhere contains water-lain deposits (especially the Moenave and Kayenta) (Lockley and Hunt, 1995). The group yields many vertebrate tracks and some skeletal remains (Lockley, 1991; Lockley and Hunt, 1995; Clark and Fastovsky, 1986).

The Moenave Formation is restricted to northern Arizona and southern Utah although other formations of the Glen Canyon Group extend throughout the Colorado Plateau region. Unlike the mainly eolian Wingate, the Moenave Formation is composed largely of water-lain deposits and is divided into the Dinosaur Canyon, Whitmore Point, and Springdale Sandstone members in ascending order (Clark and Fastovsky, 1986). Tracks of dinosaurs (*Grallator* and *Eubrontes*), crocodile-like reptiles (*Batrachopus*) and synapsids (cf. *Laoporus* or *Brasilichnium*) were reported from the formation (Lockley and Hunt, 1995; Miller *et al.*, 1989; Schultz-Pittman *et al.*, 1996).

A new Early Jurassic dinosaur tracksite, the St. George Dinosaur Discovery Site at Johnson Farm (SGDS), Utah, was discovered in 2000 (Fig. 2A, B). The site consists mainly of whitish or red and chocolate colored alternating beds of sandstone and mudstone and contains intercalated limy caliches (Fig. 2C). These sedimentary rocks are interpreted as channel sandstones and floodplain and lacustrine mudstones, siltstones and fine sandstone (Kirkland and Milner, 2005a). The site
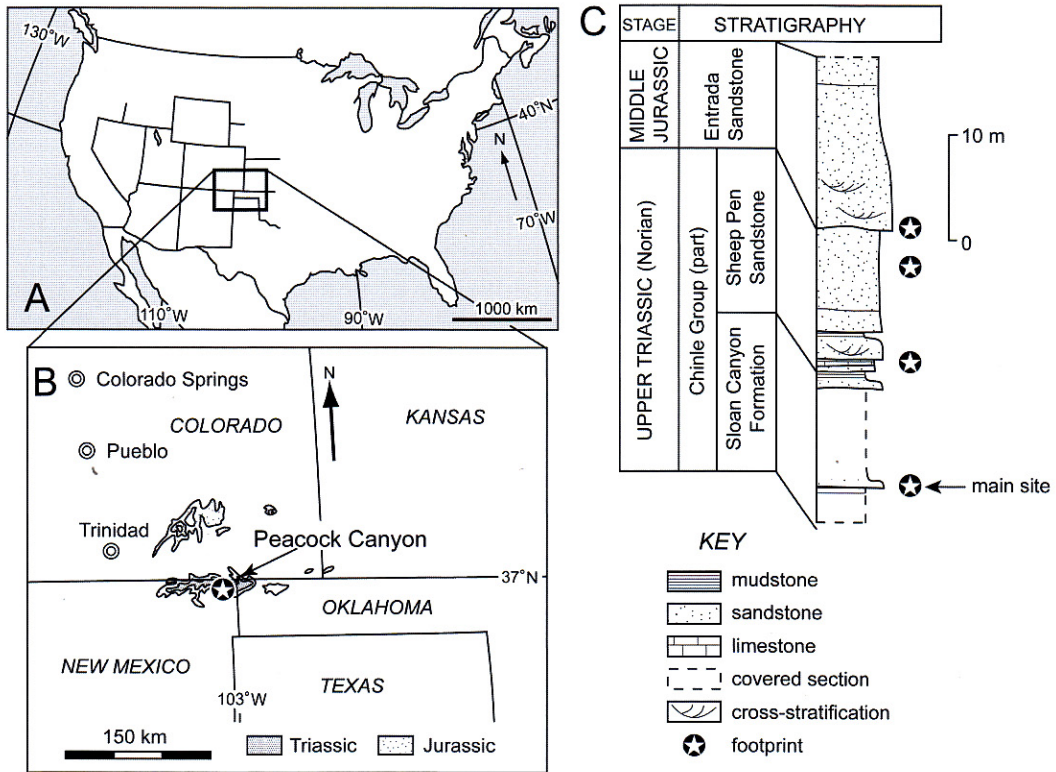
**Fig. 1** Investigated area of the Upper Triassic Chinle Group at the Peacock Canyon site, Cimarron area, New Mexico.
(A) Index map of the investigated area. (B) The location of the investigated area and outcrops of Triassic and
Jurassic rocks. (C) Stratigraphic section showing the locations of fossil tracks. Geological map and stratigraphy
based on Conrad et al. (1987) and Lockley and Hunt (1995).

yields well-preserved theropod (*Grallator* and
*Eubrontes*) and crocodile (*Batrachopus*) tracks, fish
scales, invertebrate and plant fossils (Kirkland *et
al.*, 2002; Lockley *et al.*, 2004; Milner *et al.*, 2005a,
b; Milner and Lockley, 2006). The main site of the
SGDS is assigned to the transition zone of the
Dinosaur Canyon Member and the Whitmore
Point Member stratigraphically, but is associated
with a number of under- and over-lying track-bear-
ing levels.

## METHOD

### Recognition of the Biota

For the purposes of ecosystem reconstruction, it
is important to understand the species that com-
prise the ecosystem and the population size. In
this paper, individual vertebrate numbers were
mainly counted based on the number of discrete

trackways (series of footprints made by a single
animal) not merely indiscriminate counts of
tracks.

### Food-Web Factors

Plants are eaten by herbivores, which are then
preyed upon by carnivores. The flow series is
known as the food-chain or food-web. In paleon-
tology, predatory species and their prey can often
be recognized (Raup and Stanley, 1978). There-
fore, food-webs for paleoecosystems can be recon-
structed.

### Energy Intake for Ancient Animals

It is important to estimate energy intake for ani-
mals because it is one of key factors controlling
energy-flow patterns.

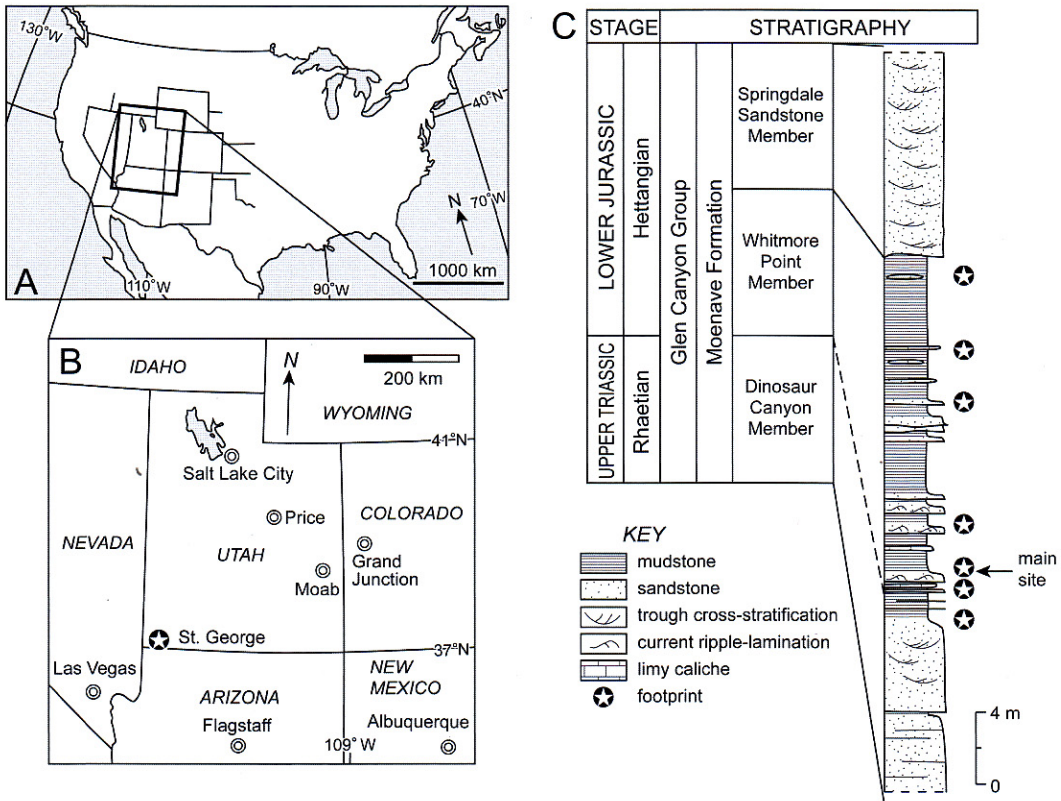Farlow (1976) showed the empirical relation

**Fig. 2** Investigated area of the Lower Jurassic Moenave Formation at the SGDS, Utah. (A) and (B) Index map of the investigated area. (C) Stratigraphic section showing the location of fossil tracks.

between weight and daily energy intake based on modern living animals and applied the relationship to dinosaurs. In this relationship, we must decide whether animals are endothermic or ectothermic. By contrast, Matsukawa *et al.* (2006) proposed new formulas that can be varied according to Standard Metabolic Rate (SMR) and the activity level. Using their formula, energy intake for herbivorous mammals can be calculated by:

$$I = 293 \times W^{0.75} \times 2 \times (1/0.5)$$
$$\approx 1,170 \times W^{0.75} \text{ (Eq. 1)}$$

where I is energy intake (kJ/day), and W is the body weight (kg). Here, $293 \times W^{0.75}$ estimates the SMR. The SMR of reptiles is 10-20% that of mammals that are of the same body weight (Fowler, 1978). Activity Metabolic Rate (AMR) is twice to

three times SMR (Fowler, 1978). In Eq. 1 the assumed AMR is twice SMR. The more active the animal is, the greater the needed AMR. 1/0.5 refers to the reciprocal of assimilation efficiency for herbivores (assimilation efficiency for carnivores is 0.8) (Begon *et al.*, 1996).

Based on the formula above, we estimated energy intake for ancient animals dealt with in this paper. As to physiology of ancient animals, therapsids had probably acquired endothermy (Ruben, 1995). However, there have been many discussions as to whether dinosaurs were endothermic or not (e.g. Bakker, 1986; Reid, 1997; Thomas and Olson, 1980). In this study, we accept a model proposed by Regal and Gans (1980) for dinosaurian metabolism whose ideal dinosaur was an animal that made optimum use of a limited food supply with a low metabolic rate (SMR). That is to say, we

consider dinosaurs ectothermic like modern lizards. But we acknowledge that metabolic rates probably varied (as addressed below). Reid (1997) also claimed that there was no evidence of high SMR for dinosaurs. Ectotherms' SMR were assumed to be 15% the SMR of endotherms, and carnivorous dinosaurs' AMR were assumed three times SMR because they are considered to be more active than herbivores (Lockley, 1991; Ostrom, 1980). Thus, in this paper, energy intakes for ancient animals were estimated or modeled as follows:

Carnivorous dinosaurs
$$I = 165 \times W^{0.75} \text{ (Eq. 2)}$$
Herbivorous archosaurs (including herbivorous dinosaurs)
$$I = 176 \times W^{0.75} \text{ (Eq. 3)}$$
Carnivorous lizards
$$I = 110 \times W^{0.75} \text{ (Eq. 4)}$$
Herbivorous therapsids
Same as Eq. 1

where I is energy intake (kJ/day), and W the body weight (kg). These models of dinosaurs are tentative. Therefore, it is important to cautiously point out that some dinosaurs' AMR were likely larger than the models because some dinosaurs were probably highly active (Ostrom, 1980; Reid, 1997).

In this study, we estimated the body weights of the Late Triassic and Early Jurassic theropod specimens: *Coelophysis bauri* (replica of AMNH 7223 housed in the Mesalands Community Colledge's Dinosaur Museum, Tcucumcari, New Mexico, U.S.A.) as ca 17 kg and *Dilophosaurus wetherilli* (TMP 83.26.02 housed in the Royal Tyrrell Museum, Drumheller, Alberta, Canada) as ca 270 kg based on Anderson *et al.* (1985). Body volume and weight increase by the cube of the linear dimensions. We estimated weights of the Late Triassic and Early Jurassic theropods from the ratio of pes skeletal length to mean value of pes track length. For example, we compare a certain specimen whose pes skeletal length is *a* and body weight *A*, and a certain trackmaker whose track length is *b*.

If the specimen and trackmaker have a similar body form, the body weight (*B*) of the trackmaker is calculated roughly as follows:

$$B = (b / a)^3 \times A \text{ (Eq. 5)}$$

As to other taxa whose skeletal remains we couldn't measure, we inferred their body sizes from track length and estimated approximate body weights.

### Setting of Assumed Geographical Area Size

To quantify possible energy and population size of creatures, we have to assume the size of area for the reconstruction of the ecosystem. One method of establishing area size is to calculate that of the exposed strata or sedimentary basins. However, living animal communities have certain activity prescribed areas. For example, the Serengeti ecosystem in Tanzania and Kenya covers an area of $2.5 \times 10^4$ km$^2$ that can be considered broadly equivalent to an ecosystem. In this study, we calculate the area size of exposed strata of each geological unit and multiply the necessary value to make the inferred area as large as the Serengeti ecosystem.

### Net Primary Productivity

Net primary productivity (NPP) represents the actual rate of production of new biomass by plants. NPP was inferred in various modern ecosystems (Whittaker, 1975). These values can be applied to the reconstruction of paleoecosystems. NPP is usually expressed in units of dry organic matter per unit area and time (e.g. g/m$^2$/year). We can estimate total actual rate of production in the inferred area by multiplying NPP and the area size together. To express values in units of energy, energy per dry unit of organic plant matter (which is 17.8 kJ/g in terrestrial plants) can be used (Whittaker, 1975).

The Late Triassic to Early Jurassic floras were dominated by ferns and gymnosperms (e.g. Ash, 1986; Kimura, 1993). However, present grassland is composed of poaceous plants not ferns. Therefore, it is important to compare the NPP of fern

and monocot grasslands. The standing crop of *Pteridium aquilinum* (fern) type grassland and *Miscanthus sinensis* (monocot) type grassland is almost the same (Shimada, 1968; Shimada *et al.*, 1968). In addition, the ecology of *Pteridium aquilinum* is similar to *Miscanthus sinensis* in its perennial nature. These ecological similarities and similar value of standing crops of two types of grassland led us to conclude that the NPP of the *Pteridium* type grassland is almost the same as that of *Miscanthus* type grassland (Matsukawa *et al.*, 2006). Therefore, we apply this information to estimate the NPP of the vegetation of ancient ecosystem, and the NPP of ancient vegetation was inferred based on that of modern vegetation as estimated by Whittaker (1975).

## Transfer Efficiency in Energy Flow-Models

When energy passes through a certain trophic level, a part of the energy is necessarily lost or transformed. The missing energy enters the decomposer chain as remains and feces or it is lost as respiratory heat or converted into energetic activity. To predict the pattern of energy-flow, three categories of transfer efficiency are useful: consumption efficiency (CE), assimilation efficiency (AE) and production efficiency (PE). Consumption efficiency (CE) is the percentage of total productivity available at one trophic level that is actually consumed by a trophic compartment 'one level up'. Assimilation efficiency (AE) is the percentage of food energy taken into the guts of consumers in a trophic compartment which is assimilated across the gut wall and becomes available for incorporation into growth or is used to do work. Production efficiency (PE) is the percentage of assimilated energy which is incorporated into new biomass. Heal and MacLean (1975) estimated these transfer efficiencies and compared predicted production with observed production in ecosystems today. Begon et al. (1996) generalized trophic structures for ecosystems based on Heal and MacLean (1975) and in this paper, we infer energy-flow patterns using transfer efficiencies estimated by these authors (Table 1).

Actual food-webs include terrestrial and aquatic herbivore systems (that part of the trophic structure of a community which depends on the consumption of living plant biomass) and decomposer systems. It is difficult to infer the interaction between terrestrial and aquatic energy-flow patterns. On the other hand, most of the productivity of the creatures enter the decomposer system without being eaten or as feces. Although the decomposer system is responsible for 98% of secondary productivity in the grassland community (Begon *et al.*, 1996), the productivity hardly influences grazer systems (Heal and MacLean, 1975, Fig. 1). Moreover, to infer the energy-flow pattern through the decomposer system based on fossil data is difficult. Therefore, in this paper, only terrestrial energy-flow pattern is considered.

## Division of Energy

The energy-flow pattern depends on a food-web. Therefore, we have to take the division of energy

**Table 1**  Transfer efficiency used in this study. Based on Begon *et al.* (1996) and Heal and MacLean (1975).

| Consumption efficiency (CE) | |
| --- | --- |
| Herbivores | |
|     Invertebrates | 5% |
|     Vertebrates (in grassland) | 25% |
|     Vertebrates (in forest) | 5% |
| Carnivores | |
|     Vertebrates on herbivorous vertebrates | 50% |
|     Vertebrates on carnivorous vertebrates | 25% |
|     Vertebrates on invertebrates | less than 5% |
|     Invertebrates on invertebrates | 25% |

| Assimilation efficiency (AE) | |
| --- | --- |
| Herbivorous vertebrates | 50% |
| Herbivorous invertebrates | 40% |
| Carnivores | 80% |

| Production efficiency (PE) | |
| --- | --- |
| Herbivorous invertebrates | 40% |
| Carnivorous invertebrates | 30% |
| Ectothermic vertebrates | 10% |
| Endothermic vertebrates | 2% |

into account.

Matsukawa *et al.* (2006) proposed an energy division model called the "equality model". In this model, the ratios of distributed energy are calculated from the required energy for an individual per day and the number of individuals. For example, we assume that there are some taxa which consume the same food resource (the number of taxa is $n$). The ratio of distributed energy for $j$ th taxon $R_j$ is estimated as follows:

$$R_j = \frac{a_j N_j}{\sum_{i=1}^{n} a_i N_i} \quad \text{(Eq. 6)}$$

where $a_i$ is required energy for an individual per day and $N_i$ is the number of individuals of $i$ th taxon. We largely adopt this model in this paper.

The equality model is based on the occurrence of individual numbers which assumes no differential bias in fossil preservation. The equality model is not applicable if differential bias exists. If similar energy patterns had been studied in the present ecosystem, we could use the patterns to model paleoecosystem. However, the examples of such study are few. In such a case, all we can do is to infer working ratios and accept that they are uncertain.

## Estimation of Population Size and Diversity Indices

Based on above calculations, total annual energy intake for each taxon is estimated. Dividing the energy intake for a taxon by that for an individual, possible animal population size in the assumed area is estimated. We also estimate population density and make an energy pyramid per 1 km$^2$.

Shannon diversity indices and equability (Begon *et al.*, 1996; Odum, 1983) for vertebrate assemblages were calculated using the estimated population size and biomass for both paleoecosystems. In this study, small lizard-like animals were omitted because we focused on the larger vertebrate fauna.

## RECONSTRUCTION OF PALEOECOSYSTEM BASED ON ENERGY-FLOW MODEL

### The Chinle Group (Upper Triassic)

In this study, the analyses are mainly based on vertebrate fossil tracks. We deal with tracks that in some cases belong to the same ichnogenus (i.e., *Grallator*) but occur from different regions and in rocks of different geological ages. We can assign these tracks to different ichnospecies with taxonomic studies that support such a classification. To avoid confusing these tracks, we distinguish them as *Grallator* ichnosp. C and *Grallator* ichnosp. M (for Chinle and Moenave respectively).

Footprints of dinosaurs, primitive archosaurs, small lizards, therapsids and invertebrates and phytosaur teeth, conchostracans and plant fossils occur from the Chinle Group at the Peacock Canyon tracksite, New Mexico (Conrad *et al.*, 1987; Lockley and Hunt, 1995; Lockley *et al.*, 2001). Concerning the terrestrial vertebrates, the following numbers of individuals have been estimated: thirty one primitive sauropods (*Tetrasauropus* ichnosp.), two prosauropods (*Pseudotetrasauropus* ichnosp.), two theropods (*Grallator* ichnosp. C), nine armored aetosaurus (*Brachychirotherium* ichnosp.), four therapsids, one indeterminate reptile (cf. *Apatopus*) and abundant lizard-like animals (*Rhynchosauroides* ichnosp.) (Fig. 3). Although the trackmaker of *Tetrasauropus* ichnosp. is controversial, the ichnotaxa can be attributed to the Sauropoda based on track morphology (Lockley *et al.*, 2001). *Neocalamites*-like plant impressions were reported from this site (Conrad *et al.*, 1987). Plant fossils of Lycopodiales, Isoetales, Equisetales including *Neocalamites*, Osmundaceae, Filicales, Bennettitales, Cycadales, Ginkgoales, Coniferales and Chlamydospermopsida are also known from the Upper Triassic system in the Colorado Plateau region (Kimura, 1993). These animal and plant fossils are listed in Table 2.

Diets of taxa from the Peacock Canyon area are inferred in Table 2. With respect to Late Triassic theropods' diet, Murry (1986) and Paul (1988) suggested that early theropods like *Coelophysis*

**Table 2** List of fossils from the Upper Triassic Chinle Group at Peacock Canyon site, New Mexico and their presumed food. Fish and phytoplankton are added as unconfirmed taxa for energy-flow model.

Tracks

| Taxa (Ichnotaxa) | Occurrence of individual numbers | Presumed food |
| --- | --- | --- |
| Sauropods (*Tetrasauropus* ichnosp.) | 31 | Plants |
| Prosauropods (*Pseudotetrasauropus* ichnosp.) | 2 | Plants |
| Armored aetosaurs (*Brachychirotherium* ichnosp.) | 9 | Plants |
| Therapsids (Therapsid track) | 4 | Plants |
| Indeterminate reptile (cf. *Apatopus*) | 1 | ? |
| Theropods (*Grallator* ichnosp. C) | 2 | Small terrestrial vertebrates, arthropods fish |
| Lizard-like animals (*Rhynchosauroides* ichnosp.) | ubiquitous | Arthropods |
| Insects (Trace fossil) | - | Plants |
| Carnivorous arthropods (Trace fossil) | - | Insects |

Other fossils

| Taxa | Occurrence of individual numbers | Presumed food |
| --- | --- | --- |
| Phytosaurs (teeth) | ? | Terrestrial vertebrates, fish |
| Plant impressions (?*Neocalamites*) | - | - |
| Root casts | - | - |
| Conchostracans | - | Phytoplankton |
| Coprolites | - | - |

Unconfirmed taxa

| Taxa | Presumed food |
| --- | --- |
| Fish | Conchostracans |
| Phytoplankton | - |

*bauri* preyed on large vertebrates like armored aetosaurs. However, they were too small to prey on armored aetosaurs and sauropods. Furthermore, stomach contents are known in a few specimens of *Coelophysis* and consist of relatively much smaller animals (Rowe and Gauthier, 1990). Therefore, we consider that they only preyed on small animals. Based on these diets, the structure of the food-web was inferred (Fig. 4). This site yields coprolites that include skeletal remains of fish. Therefore, fish and phytoplankton which were not preserved as fossils are added to the food-web model. Indeterminate reptiles were removed from the food-web because their diet can't be inferred.

Body weights of theropods were estimated as ca 7.4 kg based on that of *Coelophysis bauri* and mean
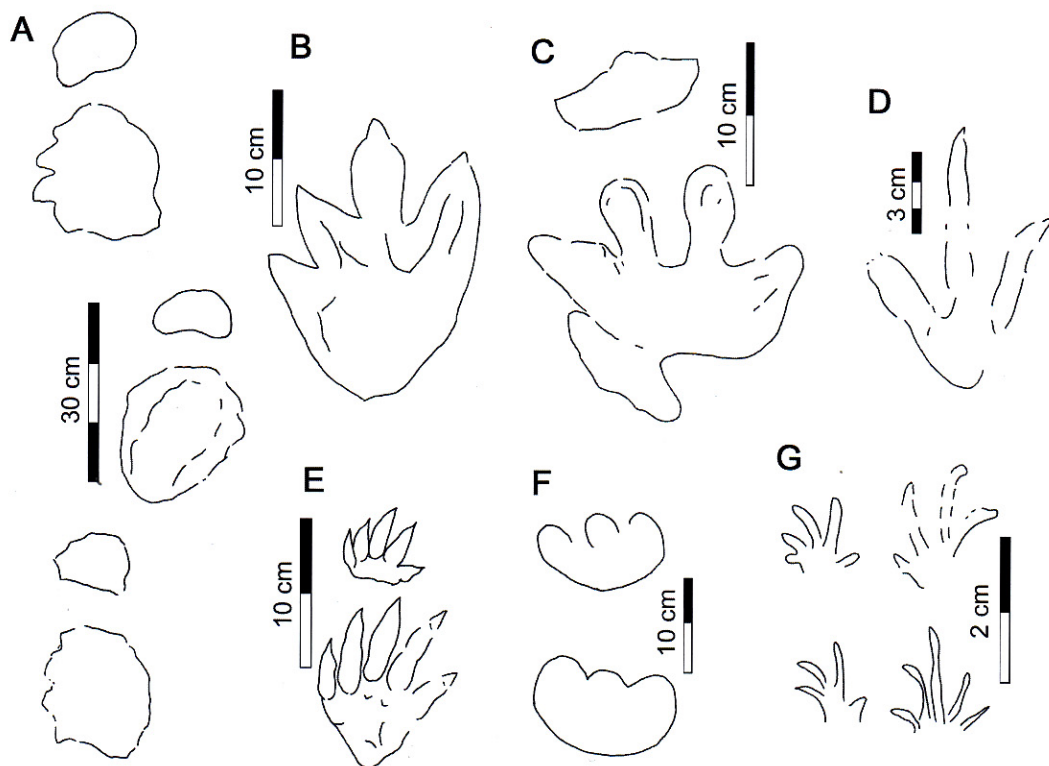
**Fig. 3** Tracks from the Upper Triassic Chinle Group at the Peacock Canyon site, New Mexico. (A) Trackway of
*Tetrasauropus* ichnosp. (B) *Pseudotetrasauropus* ichnosp. (C) *Brachychirotherium* ichnosp. (D) *Grallator* ichnosp. C.
(E) cf. *Apatopus.* (F) therapsid track. (G) *Rhynchosauroides* ichnosp.

value of track length of *Grallator* ichnosp. C. Body weights of other taxa were inferred based on the size of tracks. Estimated body weight and energy intake are shown in Table 3.

Triassic exposure around the Cimarron area extends about 90 km east and west and 20 km north and south, and covers $1.8 \times 10^3$ km$^2$ (Conrad *et al.*, 1987). For convenience, we assumed a geographic area size 10 times as large as the exposure area to make the inferred area as large as the Serengeti ecosystem in east Africa.

The Late Triassic was generally a time of distinctly seasonal precipitation called the "megamonsoon" in western North America (Dubiel *et al.*, 1991). Based on fossil flora, we compared the vegetation of Peacock Canyon area in the Late Triassic with a savannah-like environment with herbs and shrubs. Net primary productivity of the present savannah was estimated as 900 g/m$^2$/year (Whittaker, 1975), and the value was applied to an

analysis of the Chinle Group. The value was converted to ca $1.6 \times 10^4$ kJ/m$^2$/year because calorific transfer efficiency of plant dry matter is 17.8 kJ/g in modern terrestrial plants (Whittaker, 1975). Thus, actual rate of production by plants in the assumed area was estimated at ca $2.9 \times 10^{14}$ kJ/year by multiplying ca $1.6 \times 10^4$ kJ/m$^2$/year by the size of the area.

Herbivorous vertebrates consumed ca $7.2 \times 10^{13}$ kJ/year and herbivorous invertebrates ca $1.4 \times 10^{13}$ kJ/year from the production base of plants. Consumption efficiency (CE) of herbivorous vertebrates in grassland is 25% and that of herbivorous invertebrates is 5%. For each taxon, consumption by herbivorous vertebrates is based on the equality model (Table 4). For example, the ratio of therapsids is 0.21. Thus, therapsids required ca $1.5 \times 10^{13}$ kJ/year. The productivity of therapsids was estimated as ca $1.5 \times 10^{11}$ kJ/year by multiplying therapsids' intake ($1.5 \times 10^{13}$ kJ/year)

**1. Primary producer**  **2. Primary consumer**  **3. Secondary consumer**
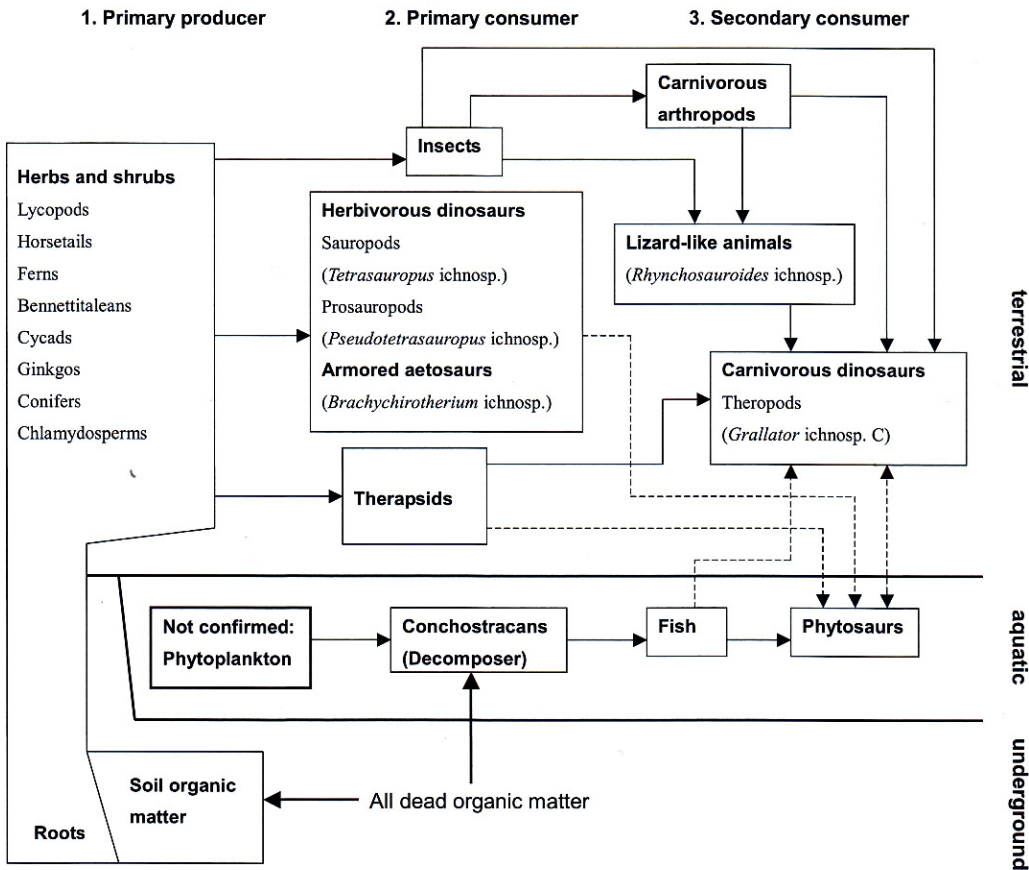


Fig. 4 Late Triassic food-web model at Peacock Canyon area, New Mexico based on taxa occurrences from the Chinle Group and unconfirmed taxa.

Table 3 Mean value of track length, hip length, body length, body weight, daily and annual energy intake and occurrence of individual numbers of terrestrial vertebrate taxa from the Upper Triassic Chinle Group at Peacock Canyon site, New Mexico.

| Taxa (Ichnotaxa) | Mean value of track length (cm) | Hip Height (cm) | Body length (cm) | Weight (kg) | Energy intake (kJ/day) | Energy intake (kJ/year) | Occurrence of individual numbers |
|---|---|---|---|---|---|---|---|
| Sauropods (*Tetrasauropus* ichnosp.) | 20.59 | 82.4 | 300-400 | 300 | $1.3 \times 10^4$ | $4.7 \times 10^6$ | 31 |
| Prosauropods (*Pseudotetrasauropus* ichnosp.) | 20.5 | 82.0 | 300-400 | 300 | $1.3 \times 10^4$ | $4.7 \times 10^6$ | 2 |
| Armored aetsaurs (*Brachychirotherium* ichnosp.) | 18.89 | 75.6 | 400 | 400 | $1.6 \times 10^4$ | $5.8 \times 10^6$ | 9 |
| Therapsids | 8.2 | 32.8 | 150 | 100 | $3.7 \times 10^4$ | $1.4 \times 10^7$ | 4 |
| Lizard-like animals (*Rhynchosauroides* ichnosp.) | 1.41 | 5.64 | 25 | 0.5 | $6.5 \times 10^1$ | $2.4 \times 10^4$ | ubiquitous |
| Theropods (*Grallator* ichnosp. C) | 9.0 | 36.0 | 150 | 7.4 | $7.4 \times 10^2$ | $2.7 \times 10^5$ | 2 |

**Table 4** Ratio intake of each taxon that consumes the same foodstuffs in the Chinle ecosystem.

| Foodstuffs | Consumers | Energy intake (kJ/day) (A) | Occurrence of indivdual numbers (B) | (A) x (B) | Ratio | Bases |
|---|---|---|---|---|---|---|
| Herbs and shrubs | Sauropods | $1.3 \times 10^4$ | 31 | $4.0 \times 10^5$ | 0.55 | Equality model |
| | Prosauropods | $1.3 \times 10^4$ | 2 | $2.6 \times 10^4$ | 0.04 | Equality model |
| | Armored aetosaurs | $1.6 \times 10^4$ | 9 | $1.4 \times 10^5$ | 0.20 | Equality model |
| | Therapsids | $3.7 \times 10^4$ | 4 | $1.5 \times 10^5$ | 0.21 | Equality model |
| Arthropods (insects) | Lizard-like animals | $6.5 \times 10^1$ | ubiquitous | - | 0.80 | No basis |
| | Theropods | $7.4 \times 10^2$ | 2 | $1.5 \times 10^3$ | 0.20 | No basis |

**Table 5** Estimated population size, population density per 1 km², head count ratio based on 31 head of sauropods, and occurrence of individual numbers of vertebrate taxa from the Upper Triassic Chinle Group at the Peacock Canyon site, New Mexico.

| Taxa (ichnotaxa) | Estimated population size | Population density per 1 km² | Head count ratio based on 31 heads of sauropods | Occurrence of individual numbers |
|---|---|---|---|---|
| Sauropods (*Tetrasauropus* ichnosp.) | $8.6 \times 10^6$ | $4.8 \times 10^2$ | $3.1 \times 10^1$ | 31 |
| Prosauropods (*Pseudotetrasauropus* ichnosp.) | $5.6 \times 10^5$ | $3.1 \times 10^1$ | $2.0 \times 10^0$ | 2 |
| Armored aetsaurs (*Brachychirotherium* ichnosp.) | $2.5 \times 10^6$ | $1.4 \times 10^2$ | $9.0 \times 10^0$ | 9 |
| Therapsids | $1.1 \times 10^6$ | $6.2 \times 10^1$ | $4.0 \times 10^0$ | 4 |
| Lizard-like animal (*Rhynchosauroides* ichnosp.) | $4.1 \times 10^6$ | $2.3 \times 10^2$ | $1.5 \times 10^1$ | ubiquitous |
| Theropods (*Grallator* ichnosp. C) | $2.9 \times 10^5$ | $1.6 \times 10^1$ | $1.1 \times 10^0$ | 2 |

Assumed terrestrial area: $1.8 \times 10^4$ km²
Estimated population size = total annual energy intake for a taxon / annual energy intake for an individual
Head count ratio = (Estimated population size × 31) / estimated population size of sauropods

and the assimilation efficiency (AE) (0.5) and production efficiency (PE) (0.02). The productivity is also used for theropod dinosaurs at higher trophic level. Because consumption efficiency (CE) of vertebrates feeding on herbivorous vertebrates is 0.5, theropods obtained ca $7.5 \times 10^{10}$ kJ/year by preying on therapsids. By the same calculations based on the food-web model, we can estimate total annual energy intake for each taxon. Moreover, population size and population density for each taxa are also calculated. Population density per 1 km² is shown as: sauropods ca $4.8 \times 10^2$, prosauropods ca $3.1 \times 10^1$, armored aetosaurs ca $1.4 \times 10^2$, therapsids ca $6.2 \times 10^1$, lizard-like ani- mals ca $2.3 \times 10^2$, and theropods $1.6 \times 10^1$ (Table 5). This estimated population size suggests the ratio of large vertebrates in the Chinle ecosystem (Fig. 5).

**The Moenave Formation (Lower Jurassic)**

Footprints of carnivorous dinosaurs, primitive crocodilians and small lizards, and fish scales of *Semionotus* sp., gastropods, ostracods, conchostracans and plant fossils occur from the Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm (SGDS), Utah. Concerning the terrestrial vertebrates, the following individual tracks can be estimated in the main site: five hun-
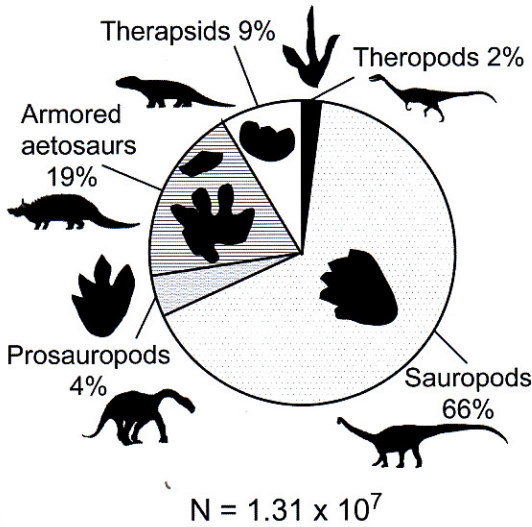
**Fig. 5** Late Triassic large terrestrial vertebrate census based on estimated population size at Peacock Canyon area, New Mexico.

dred fifty *Grallator* ichnosp. M. (small theropods), twenty three *Eubrontes* ichnosp. (large theropods), three hundred seventy five *Batrachopus* ichnosp.

(crocodilians), and a few lizard tracks. Based on these tracks, two hundred forty seven *Grallator* ichnosp. M trackways and four *Eubrontes* ichnosp. trackways were recognized. It is difficult to count the trackway numbers of *Batrachopus* ichnosp. because *Batrachopus* tracks are too small. Hence, one hundred individual numbers of crocodilians were tentatively used for energy-flow analysis. These fossils and their diets were shown in Table 6. There is no evidence of large herbivorous vertebrates from this site. Therefore, the structure of the food-web model shows that large and small theropods had preyed on only small animals including fish (Fig. 7). Insects (arthropods) and phytoplankton were added to the list and the food-web model based on numerous, as yet unidentified, invertebrate (arthropod) traces.

The body weight of small theropods was compared with that of an individual of *Coelophysis bauri* and modified based on mean value of track length of *Grallator* ichnosp. M. The body weight of large theropods was estimated based on that of an indi-
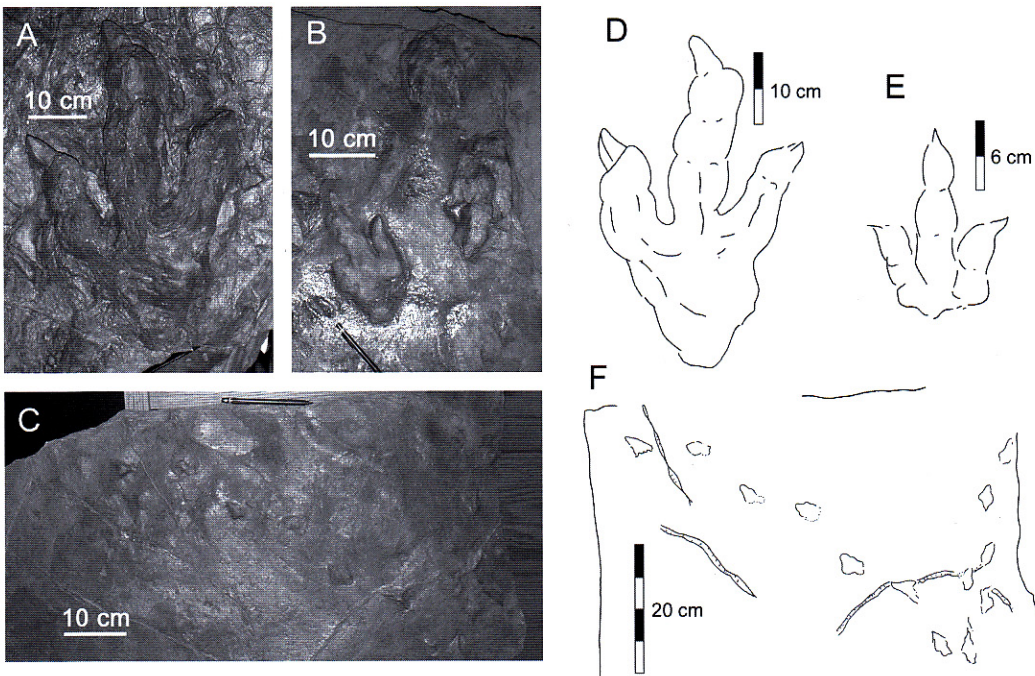


**Fig. 6** Tracks from the Lower Jurassic Moenave Formation at the SGDS, Utah. (A) and (D) *Eubrontes* ichnosp. (B) and (E) *Grallator* ichnosp. M. (C) and (F) Trackways of *Batrachopus* ichnosp.

**1. Primary producer          2. Primary consumer          3. Secondary consumer**



**Fig. 7** Early Jurassic food-web model at St. George area, Utah based on taxa occurrences from the Moenave Formation and unconfirmed taxa.

vidual of *Dilophosaurus wetherilli* (TMP 83.26.02) and mean value of track length of *Eubrontes* ichnosp. Body weight of crocodilians was inferred from their body size. Estimated body weight and energy intake for vertebrate taxa are shown in Table 7.

The Moenave Formation is restricted to northern Arizona and Southern Utah (Clark and Fastovsky, 1986). A geographic area size of $1.0 \times 10^4$ km$^2$ was assumed for energy-flow analysis.

The SGDS yields fossil plant fragments. Alternating beds of sandstone and mudstone reveal a fluvial and lucustrine system and intercalated caliche represents dry conditions. Therefore, the environment around the investigated area in the Early Jurassic was assumed to have rivers and lakes surrounded by semi-desert shrub. Mean net primary productivity of semi-desert shrub, or 90 g/m$^2$/year (Whittaker, 1975), was used to model energy-flow analysis.

The subsequent calculation process for energy-flow patterns is the same as that of the Chinle ecosystem. Here, the ratio of distributed energy is shown in Table 8. As a result, total annual energy intake for each taxa, population size, and population density are estimated. Namely, population density per 1 km$^2$ is shown as: small theropods ca $6.7 \times 10^{-2}$, large theropods ca $4.8 \times 10^{-4}$, crocodilians ca $2.7 \times 10^{-2}$, and small lizards ca $2.6 \times 10^1$ (Table 9). The ratio of large vertebrates is also estimated in Figure 8.

## DISCUSSION

### The Chinle Ecosystem (Late Triassic)

Energy-flow modeling on the Peacock Cayon site of the Chinle Group shows many individuals can exist in the assumed area: population density of herbivorous vertebrates per 1 km$^2$ could reach 700 (Table 5). By comparison, population density of herbivorous vertebrates in the Serengeti ecosys-

**Table 6** List of fossils from the Lower Jurassic Moenave Formation at the SGDS, Utah and their presumed food. Phytoplankton is added as unconfirmed taxa for energy-flow model.

Tracks

| Taxa (Ichnotaxa) | Occurrence of individual numbers | Presumed food |
|---|---|---|
| Small theropods (*Grallator* ichnosp. M) | 247 | Arthropods, small lizards, crocodilians, fish |
| Large theropods (*Eubrontes* ichnosp.) | 4 | Small lizards, crocodilians, small theropods, fish |
| Crocodilians (*Batrachopus* ichnosp.) | 100 | Arthropods, small lizards |
| Small lizards | - | Arthropods |

Other fossils

| Taxa | Occurrence of individual numbers | Presumed food |
|---|---|---|
| *Semionotus* sp. (Fish scales) | - | Gastropods, ostracods, conchostracans |
| Gastropods | - | Phytoplankton |
| Insects (trace fossil) | - | Plants |
| Carnivorous arthropods (trace fossil) | - | Insects |
| Ostracods | - | Phytoplankton |
| Conchostracans | - | Phytoplankton |
| woods | - | - |

Unconfirmed taxa

| Taxa | Presumed food |
|---|---|
| Phytoplankton | - |

tem in Tanzania and Kenya today is 140 per 1 km$^2$ (Houston, 1979). NPP of the savannah environment in the Serengeti ecosystem, which is categorized as a grazing ecosystem, is 1.1 x 10$^4$ kJ/m$^2$/year (Frank *et al.*, 1998). Although the value is less than the NPP applied to the Chinle ecosystem, or 1.6 x 10$^4$ kJ/m$^2$/year, population density of the Chinle fauna in the study area was evidently much larger than that of the Serengeti ecosystem. In this study, early dinosaurs and reptiles are considered as ectothermal animals, and their energy intakes are estimated as less than those of mammals of similar body weights. The

difference between modern and Late Triassic population density of vertebrate taxa is probably due to differences in the metabolic rate between these animals.

The results of the energy-flow analysis provide the information regarding possible energy and animal's population size for each trophic level in the assumed area. Therefore, the proportion of animals that belong to different trophic levels may be different between censuses based on estimated population size and actual fossil data. Thus, it is important to discuss whether the difference is significant. Late Triassic terrestrial vertebrate propor-

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**Table 7** Mean value of track length, hip height, body length, body weight, daily and annual energy intake and occurrence of individual numbers of vertebrate taxa from the Lower Jurassic Moenave Formation at the SGDS, Utah.

| Taxa (Ichnotaxa) | Mean value of track length (cm) | Hip Height (cm) | Body length (cm) | Weight (kg) | Energy intake (kJ/day) | Energy intake (kJ/year) | Occurrence of individual numbers |
|---|---|---|---|---|---|---|---|
| Small theropods (*Grallator* ichnosp. M) | 17.1 | 68.6 | 250 | 50 | $3.1 \times 10^3$ | $2.7 \times 10^5$ | 247 |
| Large theropods (*Eubrontes* ichnosp.) | 32.2 | 128.9 | 600 | 330 | $1.3 \times 10^4$ | $1.1 \times 10^6$ | 4 |
| Crocodilians (*Batrachopus* ichnosp.) | 4.3 | 17.0 | 100 | 4.0 | $3.1 \times 10^2$ | $2.7 \times 10^4$ | 100 |
| Small lizards | - | - | 25 | 0.5 | $6.5 \times 10^1$ | $5.7 \times 10^3$ | - |

**Table 8** Ratio of each taxon's intake which consumes same foodstuffs in the Moenave ecosystem.

| Foodstuffs | Consumers | Energy intake (kJ/day) (A) | Occurrence of indivudual numbers (B) | (A) x (B) | Ratio | Bases |
|---|---|---|---|---|---|---|
| Insects, arthropods | Small lizards | $6.5 \times 10^1$ | - | - | 0.900 | No basis |
| | Crocodilians | $3.1 \times 10^2$ | 100 | $3.1 \times 10^4$ | 0.004 | Equality model |
| | Small theropods | $3.1 \times 10^3$ | 247 | $7.7 \times 10^5$ | 0.096 | Equality model |
| Small lizards | Crocodilians | $3.1 \times 10^2$ | 100 | $3.1 \times 10^4$ | 0.04 | No basis |
| | Small theropods | $3.1 \times 10^3$ | 247 | $7.7 \times 10^5$ | 0.90 | Equality model |
| | Large theropods | $1.3 \times 10^4$ | 4 | $5.2 \times 10^4$ | 0.06 | Equality model |
| Crocodilians | Small theropods | $3.1 \times 10^3$ | 247 | $7.7 \times 10^5$ | 0.94 | Equality model |
| | Large theropods | $1.3 \times 10^4$ | 4 | $5.2 \times 10^4$ | 0.06 | Equality model |

**Table 9** Estimated population size, population density per 1 km², head count ratio based on 4 head of large theropods, and occurrence of individual numbers of vertebrate taxa from the Lower Jurassic Moenave Formation at the SGDS, Utah.

| Taxa (Ichnotaxa) | Estimated population size | Population density per 1 km² | Head count ratio based on 4 heads of large theropods | Occurrence of individual numbers |
|---|---|---|---|---|
| Small theropods (*Grallator* ichnosp. M) | $6.7 \times 10^2$ | $6.7 \times 10^{-2}$ | $5.5 \times 10^2$ | 247 |
| Large theropods (*Eubrontes* ichnosp.) | $4.8 \times 10^1$ | $4.8 \times 10^{-3}$ | $4.0 \times 10^0$ | 4 |
| Crocodilians (*Batrachopus* ichnosp.) | $2.7 \times 10^2$ | $2.7 \times 10^{-2}$ | $2.2 \times 10^2$ | 100 |
| Small lizards | $2.6 \times 10^5$ | $2.6 \times 10^1$ | $2.1 \times 10^5$ | - |

Assumed terrestrial area: $1.0 \times 10^4$ km²
Estimated population size = total annual energy intake for a taxon / annual energy intake for an individual
Head count ratio = (Estimated population size × 4) / estimated population size of large theropods

tions based on estimated population size are almost the same as those based on occurrence of individual numbers (Table 5). This means that ichnotaxa censuses are probably accurate representations of ancient animal censuses. Therefore, energy-flow models become useful tools to evalu-
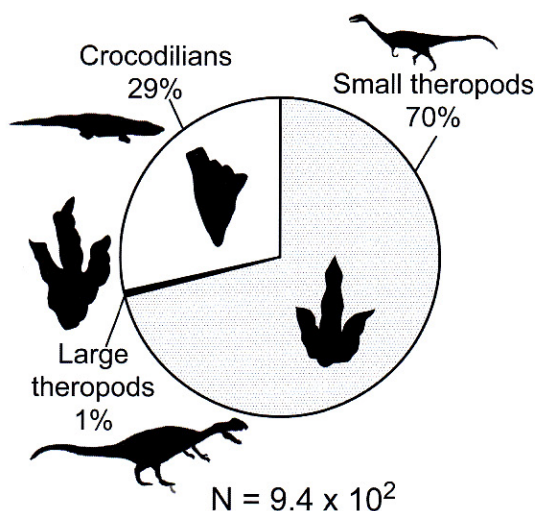
**Fig. 8** Early Jurassic terrestrial vertebrate census based on estimated population size, St. George area, Utah.

ate the degree of fossil assemblage preservation between fossil taxa which belong to different trophic levels.

### The Moenave Ecosystem (Early Jurassic)

The St. George Dinosaur Discovery Site at Johnson Farm (the investigated area of the Moenave Formation) yields no footprints or skeletal remains of herbivorous vertebrates. Thus, the inferred food-web model shows that carnivorous vertebrates likely lived on small animals like insects and small lizards (Fig. 7). Therefore, possible carnivorous vertebrate numbers (mostly theropods) were estimated at much lower numbers than those of the Late Triassic Chinle ecosystem, although NPP of the Moenave Formation is inferred as less than that of the Chinle ecosystem. In this study, the interaction between terrestrial and aquatic energy-flow is ignored. However, at the St. George site, the field evidence suggests that carnivores may have fed on fish (Kirkland and Milner, 2005b). Lockley and Hunt (1995) also suggested that theropods may have fed on aquatic crustaceans. Therefore, actual population size of the Moenave ecosystem may have been larger than that estimated by the energy-flow model because of feeding on aquatic animals. Even so, aquatic

area size (rivers and lakes) was normally less than terrestrial area size, and carnivores ought mostly to have crowded around the rivers and lakes. Therefore, considering the large assumed area size (in this study $1.0 \times 10^4 \ km^2$), averaged population density of the Moenave ecosystem was inferred as smaller than the Chinle ecosystem where herbivorous vertebrates existed.

### The Faunal Change across the Triassic-Jurassic Boundary

There were many kinds of large vertebrates in the Late Triassic Chinle ecosystem at Peacock Canyon including dinosaurs, aetosaurs, and therapsids (Table 5; Fig. 5). In the beginning of the Early Jurassic, the results of this study also show that the Early Jurassic terrestrial vertebrate fauna at the St. George site was mostly occupied only by carnivorous dinosaurs (Table 9; Fig. 8). The pattern was mostly global. Furthermore, diversity indices for the Early Jurassic Moenave ecosystem are lower than those for the Late Triassic Chinle ecosystem (Table 10). To sum up the above description, the highly diverse reptile fauna in the Late Triassic is interpreted to have changed to the low diversity fauna dominated by dinosaurs. This consideration is consistent with the evidence from the track assemblages (Lockley and Hunt, 1995).

Energy-flow through the food-web is illustrated by the ecological pyramid. In this study, pyramids of energy were calculated based on the productivities of each trophic level (Fig. 9). The pyramid for the Chinle ecosystem is a convex-up form, and it is the typical shape of an ecological pyramid. However, the shape of the ecological pyramid for the Moenave ecosystem is somewhat different: there were no herbivorous vertebrates. This means that the ecological niche of herbivorous vertebrates was empty, and the population size of carnivorous vertebrates was probably smaller size. In the Lower Jurassic Wingate, Moenave, and Kayenta deposits, fossil footprint assemblages are dominated by bipedal theropods (Lockley and Hunt, 1995), and the investigated area was no the exception. It can be inferred that there was an unusual ecosystem

**Table 10** Diversity indices of terrestrial large vertebrate assemblages of the Chinle and Moenave ecosystems based on estimated population size and biomass. Biomass: estimated population size x body weight. Shannon diversity indices (H) = -Σ Pi lnPi where Pi is the proportional abundance of the i th species. Equitability (J) = H/lnS, where S is the total number of species in the community.

| | Species richness (S) | Shannon diversity index (H) | | Equitability (J) | |
|---|---|---|---|---|---|
| | | Estimated population size | Biomass | Estimated population size | Biomass |
| Chinle ecosystem | 5 | 1.02 | 0.86 | 0.57 | 0.48 |
| Moenave ecosystem | 3 | 0.63 | 0.31 | 0.57 | 0.28 |

where herbivorous vertebrates were rare in this place and time. Low diversity indices are generally interpreted as indicative of an ecosystem that exist under physically or chemically stressed conditions (Odum, 1983). Thus, the decline in biodiversity in the Early Jurassic ecosystem suggests a stressed ecosystem without herbivorous vertebrates and a dominantly arid climate.
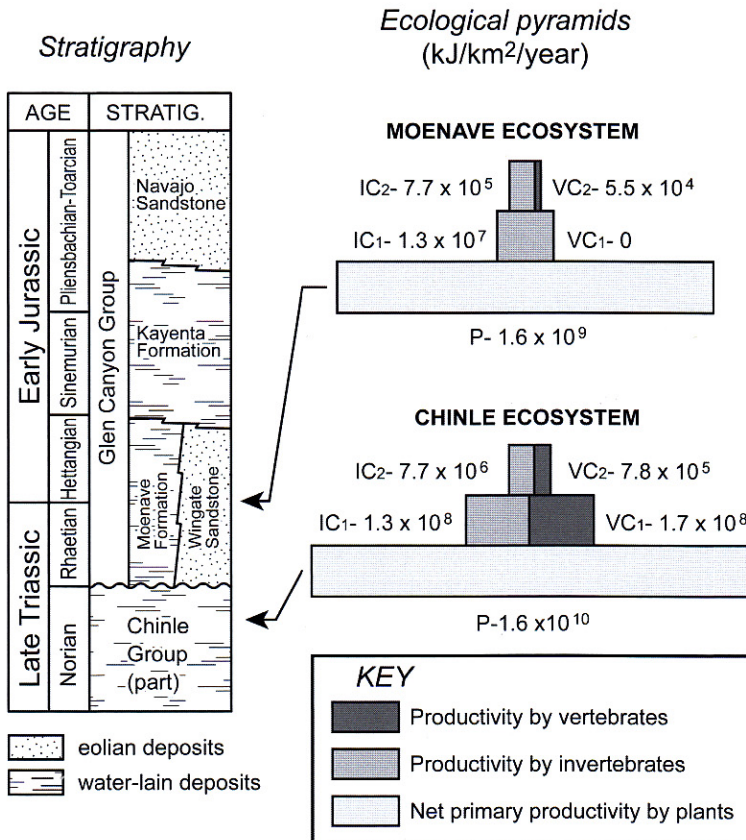


**Fig. 9** Ecological pyramids of the Chinle and Moenave ecosystem based on productivities of each trophic level. P: producer, $IC_1$: invertebrate primary consumer, $IC_2$: invertebrate secondary consumer, $VC_1$: vertebrate primary consumer, $VC_2$: vertebrate secondary consumer. Stratigraphy based on Lucas *et al.* (2005a, b).

## Significance and Problems of the Energy-Flow Model

As discussed by Matsukawa *et al.* (2006), the most important significance of paleoecosystem reconstruction using energy-flow is that we can infer the absolute abundances of ancient animals which are never estimated by only counting the fossil numbers, and compare every paleoecosystem using the same methods. We can also evaluate changing paleoecosytem, species composition, and infer some processes of evolution. Besides, energy-flow models may enable us to evaluate the degree of fossil preservation as mentioned above.

On the other hand, some problems were also suggested by Matsukawa *et al.* (2006). For example, fossil data does not provide all animal data for the paleoecosystem, and fossil communities constitute time averaged assemblages. To predict energy-flow pattern, an equality model isn't necessarily applicable because animals have food preferences (Farlow, 1980; Begon *et al.*, 1996), and the changes in the animals' body size during life is ignored. In addition, animal populations are restricted by other factors such as intraspecific and interspecific competition, and density dependent effects (Begon *et al.*, 1996). Although these problems were not addressed in this study, they should be considered as limiting factors in the analyses because to solve the problems is very difficult or impossible. Therefore, we should acknowledge that the results of energy-flow analyses may include some errors caused by the above problems.

## CONCLUSIONS

In the Colorado Plateau region, western United States, nonmarine deposits throughout the age of dinosaurs are widely distributed. For the paleoecosytem reconstruction, the Upper Triassic Chinle Group at the Peacock Canyon track site, New Mexico, and the mainly Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, Utah were investigated. The Peacock Canyon track site yields footprints of primitive sauropods, prosauropods, theropods, aetosaurs, therapsids, and small lizards. Footprints of abundant carnivorous dinosaurs, primitive crocodilians, small lizards and other terrestrial vertebrates occur from the St. George Dinosaur Discovery Site at Johnson Farm. We tried to reconstruct two paleoecosystems based on food-web and energy-flow modeling. As a result, the following approaches and conclusions are suggested:

(1) Energy-flow of paleoecosystems in the early age of dinosaurs can be represented, and population sizes of ancient animals were estimated using quantification models.

(2) Population density of vertebrate assemblages in the Chinle ecosystem was calculated to be much larger than that of animals in the Serengeti ecosystem today. The difference was likely caused by the different metabolic strategies between ancient mostly reptilian taxa and modern mammalian vertebrate taxa in the respective ecosystems.

(3) Population density of animals living in the Moenave ecosystem was extremely low. This was caused by an unusual food-web that lacked herbivorous vertebrates in addition to relatively small net primary productivity (NPP).

(4) Ecological replacement of vertebrate faunas and change in biodiversity patterns around the Triassic-Jurassic boundary were modeled by energy-flow and estimated population size. A high diversity terrestrial reptile community in the Late Triassic was succeeded by a low diversity dinosaur community in the early Early Jurassic.

(5) Low diversity indices of the Early Jurassic ecosystem suggest that it was an ecologically stressed community under an arid climatic regime.

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## POSTSCRIPT

Recently, the plant-eating dinosaur tracks (*Anomoepus* ichnosp.) were discovered at the St. George Dinosaur Discovery Site at Johnson Farm in 2005 (Milner and Lockley, 2006). This suggests that the food-web structure of the Early Jurassic ecosystem in the St. George area might be natural as an ecological niche for herbivorous vertebrates was occupied. Therefore, actual population size of the carnivorous dinosaurs in the Early Jurassic St. George ecosystem might be larger than that estimated because of feeding on the herbivorous dinosaurs. However, the number of the plant-eating dinosaur tracks is quite a few (Milner, personal communication, 2006). Therefore, a low diverse, carnivore dominant, unusual ecosystem might have existed in the Early Jurassic St. George area as discussed in this paper.