Journal of Human Evolution 92 (2016) 91–100

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Life history, cognition and the evolution of complex foraging niches

Caroline Schuppli[*, 1], Sereina M. Graber [1], Karin Isler, Carel P. van Schaik

Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

ARTICLE INFO

Article history:
Received 30 July 2014
Accepted 12 November 2015
Available online 24 February 2016

Keywords:
Niche complexity
Skill learning
Food processing
Development
Provisioning
Brain size

ABSTRACT

Animal species that live in complex foraging niches have, in general, improved access to energy-rich and seasonally stable food sources. Because human food procurement is uniquely complex, we ask here which conditions may have allowed species to evolve into such complex foraging niches, and also how niche complexity is related to relative brain size. To do so, we divided niche complexity into a knowledge-learning and a motor-learning dimension. Using a sample of 78 primate and 65 carnivoran species, we found that two life-history features are consistently correlated with complex niches: slow, conservative development or provisioning of offspring over extended periods of time. Both act to buffer low energy yields during periods of learning, and may thus act as limiting factors for the evolution of complex niches. Our results further showed that the knowledge and motor dimensions of niche complexity were correlated with pace of development in primates only, and with the length of provisioning in only carnivorans. Accordingly, in primates, but not carnivorans, living in a complex foraging niche requires enhanced cognitive abilities, i.e., a large brain. The patterns in these two groups of mammals show that selection favors evolution into complex niches (in either the knowledge or motor dimension) in species that either develop more slowly or provision their young for an extended period of time. These findings help to explain how humans constructed by far the most complex niche: our ancestors managed to combine slow development (as in other primates) with systematic provisioning of immatures and even adults (as in carnivorans). This study also provides strong support for the importance of ecological factors in brain size evolution.

1. Introduction

There is extensive variation in the foraging niches different mammal species occupy. Whereas some foraging niches seem to be simple because they involve no pre-ingestive processing (e.g., those occupied by grazing ungulates), others appear to be more complex, because obtaining access to food requires multiple processing steps, executed in the correct order and timed properly (as occupied by many primates [e.g., Gibson, 1986; Byrne et al., 1993; Gunst et al., 2010]). Living in a complex foraging niche may bring palpable fitness benefits (Gibson, 1986). First, foods that require a high level of processing, such as underground storage organs, insects or other animal prey consistently show a high nutritive content. Second, because extracted foods are often available year-round, species able to exploit them can live in seasonal environments in which they would otherwise experience a lean season. Understanding the evolution of complex niches is important for human evolution because, unique among primates, human hunter-gatherers (as models for ancestral humans), and indeed humans in general, rely on highly complex forms of extractive foraging and hunting, and so manage to maintain a relatively stable energy intake in a great variety of different environments (Leonard and Robertson, 1997; Kaplan et al., 2000; Berbesque et al., 2014).

So far, no study has systematically examined the factors that allow species to evolve into such complex foraging niches. Occupying a complex foraging niche will generally require lengthy periods of learning, during which failure is common and net yields are low. Since these learning periods are costly we expect them to be connected to life history features that counterbalance these costs. Indeed, we recently found that species with a late age at skill competence (the age at which adult-level skill levels are attained) are those that show one of two enabling factors: post-weaning provisioning or slow, conservative development (Schuppli et al.,

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[*] Corresponding author.
E-mail addresses: caroline.schuppli@aim.uzh.ch (C. Schuppli), sereina.graber@uzh.ch (S.M. Graber), karin.isler@biol.uzh.ch (K. Isler), vschaik@aim.uzh.ch (C.P. van Schaik).

[1] Both authors contributed equally to the manuscript.

http://dx.doi.org/10.1016/j.jhevol.2015.11.007

2012). Both factors work as an energetic buffer against failures during periods of learning and therefore allow the learning period to be extended (Fig. 1). We also found evidence that species with complex foraging niches (with complexity defined as the level of processing required) reach adult-level feeding skills later in development than those that live in simpler niches (Schuppli et al., 2012).

In this paper, we ask whether foraging-niche complexity coevolved with long periods of learning or provisioning and with brain size. Such a three-way relationship has often been suggested by anthropologists, who proposed that slowly developing species do so because they need time to learn skills essential to sustain reproduction (Janson and van Schaik, 1993). A recent study in which this was quantified, however, showed that the time needed to learn these skills limited the duration of development only in a subset of species, including humans (Schuppli et al., 2012), and that the most widespread limiting factor is a tradeoff between energy allocation to needs of a growing body and a growing and differentiating brain. As a result, larger-brained species develop more slowly (Isler and van Schaik, 2009; Barton and Capellini, 2011) and thus reach maturity at a later age, which is compensated for by their improved adult survival (Isler and van Schaik, 2009; Gonzalez-Lagos et al., 2010). In humans, this tradeoff is responsible for our highly delayed maturation and the adolescent growth spurt (Kuzawa et al., 2014), although in humans adult-level skills are reached even later (Kaplan et al., 2000).

Nonetheless, there are good reasons to assume there is a link between niche complexity and brain size. First, larger brains are found in species with higher overall diet quality (Fish and Lockwood, 2003) or those that engage in extensive extractive foraging or tool use (Byrne, 1997; Reader and Laland, 2002; Barton, 2012). Second, larger brains are found in species that can maintain a high and stable energy intake all year round (van Woerden et al., 2010, 2012, 2014), often as a result of extractive foraging techniques (Gibson, 1986) or perhaps because of the ability to locate ephemeral food sources (Milton, 1988). This same argument has also been applied to human evolution. It has repeatedly been suggested that the need to invent complex foraging techniques in an increasingly seasonal habitat was a driving force in the evolution of human intelligence (e.g., Parker and Gibson, 1977; Byrne, 1997; Anton et al., 2014). However, so far only very few studies have looked at the relation between brain size and niche complexity, and the ones that have focused on a few taxa only and produced inconsistent results (Parker and Gibson, 1977; Milton, 1981; Gibson, 1986; Walker et al., 2006).

Here, we first examine whether the two factors that allow for extended periods of learning during development (slow development and post-weaning provisioning) are also a prerequisite for evolving into a more complex foraging niche (Fig. 1). Focusing on the direct link between niche complexity and provisioning and pace of development allows us to include a much broader sample of species than in the previous study (Schuppli et al., 2012) where limited data on age of skill competence led to small sample size. Second, in order to attain a better understanding of the cognitive aspect of niche complexity, we examine how different aspects of niche complexity relate to brain size. If we find a relationship between foraging-niche complexity and relative brain size across different species, this may help to explain why species with complex foraging niches are relatively rare and why humans occupy by far the most complex niche.

A key decision in a study of foraging-niche complexity is how to define complexity. Previous studies have ranked the skill requirements of different food types and consistently classified leaves and grasses as less skill intensive than items, such as fruit, that require some kind of manipulation with hands or coordinated movements involving both hands and parts of the mouth (teeth, lips). The ingestion of embedded food items, such as nuts, which require more processing steps is generally considered to require more complex skills (Dittus, 1977; Kaplan et al., 2000; Johnson and Bock, 2004). All these studies thus used the amount of processing with hands or hands and mouth required as a measure of complexity, such that items that need few or no processing steps are rated as less skill-intensive than items that require a feeding technique composed of several steps of processing. Other studies have classified specific elements of the diet or certain processing techniques, such as tool use, extractive foraging or cooperative hunting, as complex since they are based on knowledge and their efficiency improves with causal understanding (Holekamp et al., 1997; Gurven et al., 2006; Lonsdorf, 2006; Gunst et al., 2010).

The patterns found in these studies suggest that ecological niche complexity can be divided into two broad dimensions: knowledge and motor complexity. Knowledge-niche complexity comprises knowing what to eat, where to look for it (which is not always obvious with embedded foods), which processing techniques to use, and how to integrate these techniques into an ordered sequence (cf. Barton, 2012). Since acquiring the requisite knowledge and understanding requires a learning period, we expect to find that species inhabiting complex knowledge niches show a long period of provisioning and/or a slow development. Motor-niche complexity, in contrast, encompasses the motor patterns involved

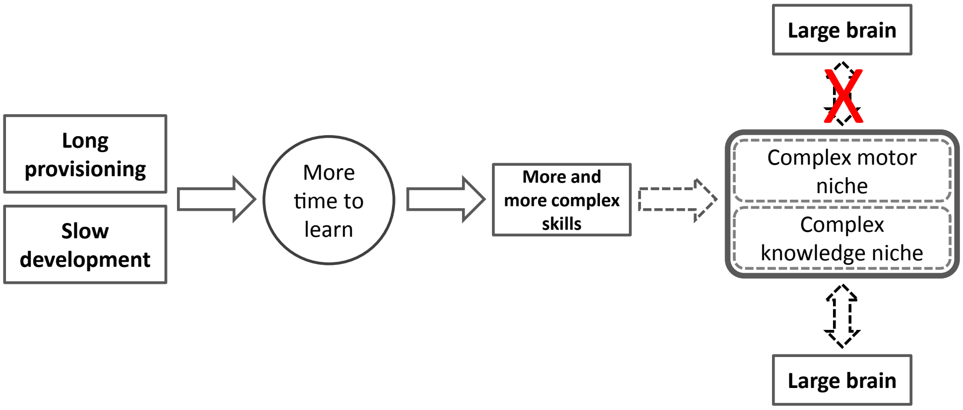

Figure 1. Slow development and extended provisioning have been shown to allow for extended periods of learning (later relative age at skill competence [Schuppli at al., 2012]). Here we ask in Part I whether the same two factors ultimately allow species to evolve into more complex niches. In Part II we are interested in how niche complexity relates to relative brain size and expect only the knowledge niche, but not necessarily the motor niche, component to be associated with large relative brain size.