A Life Table for *Psittacosaurus lujiatunensis*: Initial Insights Into Ornithischian Dinosaur Population Biology

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ABSTRACT
Very little is known about nonavian dinosaur population biology. Multi-individual sampling and longevity estimation using growth line counts can be used to construct life tables—the foundation for population analyses in ecology. Here we have determined the size and age distribution for a sample consisting of 80 individuals of the small ornithischian, *Psittacosaurus lujiatunensis* from the early Cretaceous Yixian Formation of China. Their ages ranged from less than a year to eleven years and the distribution was strongly right-skewed. This is consistent with taphonomic interpretations that these animals derive from a catastrophic death assemblage. The static life table analysis revealed the same general pattern of survivorship as tyrannosaurs including increased attrition before the attainment of full adult size. This may reflect increased physiological demands and/or predation exposure associated with reproduction. Collectively these findings suggest that most nonavian dinosaurs may have had a similar life history strategy. Anat Rec, 292:1514–1521, 2009. © 2009 Wiley-Liss, Inc.

Key words: life history; survivorship; growth rates; growth curve; reproduction

INTRODUCTION

The field of population biology was revolutionized in the 1930s and 40s with the application of actuary tables derived from the insurance industry to infer population dynamics—the balance between mortality rates and attrition that creates the demography of a population (Pearl and Miner, 1935; Deevey, 1947). Life tables, as they are referred to in ecology, serve as a foundation from which one can study influences on population structure such as predation, accidents, disease, growth rates, resources, number of progeny, and reproductive age. Commonly observed patterns in bivariate plots of survivorship against age are known as Deevey Types in honor of the ecologist who popularized their usage, and are used today for heuristic purposes to describe age-related patterns in stable populations (Ebert, 1999;

Fig. 1). Deevey Type I survivorship shows a convex pattern characterized by negligible attrition throughout the majority of ontogeny, with massive die-offs occurring following the onset of old age. This pattern is seen only in humans from developed countries, and captive
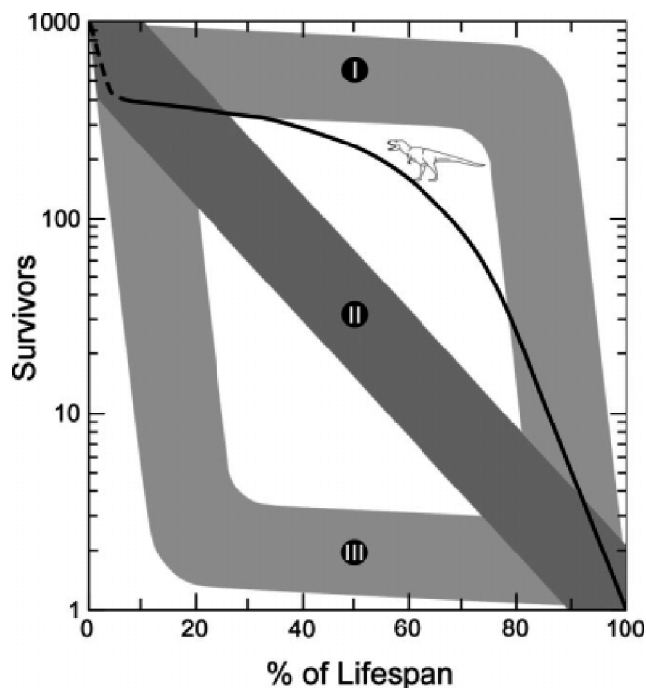
Fig. 1. Hypothetical ecological extremes used to characterize and contrast log-survivorship patterns among human and animal populations. The convex Type I pattern shows relatively low initial mortality followed by massive, senescence-driven die-offs as maximal lifespan is approached. The diagonal, Type II pattern occurs in animals whose mortality is relatively constant throughout life. Populations with the concave, Type III pattern experience high early attrition, with the few survivors that reach a threshold size standing to experience low mortality and reach maximal lifespan. The sigmoidal, Type B_1 pattern (represented by *Albertosaurus*; data from Erickson et al., 2006) shows high initial mortality rates, subsequent lower mortality, and increased attrition before extinction of the cohort.

animals where there is access to medical care, predation pressures are negligible, resources are unlimited, and numbers of offspring are low. Type II survivorship shows a diagonal pattern in which mortality is equally likely throughout life. This is a common pattern seen in wild populations of small reptiles, mammals, and birds that do not reach sizes at which predation pressures subside appreciably. Numbers of offspring are typically moderate. Type III survivorship shows a concave pattern, where extremely high juvenile attrition subsides once a threshold size is reached at which predation pressure decreases. The few survivors stand to have a long reproductive lifespan and numbers of offspring tend to be moderate to large. This pattern is characteristic of wild populations of large reptiles such as tortoises and crocodilians. Another common pattern that is seen in wild populations of large mammals and birds, as well as large tyrannosaurs (Erickson et al., 2006), shows characteristics of both Deevey Types I and III. This composite pattern was designated Type B_1 by its discoverers, Pearl and Miner (1935). High attrition in young individuals gives way to lower stabilized values once a threshold size is obtained; however, later in ontogeny mortality rates increase (typically from the effects of senescence) leading to the extinction of the cohort. Increases in mor-

tality that occur in middle-life often correspond with the onset of sexual maturity and breeding competition rather than senescence (e.g., Spinage, 1972; Flowerdue, 1987; Newton, 1989; Estes, 1991; Erickson et. al., 2006).

In practice, life table construction requires a large, random sample from a stable population (neither increasing nor decreasing in size) for which the age of the individuals can be ascertained. These simple requirements have limited the application of life tables to just a few fossil taxa (mainly humans and Cenozoic mammals: Kurten, 1953; Voorhies, 1969; Clark and Guensburg, 1970; Wolpoff and Caspar, 2006) owing to difficulties in establishing individual ages and lack of adequate sample sizes. For nonavian dinosaurs, means to determine longevity is no longer an obstacle. The use of growth line counts such as those used in the aging of extant reptiles and amphibians was firmly established in the early 1990s (Chinsamy-Turan, 2005; Erickson 2005). However, use of these data to construct life tables was precluded by insufficient intraspecific sampling. Few nonavian dinosaurs are known from more than one or a few specimens (Wang and Dodson, 2006), either because of their rarity as fossils or collection practices with a taxonomic emphasis favoring collection of single representative specimens over redundant same-species sampling (Erickson, 1999).

We were recently afforded the opportunity to study the age distribution for a large sample (N = 80) of the basal ceratopsian dinosaur *Psittacosaurus lujiatunensis* that is suitable for life table analysis. The animals derive from the Lujiatun Bed of the Lower Cretaceous Yixian Formation, Liaoning Province of China (He et al., 2006). They appear to have perished simultaneously in a volcanic mudflow (lahar; He et al., 2006) that trapped individuals irrespective of size (Fig. 2). Consequently, representatives throughout development were preserved, and presumably in proportions equivalent to the population's age structure. (The skewedness to the distribution is consistent with this assumption [see results].) These specimens provided the unique possibility to explore variation in life history patterns among nonavian dinosaurs by contrasting survivorship patterns for *P. lujiatunensis* with those in North American tyrannosaurs (Erickson et al., 2006), the only other nonavian dinosaurs for which life tables have been rigorously reconstructed. (Lehman [2007] studied the population biology of the ceratopsian *Chasmosaurus mariscalaensis* from skeletal material, and Lockley [1994] that of sauropods from trackways. Neither definitively established specimen longevity or met assumptions for life table construction.) Because these dinosaurs differ substantially with regard to phylogeny (Ornithischia versus Saurischia), maximum size [37 kg versus 5,600 kg (*Tyrannosaurus*; Erickson et al., 2004)], trophic ecology [herbivorous versus carnivorous] and presumably other life history related parameters (e.g., longevity, growth rates, developmental timing, neonate and clutch size, predation pressure, behavior, etc.), it seemed likely that this comparison would reveal differences in life history pattern among nonavian dinosaurs, should they exist. Explicit questions we sought to address with the *P. lujiatunensis* life table and growth curve include: (1) What was the age structure, growth pattern, and lifespan for this taxon? (2) Did it show Type B_1 survivorship, like tyrannosaurs and most comparable-sized birds (avian dinosaurs) and mammals? (3)

Fig. 2. Typical fossils of *Psittacosaurus lujiatunensis* from the Lujia-
tun Ash Bed. Two individuals (LPM R00137) are shown (a large animal
and a smaller individual in the lower left quadrant) showing the tightly
aggregated nature of the lahar-trapped dinosaurs, the disparity in
sizes among individuals, and the excellent state of their preservation.

What were the reproductive dynamics (e.g., age at sex-
ual maturity, reproductive lifespan and population size,
generation time, etc.) for this taxon?

MATERIALS AND METHODS

A growing body of literature and unprecedented access
to sampling of specimens in our care provided data for
80 articulated, and mostly matrix-embedded specimens
of *P. lujiatunensis* from the Lujiatun bed (He et al.,
2006) (Table 1). We are aware that many more speci-
mens of this taxon from the Lujiatun Bed exist, but
these are either uncataloged, exist in private collections,
or represent composite skeletons, rendering them unus-
able for our purposes. Most Lujiatun specimens have
been purchased from local farmers and collectors whose
collection practices, specimen documentation, and com-
mercial filtering are not recorded. Thus it is unavoidable
that artificial biases may have altered the natural
demography of our sample. Nevertheless, because the
age-size distribution strongly conforms to expectations
for a natural, randomly sampled catastrophic population
assemblage (see results) we are confident that such
biases, if present did not affect the overall biological
inferences made here. Finally, in our analysis we
included specimens of *P. major* (JZMP V11, LHPV1; see
Table 1) that were presumably exhumed from the same
region and same or similar lahar beds. The holotype and
referred specimens of this taxon are exclusively large

**TABLE 1. Specimen numbers, sizes, and
longevity estimates**

Specimen number	Femoral length (mm) (s)	Age (est.) years
IVPP 14155	31	<1[a]
D2156 (N = 34)	31	<1
IVPP 12704	30	<1
PKUVP V1058 (N = 2)	30	<1[a]
LPM R00142 (N = 4)	34	1[a]
IVPP V14341	53	1
IVPP V12704	48	1
LPM R00137	45	1[a]
LPM R00118	64	2
IVPP V14341	57	2
IVPP V14341	62	2
IVPP V14341	68	2
IVPP V14341	72	2
IVPP R00142	52	2[a]
PM R00141	85	3[a]
PM R00132	80	3[a]
PM R00136	103	3[a]
IVPP uncat.	76	3
LPM R00121	73	3
LPM R00124	100	4
LPM R00140	101	4[a]
PKUVP V1057	98	4[a]
LPM R00137	119	5
LPM R00133	113	5
LPM R00119	113	5
LPM R00135	108	5[a]
LPM R00143	111	5[a]
IVPP V12617	138	6
LPM R00133	133	6
LPM 00126	130	6
D2156	132	6
LPM R00138	144	7[a]
PKUVP V1053	149	7[a]
PKUVP V1056	135	7[a]
LPM R00128	135	7[a]
JZMP V11	165	8
PKUVP 1054	164	8[a]
LPM R00122	155	8[a]
PKUVP V1055	148	8[a]
LHPV1	172	9
ZMNH M8137	189	9[a]
LPM R00117	201	10[a]
ZMNH M8138	202	11[a]

[a]Longevity estimated from histology. Institutional abbrevia-
tions: LPM, Liaoning Paleontological Museum, Shenyang
Normal University, Shenyang, China; D, Dalian Natural His-
tory Museum, Dalian, Liaoning Province, China; PKUVP,
School of Earth and Space Sciences, Peking University, Bei-
jing, China; IVPP, Institute of Vertebrate Paleontology and
Paleoanthropology, Beijing, China; JZMP, Jinzhou Museum
of Paleontology, Jinzhou City, Liaoning Province, China:
ZMNH, Zhejiang Museum of Natural History, Hangzhou,
Zhejiang, China; LHPV, Lang Hao Institute for Paleontology,
Hohhot, Nei Mongol Autonomous Region China.

individuals (Lü et al., 2007; Sereno et al., 2007; You et al.,
2008) that are diagnosed by the pronounced nature of cra-
nial display structures (e.g., prominent, laterally directed
jugal horns, deep dentary flanges with stepped rostral
edges). Placed in the context of *P. lujiatunensis* ontogeny,
these extend the developmental trends seen in smaller,
skeletally immature individuals. The alternative, namely
the coexistence of two closely related, same-sized species
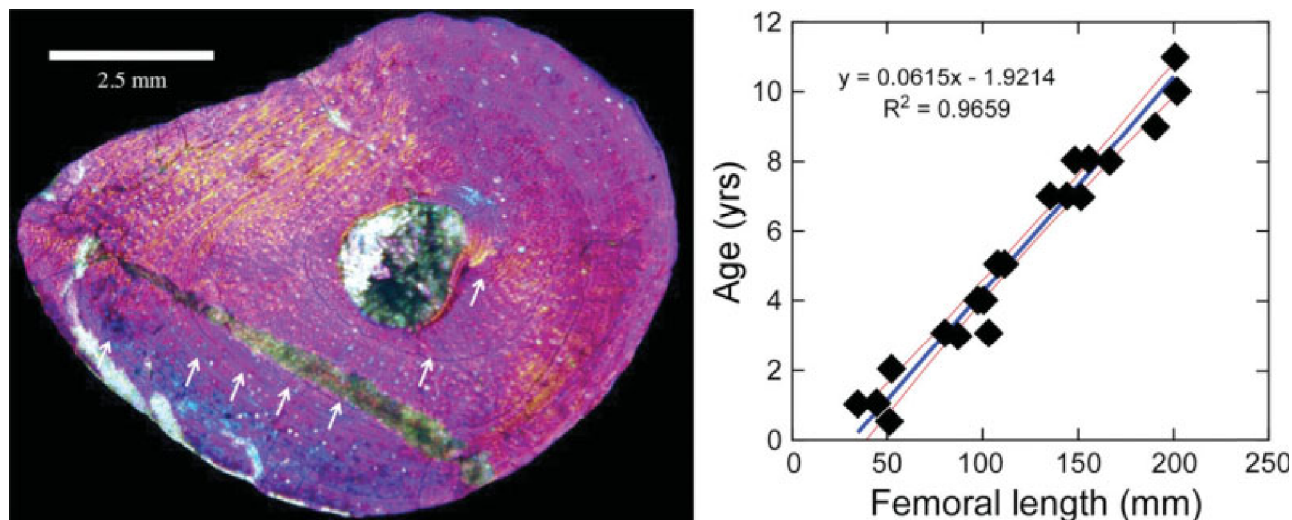with no significant difference in their dental morphology

Fig. 3. *Psittacosaurus lujiatunensis* long bone histology and regression analysis of age estimates versus femoral length. Left: Transverse section of a fibula (PKU VP 1056) viewed with polarized microscopy showing lines of arrested growth (arrows). Right: Regression analysis based growth line counts. The 95% confidence interval (red) brackets the regression line.

within the same environment runs counter to what is known for most extant ecosystems.

We established the size structure for this sample through measurements of femoral length (Table 1). We directly examined and measured 49 specimens. Remaining measurements were obtained through colleagues or from the literature. Scaling equations based on complete specimens throughout ontogeny were used to estimate femoral length for specimens where femoral measurements were not accessible, incomplete, or missing. Twenty-six specimens spanning almost the entire range of sizes known for the taxon were selected for histological analysis and longevity estimation through diaphyseal growth line counts. Fibulae (supplemented by radii and humeri for some specimens) were sectioned because preliminary analyses (Makovicky et al., 2006) revealed that this element preserves the majority of the growth record in psittacosaurs. The thin sections were viewed with polarized and reflected light microscopy and total growth line counts made (Fig. 3). Growth lines lost to medullar expansion and remodeling in older individuals were accounted for using diameter measurements and ring counts from the bones of younger individuals and checked through superposition of thin sections. A regression line ($y_{age\ (yrs)} = 0.062 x_{length\ (mm)} - 1.92$; $r^2 = 0.97$) was fitted to the femoral length and longevity data using R 2.8.1 (R Development Core Team, 2008) from which longevity for the remaining specimens was determined (Fig. 3). Two specimens from the histological analysis showed extensive fungal damage (see below), so their ages were also inferred from the regression.

An age-frequency distribution using yearly increments was compiled for the entire assemblage (Fig. 4). Static life table analysis was conducted, whereby the population was assumed to have been stable and our sampling was random. The number of individuals for age class four was averaged across the bounding classes to allow construction of the static life table (Table 2). The number surviving at the beginning of each age interval (l_x) and
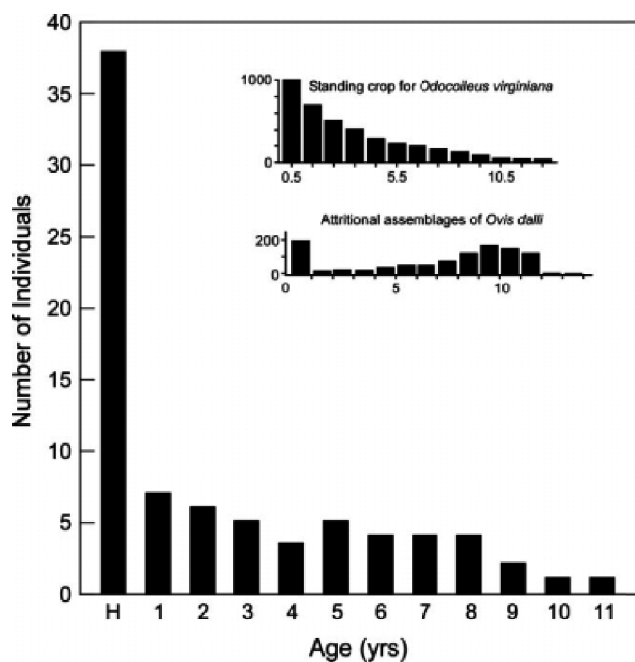

Fig. 4. Demography for *P. lujiatunensis* from the Lujiatun Bed of the Lower Cretaceous Yixian Formation, Liaoning Province of China showing right-skew. Inset: Demography depictions for an idealized standing crop of white-tailed deer (*Odocoileus*; top) from Voorhies, 1969 (data from Quick, 1962) characterized by right-skew when compared with an attritional assemblage for a mountain sheep population (*Ovis*; data from Deevey, 1947) with a bimodal distribution and left-skew among the postneonates.

number dying during each age interval (d_x) was calculated to generate a log survivorship curve (Fig. 5) (the standard in ecology for making interpopulation comparisons; Deevey, 1947; Spinage, 1972; Ebert, 1999) and

TABLE 2. Static life table for lujiatun bed
Psittacosaurus lujiatunensis

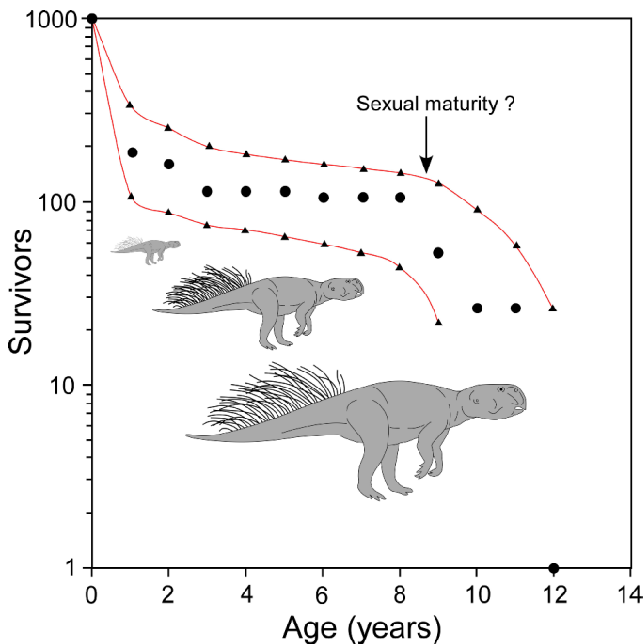| Age (yrs)	Number of individuals	l_x	d_x
<1	38	1000	816
1	7	184	26
2	6	158	44
3	(5) 4.33[a]	114	0
4	(3) 4.33[a]	114	0
5	(5) 4.33[a]	114	9
6	4	105	0
7	4	105	0
8	4	105	53
9	2	52	26
10	1	26	0
11	1	26	26
12	0	0	0

[a]Averaged.

Fig. 5. Survivorship for Lujiatun *P. lujiatunensis*. Bootstrap confidence intervals (90%) are shown in red.

the pattern described with respect to the aforementioned Deevey/Pearl-Miner types. Confidence intervals were estimated from 10,000 bootstrapped samples using R 2.8.1 (R Development Core Team, 2008). The sample was standardized to a hypothetical initial cohort size of 1,000 (a standard in ecology; Ebert, 1999).

A longevity/body mass growth curve (Fig. 6) was made using the empirically aged specimens and Developmental Mass Extrapolation (Erickson and Tumanova, 2001). Representative adult mass was deduced using the minimal diaphyseal femoral circumference measurement for the large 201 mm femoral length specimen (LPM R00117) using the Anderson et al. (1985) regression equation for bipedal taxa, as *Psittacosaurus* is interpreted as being a facultative biped (You and Dodson, 2004). Sigmoidal growth equations were fit using least
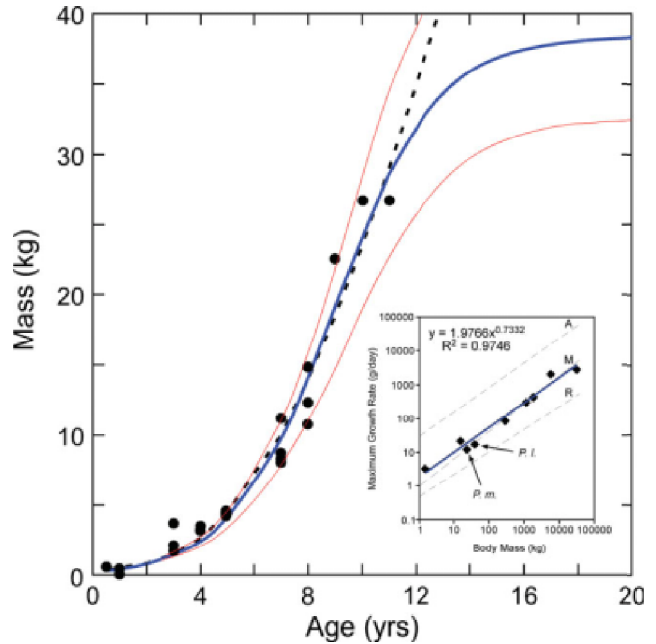

Fig. 6. Growth curve and growth rate comparison for the Lujiatun bed population of *P. lujiatunensis*. A logistic equation (solid blue line extended with long dashes beyond sample range) shows the best fit for these data (mass = 37.38 × exp(0.55 × age)/(37.38 + (exp(0.55 × age) − 1)). A Gompertz equation (black dashed line) shows similar fit for the empirical data but predicts an unreasonable asymptotic size (107-kg). The 95% confidence interval is shown (thin red bounding lines). A von Bertalanffy equation provided poor fit in both regards and is not shown. Inset: Exponential stage growth rates for *P. lujiatunensis* (*P. l.*) are comparable to those in *P. mongoliensis* (*P. m.*) and for same-sized nonavian dinosaurs. Growth in *P. lujiatunensis* was not aberrant for a nonavian dinosaur (black diamonds) that collectively grew at rates (blue regression line) along the lower bound seen in extant endotherms like marsupials (Erickson and Curry Rogers, 2000; Erickson and Tumanova, 2001) for which they presumably had similar thermal and energetic physiology (e.g., basal metabolic rates). Data from Erickson et al., 2001 (Apatosaurus, Maiasaura excluded); Erickson et al., 2004; Wings et al., 2007; A = altricial birds, M = marsupials, R = extant nonavian reptiles (Case, 1978).

squares regression and used to describe these data. These results, along with the longevity data, were used to describe the developmental timing and stages at which major changes in mortality rates occurred. Reproductive attributes including timing of sexual maturity, reproductive population size, and hypothetical fecundity schedules required to balance births and deaths (Pianka, 1994) were based on sexual maturity occurring no later than when growth rates begin to slow appreciably before attaining their asymptote. This is the outgroup condition seen in living lepidosaurs and Crocodylia (Andrews, 1982; Shine and Charnov, 1992; Thornbjarnarson, 1996) and has been histologically demonstrated from brooding nonavian dinosaurs (Erickson et al., 2007) and specimens thought to show medullary bone (Schweitzer et al., 2005; Lee and Werning, 2008).

RESULTS

The longevity analysis revealed that the specimens in our sample ranged from neonates to 11 years of age

(Fig. 4). The age structure is decidedly right-skewed (i.e., dominated by neonates and juveniles; Fig. 4). This is consistent with expectations (see cf. Plate 13 in Voorhees, 1969) based on taphonomic findings that the assemblage was produced catastrophically and represents standing crop rather than an attritional accumulation (He et al., 2006). This distribution would hold even if the specimens derive from multiple distinct lahars (= multiple event sampling of the Lujiatun *P. lujiatunensis* population), rather than a single massive event. The life table (Table 2) and graphic survivorship curve derived from it follow a sigmoidal Type B_1 pattern (Fig. 5). The highest mortality rates (estimated at 82%) were experienced in the first year of development. These continued to be relatively high (14–28%) through year three until a threshold size approximating 2-kg was attained. Attrition thereafter stabilized and was negligible throughout the most of the exponential growth stage when the majority of body mass was rapidly accrued. By the age of nine mortality rates increased to as high as 50% and were maintained at high levels up to the extinction of the cohort by age 12. The growth curve shows that these increases in attrition happen just prior to the slowing of growth that occurs during the transition to the stationary phase of development (Fig. 6). Notably, none of the specimens in our sample reached the asymptote marking the near-cessation of somatic growth. The latter is consistent with the histology, whereby none showed EFS structuring (tightly packed growth lines indicative of substantial truncation in growth). Sexual maturity appears to have begun no later than the tenth year of life. Increased mortality (see above) and development of traits often considered to be secondary sexual characteristics (e.g., enlarged, flaring jugal horns) at this time is consistent with entrance into the reproductive population which would represent 10% of the posthatchling population. Assuming that these animals reproduced annually and both primary and adult sex ratios were equal, this population would have been stable (with equal births and deaths each year) with a generation time of 10 years based on clutch sizes of approximately 34 individuals (the size of the neonate aggregation described by Meng et al., 2004), and successful reproduction by most 9 year olds uncommon.

DISCUSSION

Perhaps the most surprising finding from this study is that *P. lujiatunensis* had Type B_1 survivorship, the same pattern also seen in the much larger North American tyrannosaurids (Erickson et al., 2006; Fig. 1). It is also the pattern characteristic of populations of moderate to large-sized birds and mammals, including species comparable in size to this psittacosaur. The factors that seem to contribute to this pattern of survivorship among the birds and mammals are moderate to large size, rapid growth rates, and attainment of threshold sizes at which predation pressures diminish. In small vertebrates with adult body masses typically below 500-g, Type II survivorship occurs, whereby the odds of predation are constant throughout post-neonate development (i.e., they never reach threshold sizes that deter predation; Deevey, 1947). Despite the great disparity in sizes between *P. lujiatunensis* and tyrannosaurs, their distant phylogenetic affinities (Ornithischia vs. Saurischia, respec-

tively), and different trophic and community ecology, these animals both exceeded sizes of small reptiles, birds, and mammals today. Furthermore, they shared a similar growth strategy characterized by rapid tissue formation (Padian et al., 2001; Chinsamy-Turan, 2005), whole body growth rates (Erickson et al., 2004), and presumably endothermic physiology typical for nonavian dinosaurs (Fig. 6). These latter factors likely overrode other influences on survivorship and contributed to their shared life history pattern. Collectively this suggests that most if not all nonavian dinosaurs had Type B_1 survivorship, as even the smallest known dinosaurs (e.g., *Microraptor*) exceeded ~500 g in body mass (Turner et al., 2007).

A second notable result of our analysis is that these animals appear to have reached threshold sizes somewhere between 3 and 4 years old (Figs. 4 and 5), as these animals were entering the transition to the exponential stage of growth (*sensu* Sussman, 1964) when they would have explosively increased in body mass (Fig. 6). In extant birds and mammals with Type B_1 survivorship, this threshold typically corresponds to diminished predation pressure (even in large predators like the cheetah, *Acinonyx*; Kelly et al., 1998) owing to being more mobile, experienced, and/or large enough to deter or evade predators. Deaths of these somewhat larger, older individuals occur at much lower rates and are primarily from larger predators and/or other causes such as accidents or disease. Such deaths appear to have been a rarity in the Lujiatun *P. lujiatunensis* population, despite individuals being initially still quite small (less than 5-kg). Known predator-scavengers in the Yixian Formation include small theropods such as the dromaeosaurids *Microraptor* and *Sinornithosaurus* and the troodontids *Mei* and *Sinovenator* (Norell and Xu, 2005), moderate-sized mammals such as *Repenomamus giganteus* and *R. robustus* (Hu et al., 2005), and larger tyrannosauroids like *Dilong* and compsognathids like *Huaxiagnathus* (Norell and Xu, 2005), some of which could plausibly have preyed upon *P. lujiatunensis* at younger growth stages. Large macropredators that would incontrovertibly be capable of preying upon the largest known *P. lujiatunensis* individuals are so far not documented from the Yixian Formation, although this may reflect taphonomic biases toward preservation of small animals rather than true absence of such forms. Either way the survivorship curve suggests that during the exponential stage of development predation must have been relatively rare. It is perhaps worth noting that approximately 3% of the biomass was continually available in the first three size classes (Fig. 7), and it is from these groups that supposed crèche aggregations have also been found (Meng et al., 2004; Zhao et al., 2007; Table 1-LPM R 00142). It is plausible that predators fixated on these more available and vulnerable prey whose clumped nature may have facilitated such behavior. The discovery of a specimen of the triconodont mammal *Repenomamus* with a neonate *Psittacosaurus* individual among its stomach contents (Hu et al., 2005) and small theropod stomach contents showing even smaller prey items such as lizards and mammals (Currie and Chen, 2001) are consistent with this hypothesis.

Entrance into the reproductive population in Lujiatun *P. lujiatunensis* is posited to have occurred sometime during the ninth year of life. Thus the reproductive
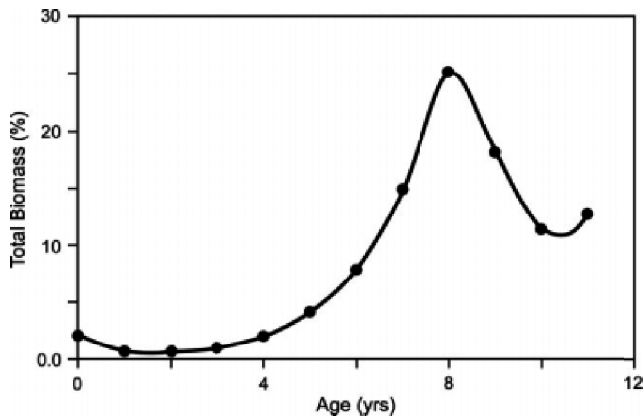
Fig. 7. Biomass proportions for the Lujiatun population of *P. lujiatunensis*. These data are based on l_x values from the life table (Table 2) and developmental masses from the growth curve (Fig. 6).

lifespan for the sampled population was just 3 to 4 years, with approximately 10% of posthatchling individuals being sexually mature at the time of their demise. That the timing of sexual maturity inferred from growth rates and the pattern of survivorship inferred from individual ages are consistent with population stability through the fecundity analysis suggests that this is a plausible life history for this taxon.

Increased attrition linked with probable sexual maturity was also found for tyrannosaurs (Erickson et al., 2006) and is observed in some populations of birds and mammals today (e.g., Spinage, 1972; Flowerdue, 1987; Newton, 1989; Estes, 1991). In these living taxa factors such as competition for mates, physiological demands of oviposition, fasting, and greater exposure to predation contribute to the increased attrition. These factors likely contributed to the same pattern seen in *P. lujiatunensis*. However, we are hesitant to speculate that this may be the case in all nonavian dinosaurs because this is certainly not true for all living taxa showing Type B_1 survivorship.

Life table analysis through the coupling of growth ring longevity estimates and actuary analysis stands to revolutionize our understanding of nonavian dinosaur population biology. This study serves as an example of how this type of investigation can be conducted and the sorts of life history information that can be garnered in the future.

ACKNOWLEDGMENTS

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