

3-2014

# Cranial Size Variation and Lineage Diversity in Early Pleistocene Homo

Jeremiah E. Scott

*Southern Illinois University Carbondale*, [jescott@siu.edu](mailto:jescott@siu.edu)

Follow this and additional works at: [http://opensiuc.lib.siu.edu/anthro\\_pubs](http://opensiuc.lib.siu.edu/anthro_pubs)

This is the peer reviewed version of the article cited below, which has been published in final form at DOI: 10.1111/evo.12215. This article may be used for non-commercial purposes in accordance with [Wiley Terms and Conditions for Self-Archiving](#).

---

## Recommended Citation

Scott, Jeremiah E. "Cranial Size Variation and Lineage Diversity in Early Pleistocene Homo." *Evolution: International Journal of Organic Evolution* 68, No. 3 (Mar 2014): 909-915. doi:10.1111/evo.12215.

This Article is brought to you for free and open access by the Department of Anthropology at OpenSIUC. It has been accepted for inclusion in Publications by an authorized administrator of OpenSIUC. For more information, please contact [opensiuc@lib.siu.edu](mailto:opensiuc@lib.siu.edu).

1 CRANIAL SIZE VARIATION AND LINEAGE  
2 DIVERSITY IN EARLY PLEISTOCENE *HOMO*

3  
4  
5 Jeremiah E. Scott  
6 Department of Anthropology  
7 Southern Illinois University  
8 Carbondale, Illinois 62901  
9 Email: [jeremiah.e.scott@gmail.com](mailto:jeremiah.e.scott@gmail.com)

10  
11  
12 Running Title: Size variation and diversity in early *Homo*

13  
14 Key Words: Anagenesis, cladogenesis, hominin, *Homo erectus*, *Homo habilis*

15  
16 Data Archival Location: Included as electronic supporting information (Appendix S1)

17  
18 Word Count: 3482

19  
20 Abstract 193  
21 Main text 2738  
22 Literature cited 289 (10 references)  
23 Figure legends 189

24  
25 Tables: 2

26  
27 Figures: 4, no color  
28

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18

**Abstract**

A recent paper in this journal concluded that a sample of early Pleistocene hominin crania assigned to genus *Homo* exhibits a pattern of size variation that is time-dependent, with specimens from different time periods being more different from each other, on average, than are specimens from the same time period. The authors of this study argued that such a pattern is not consistent with the presence of multiple lineages within the sample, but rather supports the hypothesis that the fossils represent an anagenetically evolving lineage (i.e., an evolutionary species). However, the multiple-lineage models considered in that study do not reflect the multiple-species alternatives that have been proposed for early Pleistocene *Homo*. Using simulated data sets, I show that fossil assemblages that contain multiple lineages can exhibit the time-dependent pattern of variation specified for the single-lineage model under certain conditions, particularly when temporal overlap among fossil specimens attributed to the lineages is limited. These results do not reject the single-lineage hypothesis, but they do indicate that rejection of multiple lineages in the early Pleistocene *Homo* fossil record is premature, and that other sources of variation, such as differences in cranial shape, should be considered.

1           In a recent paper published in this journal, Van Arsdale and Wolpoff (2013) evaluated  
2 size variation in early Pleistocene hominin crania representing genus *Homo* from eastern Africa  
3 and Dmanisi, Georgia. These authors concluded that the pattern of variation exhibited by the  
4 sample was most consistent with the hypothesis that these fossils were part of an anagenetically  
5 evolving lineage (i.e., an evolutionary species; Simpson, 1951; Wiley, 1978) characterized by  
6 directional trends toward brain expansion and reduction of the masticatory apparatus. Van  
7 Arsdale and Wolpoff reasoned that if the single-lineage hypothesis is correct, then variation  
8 should be lowest within time intervals and greatest between time intervals, with variation  
9 between the most disjunct time intervals being greatest (Fig. 1a). This pattern is the one that they  
10 observed in their sample. Here I show using a simulation approach that such a pattern can also  
11 characterize a fossil assemblage containing two lineages under certain conditions. These results  
12 do not falsify the single-lineage hypothesis, but they do show that multiple-lineage alternatives  
13 remain viable.

14           Van Arsdale and Wolpoff contrasted their single-lineage model with two models of  
15 lineage diversity: the first characterized by two static lineages in which variation is more or less  
16 equally high within and between time intervals (Fig. 1b), and the second characterized by two  
17 diverging lineages in which variation is lowest within the earliest time interval and greater both  
18 within subsequent time intervals and in comparisons between time intervals (Fig. 1c). However,  
19 framing the alternatives in this way is problematic because these models assume (1) that both  
20 lineages exist throughout the entire period of time considered, and (2) that representatives from  
21 each hypothesized lineage are equally likely to be sampled in each time interval. Importantly,  
22 neither of these assumptions fits well with the multiple-lineage hypotheses that have been  
23 proposed for early Pleistocene *Homo*. It is also worth noting that one of Van Arsdale and

1 Wolpoff's analyses identified a sample that included specimens of early *Homo* and  
2 *Australopithecus boisei*—which most paleoanthropologists accept as separate lineages—as  
3 conforming to the predictions of the single-lineage hypothesis. This result suggests that the  
4 resampling test used by Van Arsdale and Wolpoff may not be able to distinguish between single-  
5 and multiple-lineage alternatives under certain conditions.

6         Paleoanthropologists have partitioned the sample of *Homo* crania analyzed by Van  
7 Arsdale and Wolpoff into as many as five species since the 1980s (see references in Van Arsdale  
8 and Wolpoff, 2013). With respect to the material from eastern Africa, the simplest multiple-  
9 lineage scheme recognizes two species, *Homo habilis* and *Homo erectus*, with fossils assigned to  
10 the former appearing earlier in the fossil record. The *H. habilis* material is often split into two  
11 species—*H. habilis sensu stricto* and *H. rudolfensis*—while the earliest African representatives  
12 of *H. erectus* are sometimes referred to as *H. ergaster*. These two taxonomic distinctions will be  
13 ignored here in favor of the more conservative two-species scenario—*H. habilis* and *H.*  
14 *erectus*—in order to simplify discussion.

15         With respect to the fossils from eastern Africa, all eight of the *Homo* crania in Van  
16 Arsdale and Wolpoff's two earliest time intervals (1.9–1.7 Ma) are representatives of *H. habilis*,  
17 or at least have been identified as such by paleoanthropologists who recognize some level of  
18 taxonomic diversity during this time period (Table 1). Conversely, all seven of the *Homo* crania  
19 in the two most recent time intervals (1.6–1.5 Ma and <1.5 Ma) represent *H. erectus*. These two  
20 groups of fossils occur together in eastern Africa only in the middle time interval (1.7–1.6 Ma).  
21 Prior to 2007, it was not possible to distinguish succession from a brief period of temporal  
22 overlap for these fossils because of uncertainty in age estimates for key specimens, particularly  
23 the *H. erectus* cranium KNM-ER 3733 (for a recent review of the dating evidence, see Suwa et

1 al., 2007). However, the recent discovery of a 1.44-million-year-old partial maxilla with teeth  
2 that are metrically distinct from those of *H. erectus* but quite similar to geologically older *H.*  
3 *habilis* specimens demonstrates that individuals bearing *H. habilis* morphology did indeed  
4 coexist with those bearing *H. erectus* morphology in eastern Africa for at least 200,000 years  
5 (Spoor et al., 2007). The reason for the rarity of such individuals in the fossil record after about  
6 1.6 Ma is unclear. Notably, such fossils are absent from Van Arsdale and Wolpoff's sample.

7 Adding the four Georgian crania to the analysis broadens this overlap. The most recent  
8 and comprehensive taxonomic analysis of these fossils was conducted by Rightmire et al. (2006),  
9 who noted resemblances between these specimens and those attributed to both *H. habilis* and *H.*  
10 *erectus*. Although they left open the possibility for the presence of a second species at the site  
11 (*Homo georgicus*), Rightmire et al. (2006) ultimately argued that the fossils are best situated  
12 within the *H. erectus* hypodigm, concluding: "On morphological grounds, it can be argued that  
13 the group from which the skulls are drawn is close to a stem from which later more derived  
14 populations [of *H. erectus*] are evolved" (p. 140). The Georgian fossils thus represent, in those  
15 authors' view, an early form of *H. erectus*, one that differs from later populations principally in  
16 its smaller size and retention of plesiomorphic traits (i.e., more *H. habilis*-like). Accepting  
17 Rightmire et al.'s (2006) classification increases the degree of temporal overlap between  
18 specimens assigned to *H. habilis* and those assigned to *H. erectus* from one time interval to two  
19 (1.8–1.6 Ma; Table 1).

20 Given the preceding discussion, it is clear that tests of lineage diversity within early  
21 *Homo* need to account for the fact that the proposed lineages are not present together in all time  
22 intervals, either because one did not exist during certain intervals or because one is poorly  
23 sampled in certain intervals (e.g., because it had a low population density or was not present in a

1 particular region), or a combination of the two. Van Arsdale and Wolpoff's multiple-lineage  
2 models do not address this issue; rather, as noted above, they specify patterns of variation that  
3 assume complete temporal overlap among the specimens that represent the hypothesized  
4 lineages. Figure 2a shows a multiple-lineage model not considered by Van Arsdale and Wolpoff,  
5 one characterized by two species that differ in size and that overlap in time for only a brief  
6 period. This scenario appears to be a more realistic representation of the multiple-lineage  
7 alternatives to Van Arsdale and Wolpoff's single-lineage hypothesis.

8         If the taxonomic distinction between the two sets of data points in Figure 2a is ignored,  
9 then the bivariate distribution superficially resembles the single-lineage model. The pattern of  
10 variation expected for this two-lineage model differs from the one expected for the single-lineage  
11 model in that variation is predicted to be low within the time intervals in which the two species  
12 do not overlap, but high within the intervals in which there is overlap, as well as in comparisons  
13 between intervals that include both species. However, given the vagaries of the fossil record,  
14 sampling error can produce a situation such as the one shown in Figure 2b, where half of the data  
15 points in Figure 2a have been deleted, creating a bivariate distribution that more strongly  
16 resembles the single-lineage model presented in Figure 1a. The possibility of this scenario  
17 undermines Van Arsdale and Wolpoff's interpretation of their results as being inconsistent with  
18 the presence of multiple lineages.

19         The validity of this critique depends on the likelihood of the sampling event depicted in  
20 Figure 2b occurring, assuming Figure 2a as the starting point. In order to address this issue, I  
21 generated 100 samples, each composed of twenty individuals: ten sampled from a population  
22 (*Taxon 1*) with a mean trait value of  $\mu = 10.00$  and a standard deviation of  $\sigma = 0.80$ , and ten  
23 sampled from a second population (*Taxon 2*) with a mean trait value of  $\mu = 12.00$  and a standard

1 deviation of  $\sigma = 0.96$ . Note that these two taxa have identical levels of relative variation  
2 (coefficient of variation =  $\sigma / \mu \times 100 = 8.00$ ) but the mean for *Taxon 2* is 20% larger. For each  
3 sample, individuals were randomly assigned to one of five time intervals as shown in Table 2,  
4 holding the number of individuals from each taxon in each time interval constant in all 100  
5 samples.

6         The parameters for the simulated populations are based on those that characterize one of  
7 the best-represented measurements in Van Arsdale and Wolpoff's sample, bi-asterionic breadth  
8 (see the electronic appendices that accompany Van Arsdale and Wolpoff's paper), which is  
9 available for twenty-one of the twenty-five *Homo* crania used in their analysis. Asterion is a  
10 bilateral craniometric point that marks the spot where the temporal, parietal, and occipital bones  
11 of the neurocranium meet; bi-asterionic breadth is therefore a measure of the posterior width of  
12 the cranial vault. The mean value for the three *H. erectus* crania in the latest time interval is 21%  
13 larger than the mean value for the four *H. habilis* specimens in the earliest time interval for  
14 which this measurement is available (114.53 mm vs. 94.35 mm, respectively). The coefficient of  
15 variation for these two samples is approximately 8.00 (8.20 and 7.47, respectively). The  
16 allocation of the simulated specimens to time intervals is similar to the observed distribution, but  
17 with some minor modifications to account for two factors: (1) that the simulated samples  
18 contains only twenty individuals rather than twenty-one, and (2) that the representation of the  
19 two taxa in each simulated sample is equal (i.e., ten and ten) rather than unbalanced (bi-  
20 asterionic breadth is available for thirteen *H. erectus* and eight *H. habilis*).

21         The use of a single trait in the simulations may at first appear to be inadequate, given that  
22 Van Arsdale and Wolpoff used dozens in their analysis. However, it is almost certainly the case  
23 that the traits included in Van Arsdale and Wolpoff's analysis are highly intercorrelated and thus



1 represent only a few independent variables. Indeed, as noted by those authors, their results  
2 largely reflect “an increase in size of the neurocranium, a reduction of the masticatory structures,  
3 and related changes to the cranial base, splanchochranium and cranial vault” (Van Arsdale and  
4 Wolpoff, 2013, p. 848). Inspection of Van Arsdale and Wolpoff’s data set suggests that the time-  
5 dependent pattern of variation observed in their results is driven primarily by a directional  
6 increase in the size of the neurocranium related to brain expansion (Leigh, 1992; Lee and  
7 Wolpoff, 2003). Therefore, the use of a single simulated trait modeled on one of the best-  
8 represented measures of neurocranial size in the sample probably does not result in the loss of  
9 much information.

10 For each of the simulated samples, all possible pairwise differences were computed as:  
11  $|\ln(x) - \ln(y)|$ , following Van Arsdale and Wolpoff. The resulting values were used to construct a  
12 matrix of average pairwise interindividual differences like the hypothetical ones shown in  
13 Figures 1 and 2. These matrices and the samples used to generate them are available in Appendix  
14 S1.

15 One way to gauge how well each of the simulated matrices fits the predictions of the  
16 single-lineage model is to summarize how the median values for the different types of time-  
17 interval comparisons in each matrix sort relative to each other. The first type of time-interval  
18 comparison includes only the diagonal cells of the matrix—i.e., the mean pairwise differences  
19 within each of the five time intervals. The median of these five values is denoted with  $M_0$ . The  
20 other types of comparisons involve the off-diagonal cells, which represent the mean pairwise  
21 differences between individuals in different time intervals. For example,  $M_1$  is the median for the  
22 four cells involving comparisons between adjacent time intervals (e.g., interval 1 vs. interval 2),  
23 and  $M_2$  is the median for the three cells involving comparisons between intervals separated by

1 one time interval (e.g., interval 3 vs. interval 5). According to the single-lineage model, these  
2 median values should be ordered as follows:  $M_0 < M_1 < M_2 < M_3 < M_4$ . Of the 100 simulated  
3 matrices, twenty-four exhibit this pattern. In comparison, Van Arsdale and Wolpoff's pairwise  
4 difference matrices for early *Homo* crania exhibit patterns in which the median for diagonal cells  
5 is not the lowest of the five values ( $M_1 < M_0 < M_2 < M_3 < M_4$  and  $M_1 < M_2 < M_0 < M_3 < M_4$ ,  
6 depending on how the data are treated and the temporal placement of KNM-ER 1813; see Tables  
7 3A,C and 4A,C in Van Arsdale and Wolpoff, 2013).

8 Another simple way of evaluating the matrices is to compute the rank sum of the five  
9 diagonal cells. Given five time intervals, there are fifteen unique cells in the matrix (i.e., the  
10 diagonal and either the cells above it or the cells below it). The single-lineage hypothesis predicts  
11 that the diagonal cells will be the lowest ranked (i.e., 11–15) and thus have a rank sum of 65. The  
12 diagonal cells in the four matrices constructed by Van Arsdale and Wolpoff for early *Homo* have  
13 rank sums of 39, 41, 42, and 43. The rank sums for 90 of the 100 simulated matrices are greater  
14 than 43. The distribution of these values is shown in Figure 3 (median = 50, maximum = 58,  
15 minimum = 34).

16 In several cases, the bivariate plots of size vs. time interval for the simulated samples  
17 present patterns that are remarkably similar to the one expected for an evolving lineage. Three  
18 examples are shown in Figure 4, along with a plot of bi-asterionic breadth vs. time interval from  
19 Van Arsdale and Wolpoff's sample, with the data points identified as either *H. habilis* or *H.*  
20 *erectus*. The plots for all of the simulated samples are available in Appendix S1.

21 The results of these simulations thus indicate that a pattern of variation similar to the one  
22 expected for a single lineage changing in a nonrandom way through time is fairly easy to obtain  
23 from a multiple-lineage assemblage under certain conditions. The population parameters used

1 here to generate the simulated samples are obviously not exhaustive, and more complex  
2 multiple-lineage models incorporating additional taxa, geographic variation, sexual dimorphism,  
3 and different patterns of temporal change within hypothesized lineages can be constructed. Some  
4 of these models would increase the likelihood of obtaining the single-lineage pattern. For  
5 example, given the fact that the Georgian *H. erectus* specimens are intermediate between *H.*  
6 *habilis* and later *H. erectus* in some aspects of cranial size (Rightmire et al., 2006), another set of  
7 simulations could be generated in which *Taxon 2* is more similar to *Taxon 1* in their first interval  
8 of overlap (e.g., 10% larger on average than *Taxon 1* rather than 20%), thereby reducing  
9 variation within this time interval. Another factor that would increase the likelihood of obtaining  
10 the single-lineage pattern is reducing the number of specimens sampled at each time interval.  
11 With a combined-taxon sample size of  $n = 20$  for each simulation, the results presented here  
12 should be considered conservative, given that the overwhelming majority of the measurements  
13 used by Van Arsdale and Wolpoff are available on fewer than half of the *Homo* specimens  
14 included in their analysis.

15         Van Arsdale and Wolpoff's examination of the temporal pattern of size variation in early  
16 Pleistocene *Homo* crania is a novel attempt to address the longstanding question of lineage  
17 diversity in this critical part of the hominin fossil record. However, given the results of the  
18 simulation analysis presented here, it is premature to conclude that their results unambiguously  
19 support the hypothesis that these crania represent a single lineage based on the time-dependent  
20 pattern of size variation that they exhibit. The approach adopted here does not falsify the single-  
21 lineage hypothesis, but it does indicate that fossil assemblages that contain multiple lineages can  
22 exhibit the pattern of size variation specified by Van Arsdale and Wolpoff's single-lineage  
23 model. The fact that this pattern characterizes early Pleistocene *Homo* cranial remains does not,

1 therefore, constitute strong evidence against the hypothesis that there are multiple lineages  
2 present in the sample. Finally, it is worth emphasizing that the case for multiple species of early  
3 Pleistocene *Homo* has never relied principally on size variation. Rather, shape variation has  
4 played an integral role in, for example, building the case for recognizing two species within the  
5 *H. habilis* hypodigm (e.g., Wood, 1992; Kimbel and Rak, 1993; Leakey et al., 2012). Clarifying  
6 the taxonomy of early Pleistocene *Homo* will thus likely come from separate considerations of  
7 both of these components of variation.

8

## 9 **ACKNOWLEDGMENTS**

10 I thank Bill Kimbel, Tierra Nalley, the editors, and anonymous reviewers for helpful  
11 comments and suggestions.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22

**LITERATURE CITED**

Kimbel, W. H., and Y. Rak. 1993. The importance of species taxa in paleoanthropology and an argument for the phylogenetic concept of the species category. Pp. 461–484 *in* W. H. Kimbel and L. B. Martin, eds. *Species, species concepts, and primate evolution*. Plenum Press, New York.

Leakey, M. G., F. Spoor, M. C. Dean, C. S. Feibel, S. C. Antón, C. Kiarie, and L. N. Leakey. 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature* 488:201–204.

Lee, S.-H., and M. H. Wolpoff. 2003. The pattern of evolution in Pleistocene human brain size. *Paleobiology* 29:186–196.

Leigh, S. R. 1992. Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. *Am J. Phys. Anthropol.* 87:1–13.

Rightmire, G. P., D. Lordkipanidze, and A. Vekua. 2006. Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *J. Hum. Evol.* 50:115–141.

Spoor, F., M. G. Leakey, P. N. Gathogo, F. H. Brown, S. C. Antón, I. McDougall, C. Kiarie, F. K. Manthi, and L. N. Leakey. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448:688–691.

Suwa, G., B. Asfaw, Y. Haile-Selassie, T. White, S. Katoh, G. WoldeGabriel, W. K. Hart, H. Nakaya, Y. Beyene. 2007. Early Pleistocene *Homo erectus* fossils from Konso, southern Ethiopia. *Anthropol. Sci.* 115:133–151.

- 1 Van Arsdale, A. P., and M. H. Wolpoff. 2013. A single lineage in early Pleistocene *Homo*: size
- 2 variation continuity in early Pleistocene *Homo* crania from East Africa and Georgia.
- 3 *Evolution* 67:841–850.
- 4 Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Syst. Biol.* 27:17–26.
- 5 Wood, B. 1992. Origin and evolution of the genus *Homo*. *Nature* 355:783–790.
- 6

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21

## Figure Legends

**Figure 1.** Models of evolution and their predicted patterns of variation proposed by Van Arsdale and Wolpoff (2013): (a) a single lineage characterized by a directional trend toward increased size; (b) two lineages that differ in size but do not change through time; (c) two lineages diverging in size through time. The expected pattern of variation for comparisons within and between time intervals for each model is illustrated in the matrices below each plot.

**Figure 2.** (a) Multiple-lineage model not considered by Van Arsdale and Wolpoff in which two lineages overlap only briefly in time. (b) Sampling error can produce a pattern that strongly resembles the single-lineage model depicted in Figure 1a.

**Figure 3.** Distribution of the rank sums for the five diagonal elements of each of the 100 simulated matrices (median = 50, maximum = 58, minimum = 34).

**Figure 4.** (a) Bi-asterionic breadth (mm) plotted against time interval for the *Homo* crania included in Van Arsdale and Wolpoff's (2013) sample (black circles: *H. habilis*; open circles: *H. erectus*; see Table 1). (b–d) Example plots from the simulated two-lineage samples exhibiting a clear temporal signal.

**Table 1. Fossil *Homo* crania included in Van Arsdale and Wolpoff's (in press) study and their taxonomic assignments and temporal placements.**

	Time intervals				
	1.9–1.8 Ma	1.8–1.7 Ma	1.7–1.6 Ma	1.6–1.5 Ma	<1.5 Ma
<i>H. habilis</i> (including <i>H. rudolfensis</i> )	OH 7	OH 16	OH 13		
	OH 24	KNM-ER 1590	KNM-ER 1805		
	KNM-ER 1470		KNM-ER 1813		
	KNM-ER 3732		KNM-ER 3891		
	KNM-ER 3735				
KNM-ER 62000					
<i>H. erectus</i> (including <i>H. ergaster</i> )			KNM-ER 730	KNM-ER 1808	OH 9
			KNM-ER 3733	KNM-ER 3883	OH 12
				KNM-ER 42700	Daka
				KNM-WT 15000	
Dmanisi, Georgia		D2280			
		D2282			
		D2700			
		D3444			



**Table 2. Temporal distribution of specimens in the simulated data sets.**

	Time intervals				
	1	2	3	4	5
<i>Taxon 1</i>	4	4	2		
<i>Taxon 2</i>		2	2	3	3

Figure 1

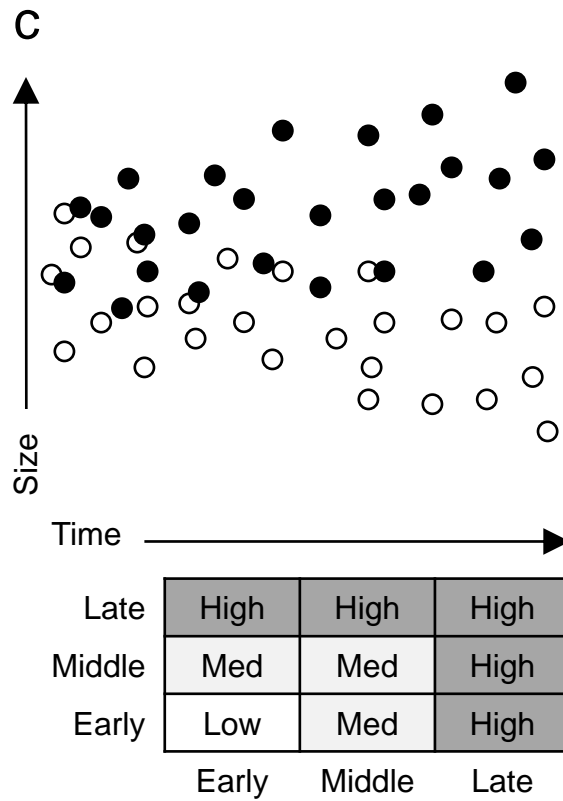
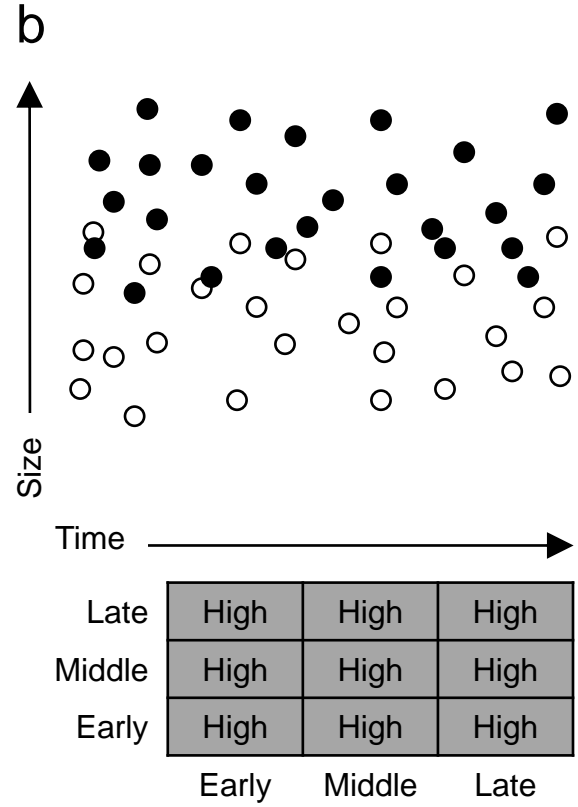
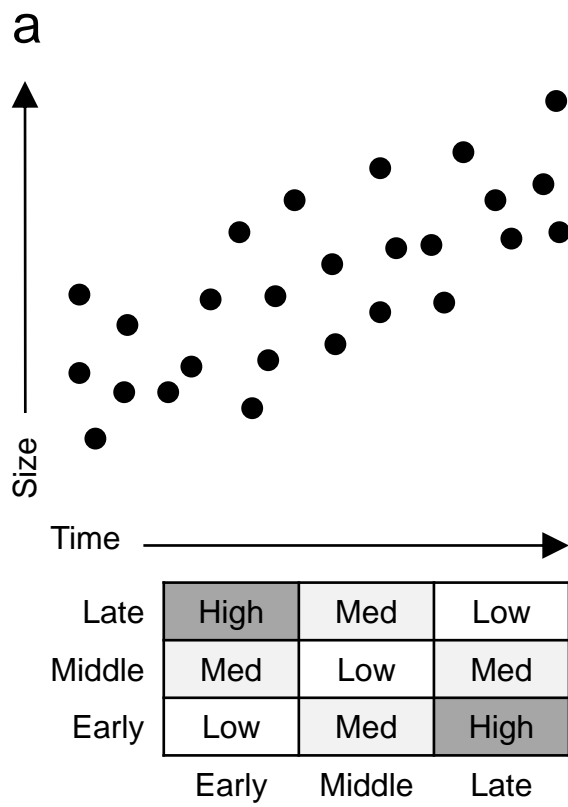


Figure 2

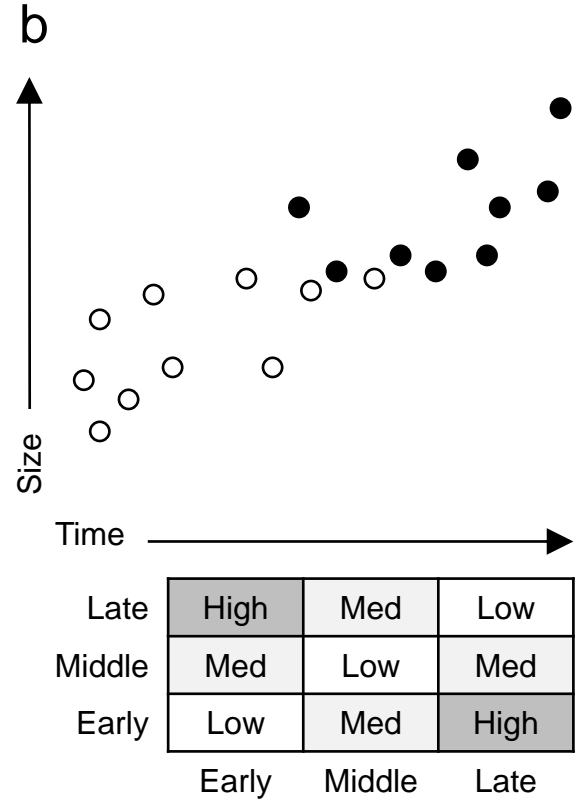
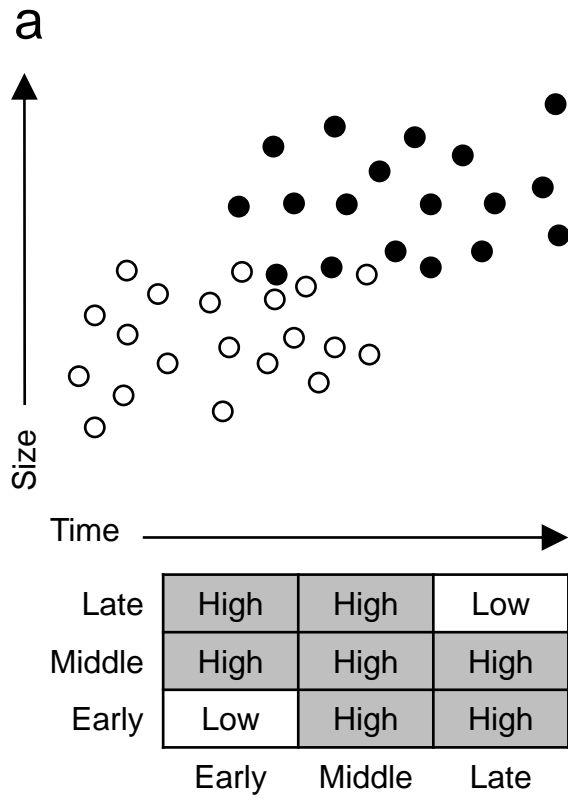


Figure 3

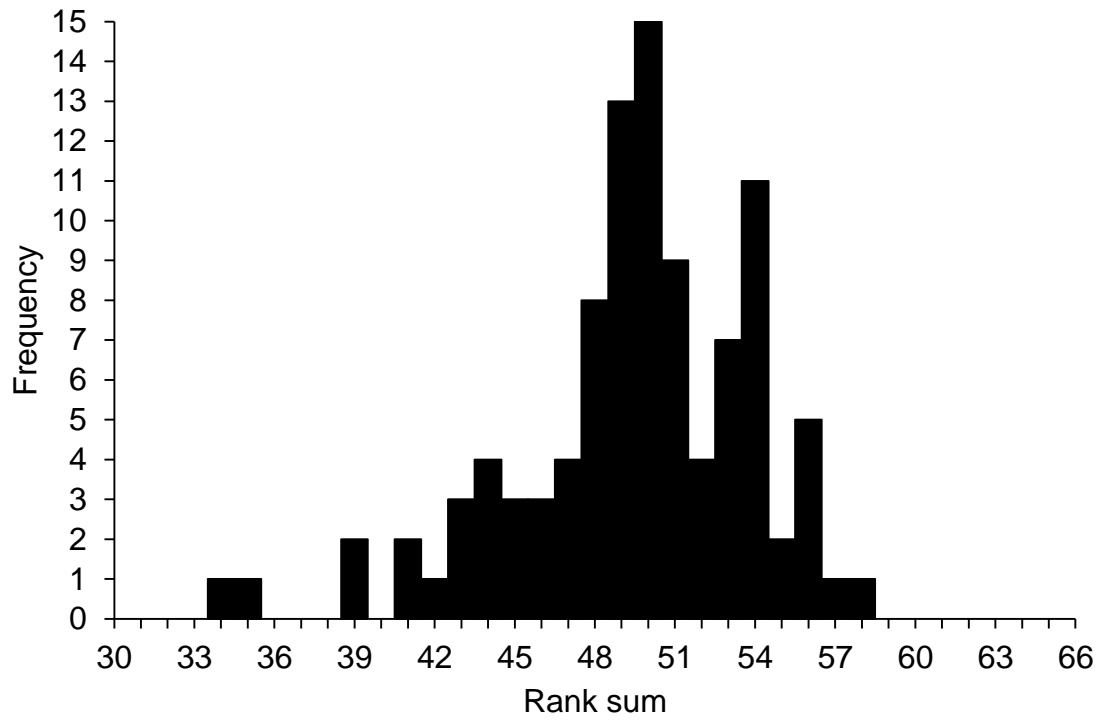
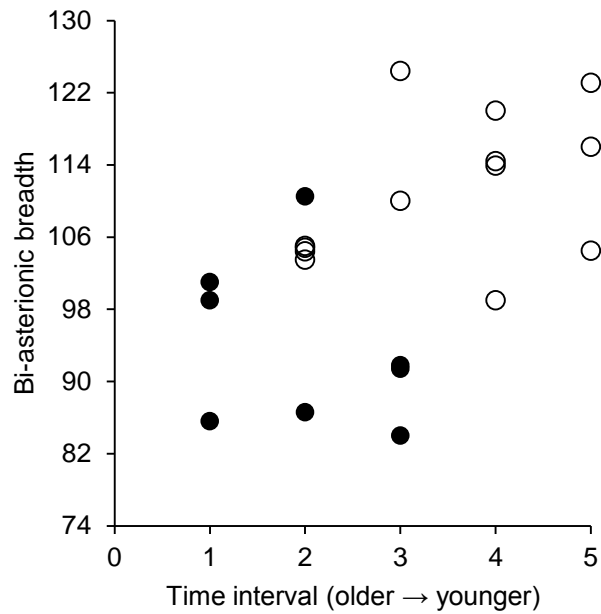
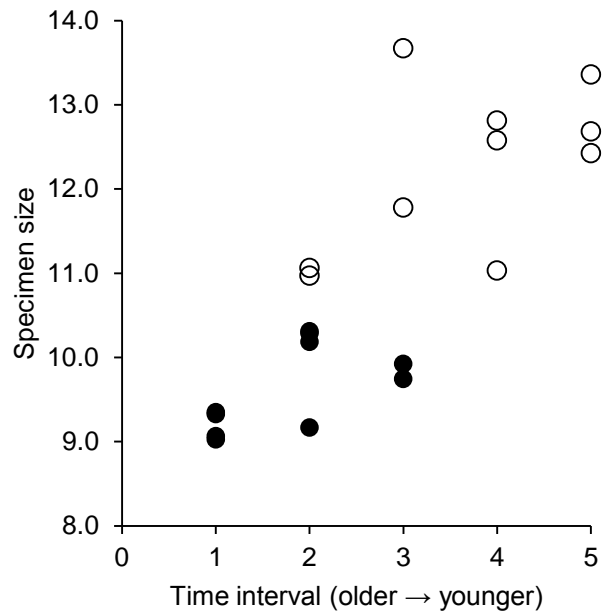


Figure 4

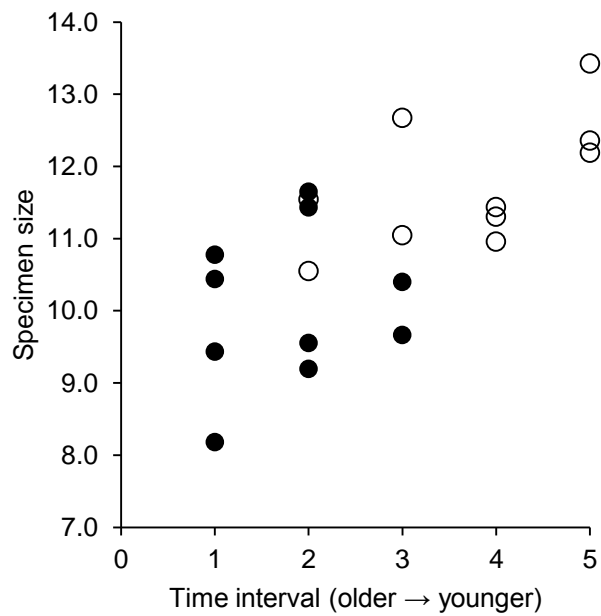
a



b



c



d

