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CHAPTER NINE

Average Body Weight for Mantled Howling Monkeys (*Alouatta palliata*): An Assessment of Average Values and Variability

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INTRODUCTION

Body weight is a universally accepted morphological descriptor for most organisms and is frequently given as a group or population average. This average is then used as a predictive tool in many fields such as ecology (Kendeigh *et al.*, 1977); behavior (Clutton-Brock and Harvey, 1977a,b); physiology (Pedley, 1977; Schmidt-Nielsen, 1979); and paleontology (Gould, 1966; Rensch, 1960).

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These predictions are only as reliable as the average body weight chosen because often there are several available. Frequently, this is not apparent to the reader of a published paper as no mention is made of the fact that there was more than one "average" available. Sometimes an average of the means from different sites is given without the original weights, standard deviations, or sample size specified (Froelich and Thorington, 1982). Further, weakening the validity of a cited average body weight is that the original source was an unpublished source.

In this paper, I present average body mass for mantled howling monkeys (*Alouatta palliata*) from two sites in Costa Rica and one in Panama, examine what a given "average" body mass number hides, and offer detailed analyses of 34 years of body mass fluctuations in one population of mantled howlers. The geographic relationship of the three study sites is given in Figure 1.

METHODS

Sites

Hacienda La Pacifica, Costa Rica

Hacienda La Pacifica (LP) (10°28′N and 85°07′W) is a 1990-ha ranch containing a mosaic of farmland, dry tropical forest, evergreen forest, and reclaimed pasture in varying degrees of secondary succession (Glander and Nisbett, 1996). The ranch experiences distinct wet (May to November) and dry (December to April) seasons with 99% of the average rainfall of 1553 mm (records for 81 years) occurring during the wet season of mid-May to mid-December.

Santa Rosa National Park, Costa Rica

Santa Rosa (SR) (10° 45′ to 11° 00′ N and 85° 30′ to 85° 45′ W) is a 10,700-ha National Park created in 1971 (Chapman *et al.*, 1995). The park experiences two distinct seasons with 98% of the 1527-mm yearly average rainfall occurring from late May to mid-December (Chapman *et al.*, 1995).

Barro Colorado Island, Panama

Barro Colorado Island (BCI) (9°09′N, 79°51′W) is a 1500-ha nature reserve

Figure 1. Location of the Costa Rican and Panamanian study sites plus sites from the northern and southern extremes of mantled howler geographic distribution. Map is modified version of the one supplied by courtesy of the General Libraries, The University of Texas at Austin. http://www.lib.utexas.edu/maps/americas/middleamerica.jpg, http://www.lib.utexas.edu/usage_statement.html

(records for 50 years) with 90% of that falling during the wet season from May through December (Rand and Rand, 1982).

Procedure

Individuals were captured using the Pneu-Dart™ system (Pneu-Dart, Inc., HC 31, Williamsport, PA 17701,USA) as part of long-term studies at each of the study sites (for a complete description of the capture methodology, see

Glander *et al.*, 1991). Once captured, the monkeys were weighed, measured, and marked for positive identification (unique collars plus tattoos as well as Avid chips (AVID, Norco, CA) for the LP individuals). Body weight in kg (to the nearest 100 g) was obtained using a 20 kg Pesola® scale.

All body weights are for fully adult individuals. Females were judged to be adult at 48 months and males at 60 months (based on known ages of 50 individuals of each sex). Weights for pregnant females were excluded after 3 months of pregnancy. The fetus weighs less than 100 g until after the fourth month. Gestation for mantled howlers is 6 months (Glander, 1980). All captured females were palpated and fetuses 3–4 weeks old can be detected.

The body weights for LP have been collected as part of a continuing long-term study begun in 1970 (Clarke, 1990; Clarke *et al.*, 2002; Clarke and Zucker, 1994; Glander, 1980, 1992; Glander and Nisbett, 1996; Glander *et al.*, 1991; Stuart *et al.*, 1998; Teaford and Glander, 1997; Ungar *et al.*, 1995; and references in these papers). The weights for SR were obtained in 1985, 1986, and 1992 (Chapman *et al.*, 1995; Glander *et al.*, 1991). The weights for BCI were collected in 1986 and 2000 (Glander and Milton, in prep.).

RESULTS

The body mass of howling monkeys from three locations (two in Costa Rica and one in Panama) was significantly different (Table 1). All three populations are sexually dimorphic with the males being significantly heavier than the females (BCI: $F = 65.71$, $p < 0.00001$); SR: $F = 65.60$, $p < 0.00001$; LP: $F = 621.72$, $p < 0.00001$). Males from BCI were significantly heavier than males from both SR ($F = 23.33$, $p < 0.00001$) and LP ($F = 295.50$,

Table 1. Average body weight for mantled howlers at three sites. BCI = Barro Colorado Island, Panama; SR = Santa Rosa, Costa Rica; LP = La Pacifica, Costa Rica. See Figure 1 for locations

	Males	Females
BCI	7562 g (±731) $N = 38$	6445 g (±553) $N = 49$
SR	6573 g (±483) $N = 15$	5161 g (±537) $N = 21$
LP	5790 g (±578) $N = 288$	4726 g (±616) $N = 663$

$p < 0.00001$). The SR males were significantly heavier than the LP males ($F = 26.54$, $p < 0.0001$). BCI females were significantly heavier than females from both SR ($F = 80.48$, $p < 0.00001$) and LP ($F = 360.50$, $p < 0.00001$). The SR females were significantly heavier than the LP females ($F = 10.25$, $p < 0.001$).

Females were significantly heavier during the wet season while males did not demonstrate a seasonal fluctuation in body weight (Table 2). Both females and males from Riparian (River) forests were significantly heavier than females and males living in Upland (Dry) forests (Table 3).

When season and habitat were considered together by sex, there were no seasonal differences in body weight either for females (Table 4) or for males (Table 5), but there was a habitat effect. Females living in Riparian Forests were significantly heavier in both dry and wet seasons than those living in Upland Forests (Table 4) just as the males living in Riparian Forests also were significantly heavier in both seasons than those in the Upland Forests (Table 5).

For individuals, the amount and percentage of change in body weight were much greater than the average. Females fluctuated 616 g on average or 13% of their body weight (Table 1), but it was as much as 1506 g for a riparian female (Purple) or 23% of her body weight (Figure 2) and 1500 g for an Upland female (Trinka) or 30% (Figure 2). Male body weights fluctuated less, both on average

Table 2. Seasonal differences in weights for La Pacifica howlers

	Dry season	Wet season	F	p-Value
Females	4598 g (±658) $N = 106$	4750 g (±607) $N = 539$	5.18	0.02
Males	5691 g (±630) $N = 48$	5807 g (±571) $N = 233$	1.58	NS

The values in the parentheses are SD.

Table 3. Body weight comparisons for La Pacifica howlers by habitat

	Upland Forest	Riparian Forest	F	p-Value
Females	4478 g (±521) $N = 262$	5006 g (±630) $N = 243$	105.91	<0.00001
Males	5695 g (±472) $N = 134$	6163 g (±598) $N = 63$	35.24	<0.00001

The values in the parentheses are SD.

Table 4. Female body weight by season and habitat at La Pacifica. Habitats within seasons affect body weights (columns) while season within the habitat does not (rows)

	Dry season	Wet season	*F*	*p*-Value
Upland Forest	4387 g (±543) $N = 66$	4509 g (±510) $N = 196$	2.70	NS
Riparian Forest	4994 g (±683) $N = 36$	5008 g (±622) $N = 207$	0.01	NS
F	24.18	77.07		
p-Value	<0.00001	<0.00001		

The values in the parentheses are SD.

Table 5. Male body weight by season and habitat at La Pacifica. Habitats within seasons affect body weights (columns) while season within habitats does not (rows)

	Dry season	Wet season	*F*	*p*-Value
Upland Forest	5606g (±570) $N = 34$	5725g (±434) $N = 100$	1.61	NS
Riparian Forest	6086g (±662) $N = 7$	6172g (±595) $N = 56$	.13	NS
F	3.92	28.98		
p value	0.05	<0.0001		

The values in the parentheses are SD.

and for specific individuals. On average, all males fluctuated 578 g or 10% of their body weight (Table 1) while a Riparian male (Bandit) oscillated 1300 g or 18% of his body weight and an Upland male (Chief) varied 1000 g or 16% (Figure 3).

DISCUSSION

It is clear from these results that there is no "average" body weight for mantled howlers. Populations of mantled howlers from three different locations in Central America differed significantly in body mass even though the two Costa Rica populations (LP and SR) are only 70 km apart. The SR males are 14% larger than the LP males while the SR females are 9% larger in average body weight (Table 1). The difference in average body weight is much greater between Panama and Costa Rican populations with BCI males being 15% larger than SR males and 31% heavier than LP males while BCI females are 25% larger

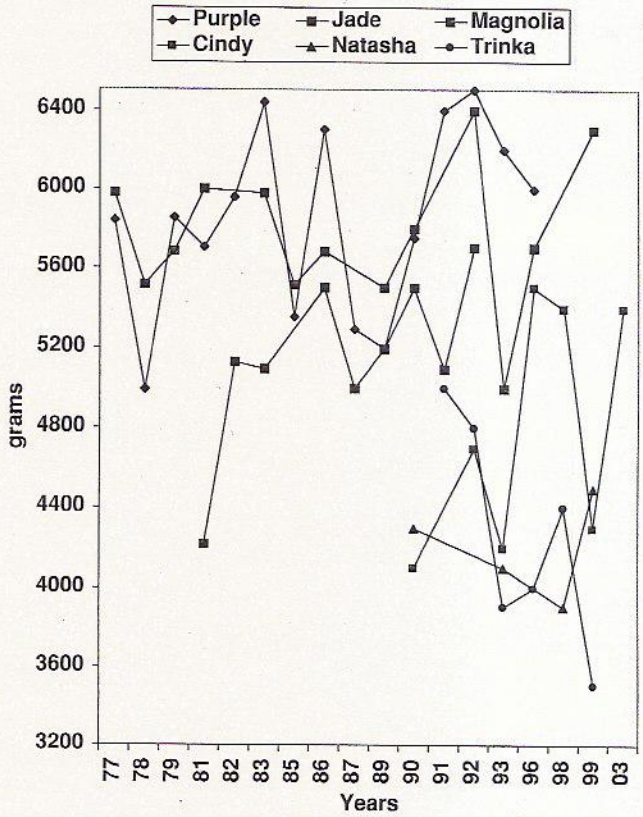

Figure 2. Weight fluctuations for females at La Pacifica. Purple, Jade, and Magnolia are from Riparian Forest while the other three are from Upland Forest.

Variation is even greater when the actual range for each population is considered rather than the range between "average" body mass. The body weight range of the LP population was 3320 g for adult females and 3000 g for adult males (Table 6). The smallest range was found in the SR population, but it was still 2000 g for females and 1500 g for males. Estrada (1982) reported similar ranges in both sexes for a Mexican population of mantled howlers (Table 6). In all documented populations, there is overlap between the sexes in body weight, that is, there were some females as large or larger than some males (Table 6).

Discussing "average" weights for various populations or even the actual ranges in body weights of a population does not value what fluctuations in body weight signify for individuals. Weight change presumes biological consequences, especially when a female loses 23–30% of her body mass (Purple and Trinka, Figure 2). Going from 5 kg to 3.5 kg (Trinka) may have a major impact

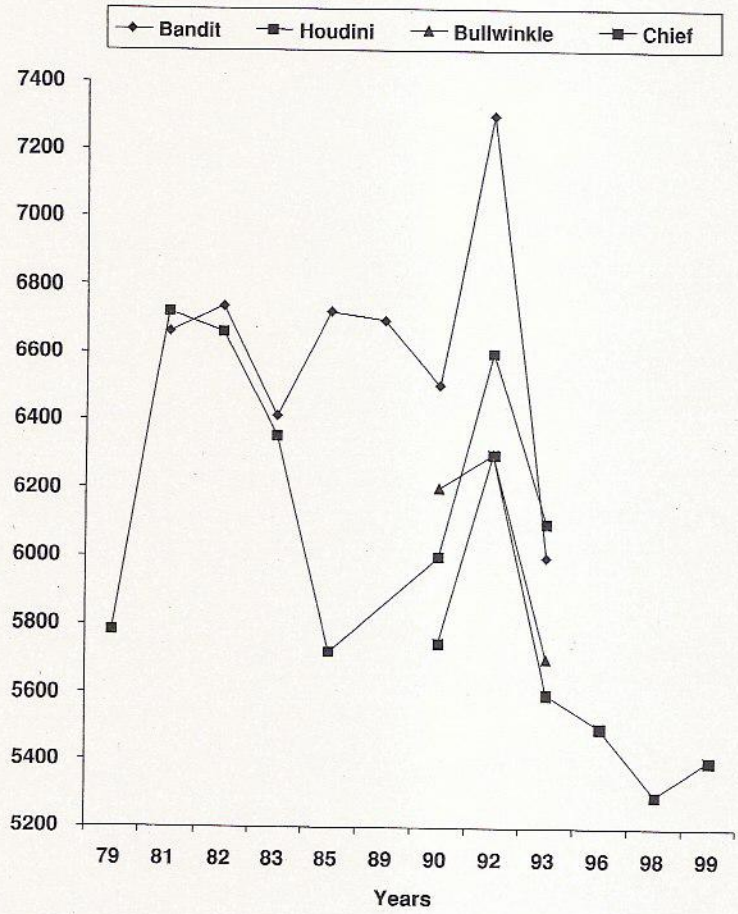

Figure 3. Weight fluctuations for males at La Pacifica. Bandit and Houdini are from Riparian Forest while the other two are from Upland Forest.

Table 6. Range of body weight from North to South in the geographic range of mantled howlers. See Figure 1 for site locations

Site	Males (g)	Females (g)	Source
Los Tuxtlas, Mexico	6430–9007 $N=5$	5000–8000 $N=7$	Estrada (1982)
Santa Rosa, Costa Rica	5750–7250 $N=15$	4000–6000 $N=21$	Glander *et al.* (1991)
La Pacifica, Costa Rica	4300–7300 $N=288$	3178–6500 $N=663$	This paper
BCI, Panama	6000–8750 $N=38$	5300–7900 $N=49$	Glander and Milton (in prep.)
Pachijal, Ecuador	7000–7150 $N=2$	na	Glander (unpublished)

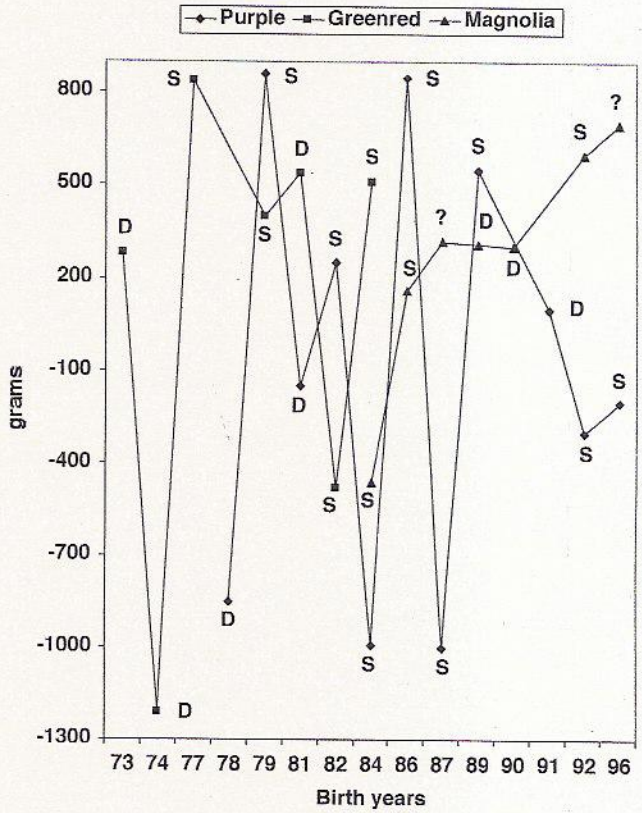

Figure 4. Weight fluctuations and infant mortality for three riparian females at La Pacifica. The first data point is the difference (plus or minus) from the previous year. The gain or loss occurred within ±6 months of the birth, thus impacts both gestation and lactation. D = died; S = survived; ? = unknown fate (D, S, and ? pertain to the infant's fate).

on life expectancy and reproduction (but see next paragraph). The males in this population experienced less actual body weight loss (900–992 g) and percentage loss (11%) (Figure 4). One reason for this may be that males are dominant and are not limited in their access to high quality food (Glander, 1992) as are the lower ranked females (Purple and Trinka were both low ranked in their groups). Also, males do not bear the burden of pregnancy or lactation that may contribute to a female's weight change.

Many models of within-group feeding competition assume that even slight differences in feeding efficiency or access to resources have a major impact on individual survivorship and fitness. Yet my data show that individuals can lose

10–30% of their body mass within a given year and still survive for many years (Figure 2). For example, Purple lost 1000 g or 15% of her body mass between July 1986 and August 1987, but lived for another 11 years. Trinka lost 900 g or 19% of her body weight between July 1992 and February 1993, but lived another 9 years. Both of these females had other dramatic weight fluctuations, as did all other females at LP without affecting their life span.

The same models suggest that a reduction in body mass should result in a reduction in fertility or infant survivorship. Again, my data contradict this assumption (Figure 4). Purple suffered weight losses of 990 and 1000 g but her infants born during and/or after these changes survived. Greenred experienced a weight loss of 480 g, but her infant also survived. These are just a few examples of many similar occurrences in the LP population. Figure 4 clearly shows that weight gain or loss is not correlated with infant mortality when viewed over the long-term.

These extreme variations in body mass of individuals or populations did not occur between members of different species but in individuals of the same species, i.e., *A. palliata*, or more commonly known as mantled howling monkeys (also referred to as howler monkeys, but I prefer the grammatically correct phrase "howling monkey" or "howlers" used by C. R. Carpenter in 1934). Mantled howlers have one of the largest geographic distributions, from southern Mexico to Ecuador (Rowe, 1996; Wolfheim, 1983). Within this geographic range, the "average" male howler weighs 4300–9007 g and the "average" female weighs 3178–8000 g (Table 6). The largest of each sex is more than double the smallest, yet all of these individuals are *A. palliata* (Ellsworth, 2000).

This tremendous range in body mass should raise a red flag for taxonomists, paleontologists, ecologists, and behaviorists who rely on body size to distinguish species, allocate species designation to fossils, study niche separation, and even predict behavior. Body size is one of the factors used to differentiate species (Groves, 2001) and differences in size are used by paleontologists to assign fossils to different species (Ciochon *et al.*, 2001). In ecological theory, body size is believed to be critical in foraging (Temerin *et al.*, 1984) as well as in community structure (Schoener, 1984; Terborgh, 1983). Vervaecke *et al.* (1999) used body size to estimate relative fighting abilities in *Pan paniscus* and predict dominance hierarchies.

The astonishing variation for each sex described here obviously calls into question the use of "average" body weights in any of these theories and models.

individuals (Lomolino, 2004). If this were the case, then LP howlers should be heavier than either the SR or BCI howlers since there are no other primates occupying the LP habitat while *Cebus capucinus* and *Ateles geoffroyi* share both the SR and BCI habitats with howlers. A similar line of reasoning suggests that smaller members of a feeding guild are usually heavier where competitors are missing (Grant, 1965; Schoener, 1970; McNab, 1971). The reality is the reverse of the expected.

Using habitat variations to explain these divergences in body mass for the mantled howlers is tempting since mantled howler geographic distribution is extensive with habitats including deciduous, riparian, evergreen, and montane forests (Crockett and Eisenberg 1987). One of the primary sources of habitat variation is food availability. And, established theory holds that reduced food availability should select for smaller body size (Hessee *et al.*, 1951; Lawlor, 1982). The BCI habitat is certainly different from the LP and SR habitats in rainfall and tree species composition and the BCI howlers are significantly heavier than either of the Costa Rican populations. However, the LP and SR habitats are similar in terms of tree species and rainfall (Chapman *et al.*, 1995; Glander and Nisbett, 1996) and the howlers at SR are also significantly heavier than those at LP despite similar habitats and similar food availability (Chapman *et al.*, 1995; Glander and Nisbett, 1996).

BCI does have more tree species and many more *Ficus* tree species and individuals (Milton, 1980) than either Costa Rican site (Chapman *et al.*, 1995; Glander and Nisbett, 1996). Certainly, the abundance of figs could help in explaining the larger body size of the BCI howlers despite the competition from two other primate species (Milton, 1982). But, there is no similar difference in food availability between the LP and the SR to explain the variation in body weights between these two Costa Rican populations.

It is also tempting to use population density as an explanation for body size variation, but the howler density of 72.7/km^2 for LP, Costa Rica (Clarke *et al.*, 2002), is less than the 91.7/km^2 on BCI, Panama (Milton, 1982). Further diluting this argument are the population densities of 4.9/km^2 at Santa Rosa National Park, Costa Rica (Fedigan *et al.*, 1985) and 23/km^2 at Los Tuxtlas in Mexico (Estrada, 1982). The largest "average" body size for both sexes is found in the habitat with the highest density of howlers (BCI) and this does not consider the added presence of two other primate species on BCI. Santa Rosa with the lowest population density has howlers that are significantly heavier than LP, but significantly lighter than BCI with the highest population density.

Based on these numbers, there is no relationship between howler population density and body size. The population density of the other primate species at some of these sites is not relevant because the competition explanation is not applicable as discussed earlier.

An argument could be made that the weight differences are due to micro-habitat differences, but these differences (if they exist) have not been discovered after long-term studies at both sites (21 years at SR and 34 years at LP).

These 34 years of research at LP and 1564 individual captures of uniquely marked animals provided an opportunity to examine body weight changes in the LP howlers over their life span (30 years), seasonally, and by habitat. Only the females showed a seasonal effect by weighing more in the wet season (Table 2). Both males and females living in the riparian forests were significantly heavier than those in the Upland forests (Table 3). It is not clear why only the females demonstrated a seasonal effect because fruit is primarily a wet season occurrence (Glander and Nisbett, 1996) and the males are dominant to all females (Glander, 1980). The habitat variation effect may be due to the availability of fruit since there are more fruiting species in the riparian habitats (Glander and Nisbett, 1996).

Despite the fact that females were significantly heavier in the wet season while the males showed no seasonal difference (Table 2), there were season and habitat effects by sex. There were no seasonal effects for females and males in either habitat. Tables 4 and 5 clearly show that habitat has a greater impact on body size than season. This points out the importance of looking at more than just overall seasonal and habitat differences. In fact, the overall seasonal impact disappears when broken down by season within habitats. The weight of females and males living in both types of habitat does not change seasonally, but both sexes living in the Riparian habitats are heavier than those living in the Upland forests.

CONCLUSION

Mantled howling monkeys (*A. palliata*) from two Costa Rican populations (SR and LP) and the island population of BCI were significantly different in body size with the "average" body weight of females ranging from 6445 g for BCI to 4726 g for LP. The "average" male body weight ranged from 7562 g for BCI

either of the Costa Rican populations while both SR sexes were significantly heavier than their LP counterparts.

As expected, the sexes were significantly different in body size; however, there was much greater variation in body weight between the populations than is usual when considering the same species. Especially, when body weights within populations exceeded that between populations. There also were seasonal and habitat variations in the weights of LP individuals and extreme individual fluctuations that did not correspond to reproductive condition nor to infant mortality.

These extreme weight differences are not explained by competition or by food availability for the Costa Rican populations. The type and variety of food in BCI may be a factor in the case of BCI howlers of both sexes being significantly heavier than the Costa Rican populations, even though the BCI population has the highest density and greater potential competition from other primate species. The heaviest individual howler of each sex is found at Los Tuxtlas, Mexico; a very different habitat from that found in BCI in terms of rainfall and tree species composition.

An "average" body mass is a myth for mantled howling monkeys. Anyone using mantled howlers as models must carefully consider the season, forest type, and population rather than simply using one average body size to represent all *A. palliata*. Unfortunately, detailed analyses of season, forest type, and populations are seldom available, but if they are, the "average" weight used for predictive purposes should be matched to the finest grained conditions available.

SUMMARY

A comparison of mantled howling monkey (*A. palliata*) body weights from the two Costa Rican populations at SR and LP plus the island population of BCI yielded average body weights of 6445 g for BCI females ($N = 49$), 5161 g for SR females ($N = 21$), and 4726 g for LP females ($N = 663$). Average male body weight for these same three populations was 7562 g for BCI ($N = 38$), 6573 g for SR ($N = 15$), and 5790 g for LP ($N = 288$). All three populations are sexually dimorphic with the males being significantly heavier than the females (BCI: $F = 65.71$, $p < 0.00001$); SR: $F = 65.60$, $p < 0.00001$; LP: $F = 621.72$, $p < 0.00001$).

The BCI females are significantly heavier than the SR females ($F = 80.48$, $p < 0.00001$) and LP females ($F = 360.50$, $p < 0.00001$). The BCI males are significantly heavier than the SR males ($F = 23.23$, $p < 0.00001$) and the

LP males ($F = 295.50$, $p < 0.00001$). The SR females are significantly heavier than the LP females ($F = 10.25$, $p < 0.001$) and the SR males are significantly heavier than the LP males ($F = 26.54$, $p < 0.0001$).

Female weight at LP showed a seasonal difference while season had no effect on male weight. There were habitat effects on both female and male weights. Individual body weights at LP oscillated from 10% to 30% within and between years. These dramatic changes in body mass did not reduce life span nor affect infant survivorship.

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