

BODY WEIGHT AND AGE INFLUENCES ON LIVER WEIGHT IN WHITE-  
TAILED DEER (*ODOCOILEUS VIRGINIANUS*): IMPLICATIONS FOR  
REPRODUCTIVE EFFORT

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## ABSTRACT

### BODY WEIGHT AND AGE INFLUENCES ON LIVER WEIGHT IN WHITE- TAILED DEER (*ODOCOILEUS VIRGINIANUS*): IMPLICATIONS FOR REPRODUCTIVE EFFORT

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The mammalian liver is integral to homeostasis, metabolism, and reproduction. Previous research into the liver has mainly examined liver function; there have been far fewer investigations into how liver weight is coupled to body weight, age, and reproductive events like lactation. Understanding how these variables are coupled to liver weight may be useful to understanding reproductive effort as animal age. I examined the scaling relationship between body weight and liver weight and the influences of age, sex, body condition (back fat), tooth wear, and lactation on liver weight to shed insight into the reproductive effort of

aging white-tailed deer. White-tailed deer (62 males, 71 females) from Kerr Wildlife Management Area, Texas, and a private ranch near Hebbronville, Texas, were measured. There was an allometric relationship between body weight and liver weight. Sex and age were predictors of liver weight at Kerr WMA and sex, back fat, and lactation were significant predictors at the private ranch. Controlling for body weight, males had heavier livers than females and age was positively related to liver weight. My findings indicate that liver weight reflects metabolic and reproductive demands and that older animals can potentially invest more effort in reproduction because of larger livers. These findings might be useful to understanding senescence and terminal investment on reproduction in older deer.

## **CHAPTER I**

### **THESIS**

#### INTRODUCTION

The liver is the largest visceral organ in the mammalian body and performs numerous metabolic and excretory functions necessary for survival and maintenance of homeostasis. Largely due to its unique circulatory anatomy with the absorptive surfaces of the gastrointestinal tract, the liver plays the initial role in the processing of nutrients ingested in the gastrointestinal tract as well as in detoxification of harmful substances absorbed through the gut (Barrett 2011). The liver is integral in oxidation of fatty acids and the conservation of nitrogen through urea cycling and also helps to regulate blood glucose levels by metabolizing carbohydrates (Barboza et al. 2009, Barrett 2011). Detoxification of blood in the mammalian body is performed by hepatocytes in the liver (Barrett 2011). The liver is also responsible for producing anticoagulants throughout life as well as red blood cells in early embryonic development (Leach 1961). Due to the integral contribution of the liver to metabolism and homeostasis, liver size should be useful in assessing the possible physiological level of reproductive effort in animals as they age. Previously, reproductive effort has been assessed through offspring size or survival, which might be confounded with parental experience (Clutton-Brock 1984, Green 1990, Ericsson et al. 2001, Hussey et al. 2010).

The varied and numerous functions performed by the liver suggest that many factors can affect liver weight. Age, body condition, and life history events such as lactation and previous births have a significant effect on the weight of mammals and in turn should affect the internal organs (Bollo et al. 1997, Therrien et al. 2008, Hewison et al. 2011). The combined effects of these various life history factors on the weight of ruminant livers, as well as the scaling relationship of body weight to liver weight, are largely unknown.

Nutrition and body condition have a direct effect on the weight of ruminant male and female livers (Johnson et al. 1990, Bollo et al. 1997). Sheep with high dietary intake exhibited a greater liver energy use intensity compared to fasting individuals (Johnson et al. 1990). Emaciated deer showed significantly smaller mean size of hepatocyte nuclei compared to those that were not emaciated (Bollo et al. 1997). Similar findings were found in a study where food-restricted deer showed significant reduction in body weight and organ cell size and number (Wolkers et al. 1994).

Van Soest (1994) found that regardless of life history events, the body weight and therefore organ weight of homeothermic animals is most likely constrained by their energy requirements. Metabolic rate presumably scales to the 0.75 power of body weight such that smaller animals exhibit a higher energy cost per unit of body weight (Van Soest 1994). Consequently, smaller animals require greater allocation to gastrointestinal size and capacity in relation to their body size than larger animals. Prothero (1982) reported interspecific liver weight scaled to the 0.89 power of body weight across adult mammals and was found to be independent of sex and habitat. In a review article of interspecific allometric patterns in mammals, Lindstedt and Schaefer (2002) reported that liver weight scaled to the 0.85-0.87 power of body weight. Prothero (1982) also found hepatic blood flow scaled to the 0.91 powers of body weight but noted that the scalar may be closer to 0.75 across the entire

mammalian range. Additionally, hepatic oxygen consumption of various mammalian species scaled to the  $0.67 - 0.77$  power of body weight (Prothero 1982).

In addition to body condition and size, age, tooth wear, and reproductive capacity influence liver size in mammals. In white-tailed deer (*Odocoileus virginianus*) fatty acid composition in the liver increased with age (Rule and McCormick 1998). In female rats, older and multiparous individuals had larger livers than nulliparous animals, even after reproductive senescence (Kennedy et al. 1958).

Lactation is the most energetically demanding activity in the lifetime of female mammals (Ericsson et al. 2001, Naya et al. 2008) and affects female body condition and size (Hewison et al. 2011). Lactating females have been observed with decreased body condition and weight as well as decreased fecundity in the next year suggesting a tradeoff between body maintenance and reproductive ability (Mitchell et al. 1976, Therrien et al. 2008). To meet the demand of lactation, lactating Holstein cows had heavier livers in relation to body weight than did steers (Johnson et al. 1990). Tooth wear may also impact the ability of individuals to adequately ingest food and assimilate nutrients leading to reduced lactation with age (Ericsson et al. 2001)

Due to the high metabolic demands of reproduction, two contrasting hypotheses have been developed to understand reproductive effort with age: terminal investment and senescence. As placental mammals age, it is predicted that their reproductive effort should increase as their reproductive value declines (Clutton-Brock 1984, Green 1990, Ericsson et al. 2001, Weladji et al. 2002, Hussey et al. 2010). Reproductive effort is often measured as an increase in offspring mass as the mother ages (Clutton-Brock 1984). Female moose exhibit a loss of viable ovarian oocytes as they age and were found to give birth to larger offspring to achieve offspring survival that was similar to that of younger moose. The older dams also

had a higher tolerance to offspring suckling, spent a longer time nursing (Green 1990, Weladji et al. 2002), and were better able to detect the offspring's critical period for suckling (Weladji et al. 2002). Indeed, it is difficult to ascertain if increases in weight and survival of offspring born to older mothers is due to increased reproductive effort or greater experience in caring for offspring (Clutton-Brock 1984, Green 1990).

Another non-mutually exclusive prediction is that reproductive effort decreases with age due to senescence, resulting in a loss of functioning and decreased performance with age (Weladji et al. 2002). Senescence is manifested as a decrease in cell-division capacity of reproductive organs and through the effect of tooth wear on food consumption, thus inhibiting the ability to assimilate nutrients and lactate (Ericsson et al. 2001). Senescence is usually detected by declining body weight and survival in older males and females (Loison and Festa-Bianchet 1999, Gaillard et al. 2000, Ericsson and Wallin 2001, Nussey et al. 2011, Robinson et al. 2012). However, few studies examine changes in size of vital organs with age while controlling for body weight (Green 1990, Weladji et al. 2002).

There is much conflict as to whether the terminal investment or senescence hypotheses best explains reproductive patterns of older animals. Due to the high metabolic demands on the mammalian liver and its significance in overall health, a positive or no relationship between age and liver weight, controlling for body weight, would support the terminal investment hypothesis. Conversely, a decline in liver weight with age, controlling for body weight, would favor the senescence hypothesis. I examined the relationships of body weight, age, tooth wear, and reproductive events to liver weight to shed insight into the reproductive effort of aging white-tailed deer.

## METHODS

### *Study areas*

White-tailed deer were collected from two study areas. One study area, Kerr Wildlife Management Area (WMA), was located in Kerr County, Texas, USA. Average annual precipitation was 69.7 cm. Average temperature on Kerr WMA was 7°C in January and 27°C in July with an average annual temperature of 18°C. The deer in this study were confined to six 0.27-ha breeding pens and three 1.62-ha rearing pens enclosed by a 2.5 m high game fence. Their primary diet was food pellets in addition to about 1 kg (dry weight) of alfalfa provided per animal, per week. Kerr Wildlife deer pellets consisted of a minimum crude protein of 16% and 18.5% acid detergent fiber (Lockwood et al. 2007).

The other study area was a 3,238 ha private ranch (hereafter, the ranch) in Jim Hogg County, Texas, USA in the brush country region of south Texas. The deer at this study site were free-ranging. The average annual precipitation was 60.5 cm. The average temperature in January was 14°C and 30°C in July with an average annual temperature of 23°C. The dominant vegetation on the ranch included honey mesquite (*Prosopis glandulosa*), cenizo (*Leucophyllum frutescens*), retama (*Parkinsonia aculeata*), western ragweed (*Ambrosia psilostachya*), tanglehead (*Heteropogon contortus*), woolly croton (*Croton capitatus*), Hooker's palafoxia (*Palafoxia hookeriana*), prickly pear (*Opuntia* spp.), sand bur (*Cenchrus spinifex*), little bluestem (*Schizachyrium scoparium*), king ranch bluestem (*Bothriochloa ischaemum*), and Johnson grass (*Sorghum halepense*).

### *Specimen and data collection*

The data at Kerr WMA were collected near the peak of the mating season in central Texas in November, 2011 (Robinson et al. 1965). The deer were dispatched using a high powered rifle and brought to a central staging area where they were processed within thirty

minutes of death. Live weight, minus blood loss, was recorded to the nearest 0.1 kg after which visceral organs were removed. The rumen-reticulum was then separated from the liver and spleen. The rumen was severed from the rest of the digestive tract at the reticulo-omasal junction and 5 cm above the junction of the esophagus and reticulum and then weighed with contents to the nearest 0.1 kg (Weckerly et al. 2003, Ramzinski and Weckerly 2007). After which the rumen was inverted, rinsed with tap water, re-weighed and weight of the contents determined to the nearest 0.1 kg by subtraction. During data analysis, rumen content weight was subtracted from the body mass to lessen the influence of the weight of gut contents on the scaling relationship. In deer, the rumen-reticulum comprises > 60 percent of the gut contents (Ramzinski and Weckerly 2007, Barboza et al. 2009). The liver was also weighed to the nearest 0.1 kg. Along with back fat measurements, sex and the number of young that females weaned that year were also noted. A juvenile was considered weaned if it survived to 90 days of age. Back fat, which is a measurable indication of body condition, was determined by making an incision adjacent to the L<sub>2</sub> to L<sub>4</sub> vertebrae and measuring the thickness of the fat with a ruler to the nearest 0.1 cm (Stephenson et al. 2002). Birth date of each deer was known and only animals  $\geq 1.5$  years of age were included in data collection.

Free-ranging deer at the ranch were collected on 16-17 October, 2010. The collection occurred before the mating season which begins in late December (Webb et al. 2007). The deer were net-gunned then restrained before being dispatched with a high-powered rifle. The animals were then brought to a central area where they were processed to a similar manner as the specimens at Kerr WMA. The right mandibular bone was also measured in cm with a tape measure. Adults (>1.5 years) at the ranch had an estimated age based on tooth wear and replacement and only animals >1.5 years were included in the study (Severinghaus 1949). Lactation was determined by whether the teats contained milk. Tooth



wear was indexed by measuring the height of the first molar (M1) to the nearest 0.01 mm using digital calipers. Measurements were taken on the lingual side of the right mandible from the tip of the tooth's cusp to the enamel/cementum line (Skogland 1988, Loe et al. 2003, Carranza et al. 2004, Veiberg et al. 2007, Ozaki et al. 2009). Validity of the tooth wear index was examined by measuring the M1 height as well as length and width of the occlusal surface to the nearest 0.01 mm with digital calipers on another set of specimens from Kerr WMA. Pearson's correlation coefficients were estimated between the M1 height and the width and length of the occlusal surface on M1 (Sokal and Rohlf 2012). An inverse correlation was found between the height of M1 and the width of the occlusal surface ( $r = -0.82$ ,  $n = 41$ ,  $p < 0.001$ ) and a positive correlation was detected between the length of the occlusal surface and the height of M1 ( $r = 0.51$ ,  $n = 41$ ,  $p < 0.001$ ). The correlations support the use of M1 height as an index of tooth wear. The tooth wear index included in analyses was adjusted for body size of the animal by dividing the height of M1 in mm by the right mandible length taken in cm.

### *Statistical analyses*

Statistical analyses were conducted using program R. Least squares regressions were performed with a complete model that had all possible predictors that could influence natural log transformed liver weight. A reduced model was then analyzed with only the significant predictors from the complete model (Sokal and Rohlf 2012). Predictors of the complete Kerr WMA model included log transformed body weight minus rumen-reticulum weight, sex, number of weaned and surviving young in the previous year, back fat in cm, and age. The complete ranch model had predictors of log transformed body weight minus rumen-reticulum weight, tooth wear, sex, back fat, and lactation.

## RESULTS

There were a total of 133 animals, 19 males and 27 females taken from Kerr WMA and 43 males and 44 females from the ranch. Back fat measurements of the deer from Kerr WMA ranged from 0 to 2.22 cm for males and 0 to 1.59 cm for females. At the ranch back fat measurements of males ranged from 0.16 to 5.08 cm and 0.16 to 3.81 cm for females. Tooth wear for the ranch animals ranged from 0.11 to 0.58 according to the tooth wear index.

For the Kerr WMA data, body weight, sex, and age were significant predictors of liver weight but back fat and number of weaned young were not (Table 1). For the ranch data, body weight, sex, back fat, and lactation were significant predictors of liver weight but tooth wear was not (Table 2). At both sites, males had larger livers and there was a positive relationship between body weight and liver weight (Fig. 1, 2). The estimated scalar (slope) for liver weight at Kerr was 0.66 and 0.72 at the ranch. There was also a positive relationship between age and liver weight in both males and females at Kerr WMA (Fig. 3).

## DISCUSSION

Results of this study offer empirical evidence supporting the terminal investment hypothesis in male and female white-tailed deer. The increase in liver weight with age observed in this study implies older animals have the potential to allocate more effort to reproduction than younger animals. Also, the body weight to liver weight scalar was allometric (0.66-0.72). The liver weight scalar is statistically indistinguishable from 0.75, the presumed scalar for metabolic rate (Van Soest 1994). My estimated liver weight scalar is consistent with the notion that the liver is indicative of the metabolism, homeostasis, and reproduction in white-tailed deer (Barrett 2011).

As animals age, their reproductive value decreases but reproductive costs remain (Clutton-Brock 1984). This study provides evidence of compensation for decreased reproductive value by an increase in reproductive effort. As the animals aged, liver weight increased. A larger liver implies greater physiological demands and increased metabolic functioning (Johnson et al. 1990, Wolkers et al. 1994, Bollo et al. 1997, Ribeiro et al. 2001). Past studies have quantified reproductive effort with offspring survival and size, which can be attributed to confounding factors (Clutton-Brock 1984, Green 1990, Ericsson et al. 2001, Hussey et al. 2010). Increased parental experience with age may account for greater offspring survival through a higher suckling tolerance, longer time spent nursing (Green 1990, Weladji et al. 2002), and a greater ability to detect critical periods when the offspring needs to nurse (Weladji et al. 2002). My study suggests that liver weight might be a physiological measure of reproductive effort that should be less influenced by parental experience.

In male ungulates, reproductive effort is reflected in weight loss and compromised body condition during the mating season (Barboza et al. 2004). In Fig. 3, the 8.5 year old male age group from the Kerr WMA data exhibited a lighter liver weight than the 4.5 and 5.5 year old age groups. The regression was estimated based on the average weight of individuals in each age group, of which there was only one individual in the 8.5 year group. The ostensibly lighter liver of the 8 year old male is due to the much lighter body weight of this animal. Other studies have reported that prime aged individuals exhibit much weight loss during the mating season (Yoccoz et al. 2002, Jennings et al. 2010). The oldest male most likely exhibited a lighter body weight due to the demands of reproductive activities. However, the limited sample size for males in particular at Kerr WMA suggests that findings and conclusions should be viewed cautiously.

At both study sites, males exhibited larger livers than those of females. Male livers, controlling for body weight, were about 8 to 14 percent larger than female livers. To my knowledge, differences in liver weights between the sexes have not been reported in ruminants when body weight differences between the sexes were controlled and female lactation status was taken into account. It is likely that the liver weight differences are due to differing reproductive demands between males and females in November. It is unlikely that the greater liver weights in males are due to differences in body condition or back fat thickness. At the ranch, males (mean = 3.15 cm) had noticeably more back fat than females (1.28 cm). At Kerr WMA, however, there were not extensive differences between males (0.68 cm) and females (0.42 cm) in back fat thickness. Interestingly, liver weights of Kerr WMA females were not influenced by whether they reared 0, 1, or 2 young that year whereas at the ranch lactating females had heavier livers. Females at Kerr WMA might have weaned young earlier than at the ranch and, thus, had sufficient time to recover energy stores lost during the demands of lactation. It is also possible that the high quality diet that Kerr WMA animals consumed allowed females to recover from the demands of lactation more quickly than the free-ranging animals at the ranch.

Tooth wear exhibited no relationship with liver weight. This finding is somewhat surprising in that chewing effectiveness declines with tooth wear and particle sizes of ingested food take longer to comminute (Perez-Barberia and Gordon 1998, Logan 2003, Myrsetrud et al. 2007). Tooth wear has also been positively associated with weight of rumen contents, suggesting that animals with more tooth wear tend to have larger particles in their gut (Veiberg et al. 2009). There are 2 possibilities to explain why an influence of tooth wear on liver weight was not detected. First, tooth wear was not great enough to affect particle comminution, and second, animals with greater tooth wear adjust chewing behavior to

compensate for the reduced effectiveness of molar teeth in comminuting particles (Perez-Barberia and Gordon 1998, Logan 2003).

The body weight to liver weight scalar that is allometric with a value less than 1.0 is similar to what has been found in humans (Muller et al. 2001). Moreover, in humans, liver weight has a strong correlation with metabolic rate. Although intraspecific scaling relationships can vary for liver, brain, kidneys, and heart, all of the scalars were still less than 1.0 indicating that intraspecific metabolic rate also has a scalar less than 1.0 (Wang et al. 2011). The scaling relationship of body weight to liver weight therefore provides some information about the metabolic demands of animals that range in body weight as well as in reproductive demands.

The interspecific body weight-liver weight scalar observed in previous studies, 0.85-0.89, is slightly higher than that estimated herein, 0.66-0.72. On an interspecific basis, mammals apparently show a larger unit weight increase in liver weight with every one unit increase in body weight (Prothero 1982, Lindstedt and Schaeffer 2002). The reasons for this disparity are difficult to ascertain. Confidence intervals are rarely reported for scaling estimates. There might be broad overlap between intra- and interspecific scalars indicating no real difference. It might also be possible that the interspecific scalar may reflect heterogeneity due to ancestry, diet, and life history (McNab 2008, Isaac and Carbone 2010).

This study found empirical evidence supporting the terminal investment hypothesis by detecting a positive relationship between age and liver size. The scalars of body weight to liver weight in white-tailed deer were also found to range from 0.66-0.72. Further research would be beneficial to extensively determine terminal investment through organ size and physiological functioning. Previous research into the liver has mainly examined liver function and its role in metabolism, homeostasis, and reproduction. This study showed liver weight

variation also can be used to understand life history. Further research is also necessary to comprehensively understand the intraspecific scalar relationship and the specific factors influencing it.

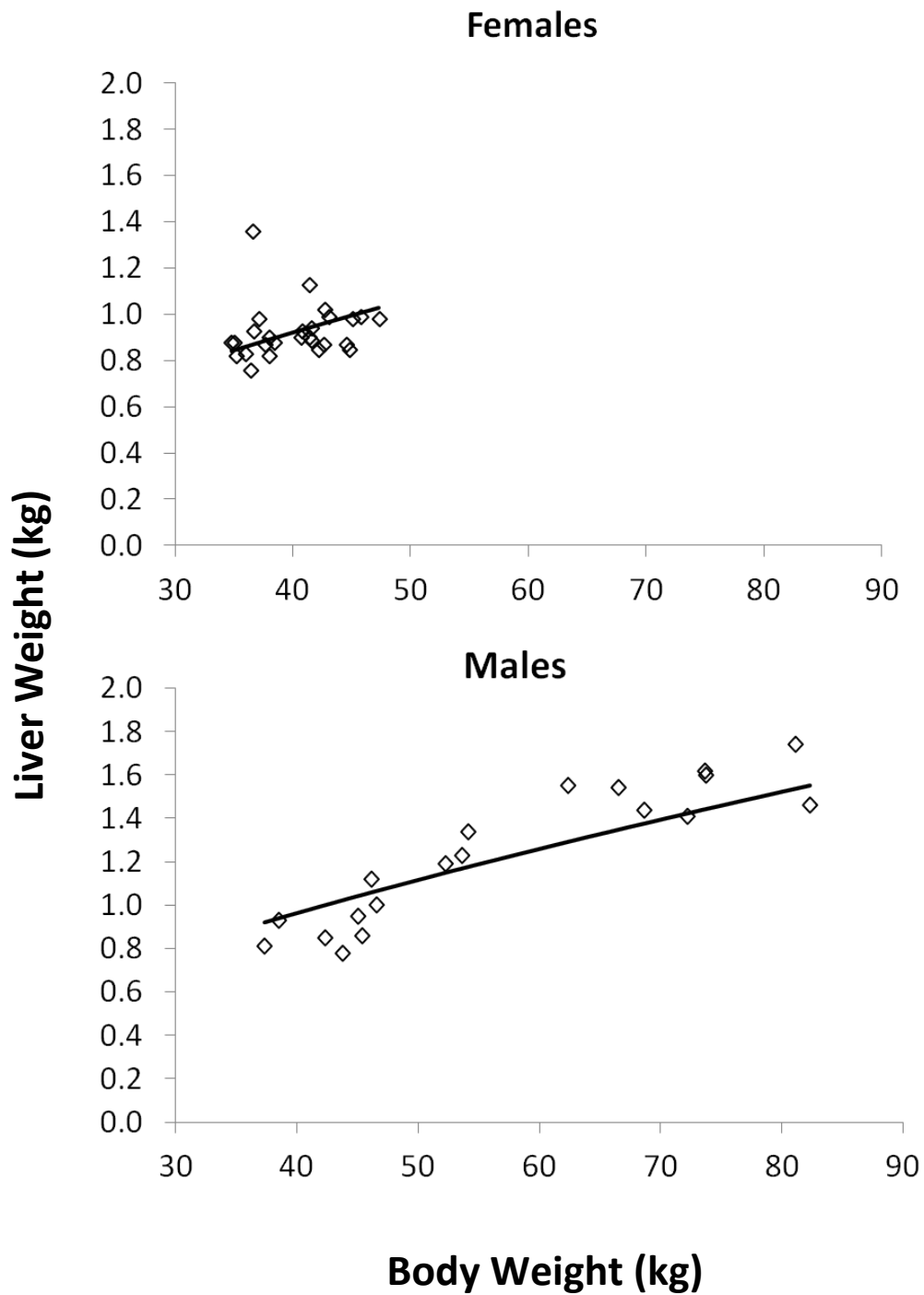
**Table 1** Estimates of regression coefficients and lower (lb) and upper bounds (ub) of 95 percent confidence intervals of intercepts and predictors of liver weight (kg) of white-tailed deer (*Odocoileus virginianus*), at Kerr WMA, Kerr County, Texas, USA, November, 2011. The reduced model contains only significant predictors from the complete model. The adjusted  $R^2$  for the complete model is 0.82 with error degrees of freedom of 39. The reduced model adjusted  $R^2$  is 0.83 with errors degrees of freedom of 42. The intercept and body weight coefficients are in natural logarithm scale. Female was the reference category for sex.

Parameter	Coefficients					
	<u>Complete</u>			<u>Reduced</u>		
	lb	Estimate	ub	lb	Estimate	ub
Intercept	-3.48	-2.53	-1.58	-3.41	-2.80	-2.18
Body Weight	0.31	0.59	0.87	0.48	0.66	0.84
Sex	0.01	0.17	0.32	0.08	0.19	0.30
1 Weaned Young	-0.19	-0.05	0.09		-	
2 Weaned Young	-0.17	-0.05	0.07		-	
Back Fat	-0.06	0.02	0.10		-	
Age	0.02	0.04	0.06	0.02	0.04	0.06

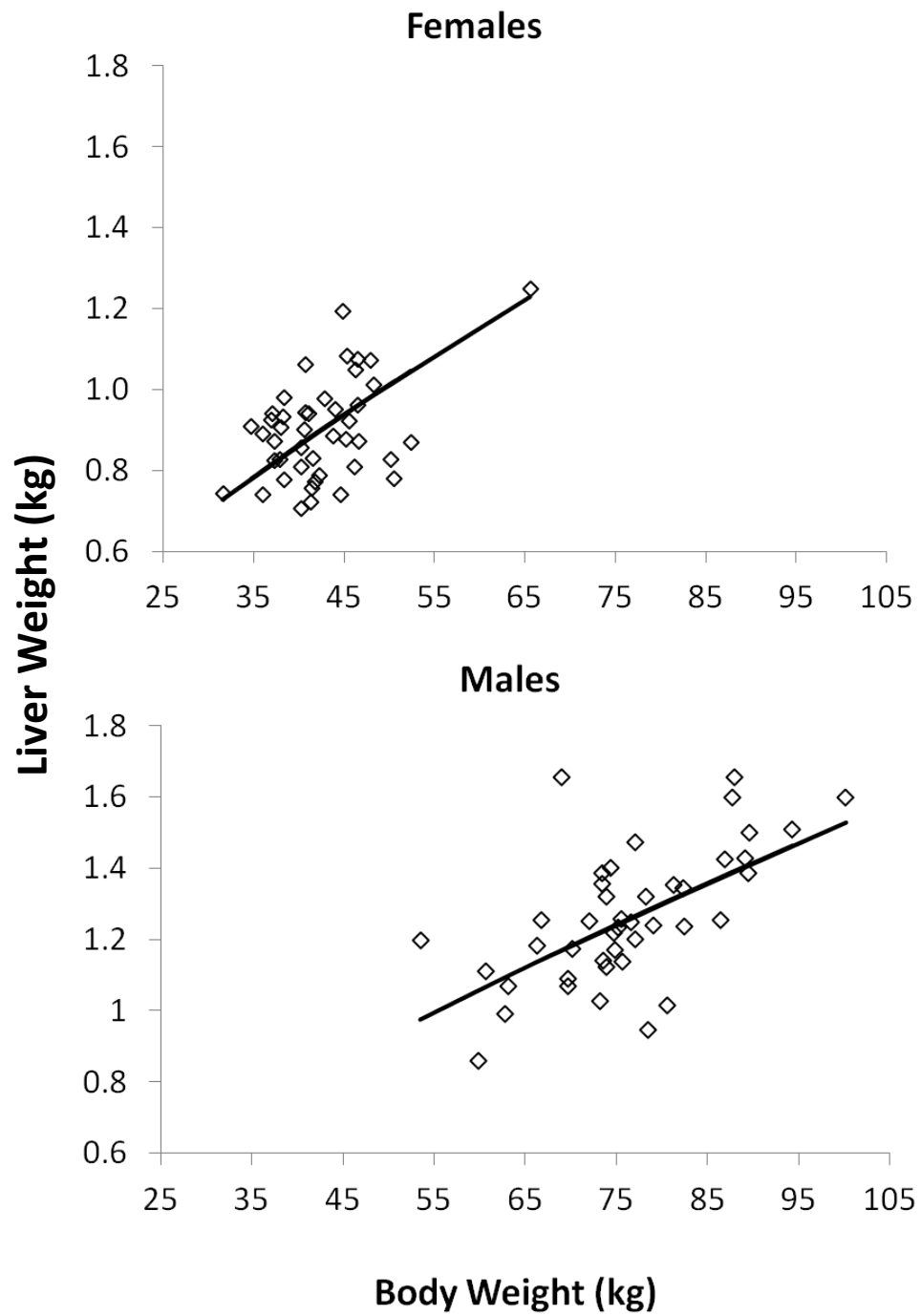
**Table 2** Estimates of regression coefficients and lower (lb) and upper bounds (ub) of 95 percent confidence intervals of intercepts and predictors of liver weight (kg) of white-tailed deer (*Odocoileus virginianus*) at the ranch in Jim Hogg County, Texas, USA, October, 2010. The reduced model contains only predictors from the complete model. The adjusted  $R^2$  for the complete model is 0.76 with error degrees of freedom of 81. The reduced model adjusted  $R^2$  is also 0.76 with 82 degrees of freedom for error. The intercept and body weight coefficients are in natural logarithm scale. Female was the reference category for sex.

Parameter	Coefficients					
	<u>Complete</u>			<u>Reduced</u>		
	lb	Estimate	ub	lb	Estimate	ub
Intercept	-3.48	-2.62	-1.76	-3.54	-2.70	-1.86
Body Weight	0.49	0.70	0.91	0.52	0.72	0.92
Sex	0.11	0.13	0.25	0.01	0.13	0.25
Tooth wear	-0.16	0.14	0.43	-		
Lactation	0.04	0.12	0.20	0.04	0.12	0.20
Back Fat	0.02	0.06	0.10	0.03	0.07	0.11

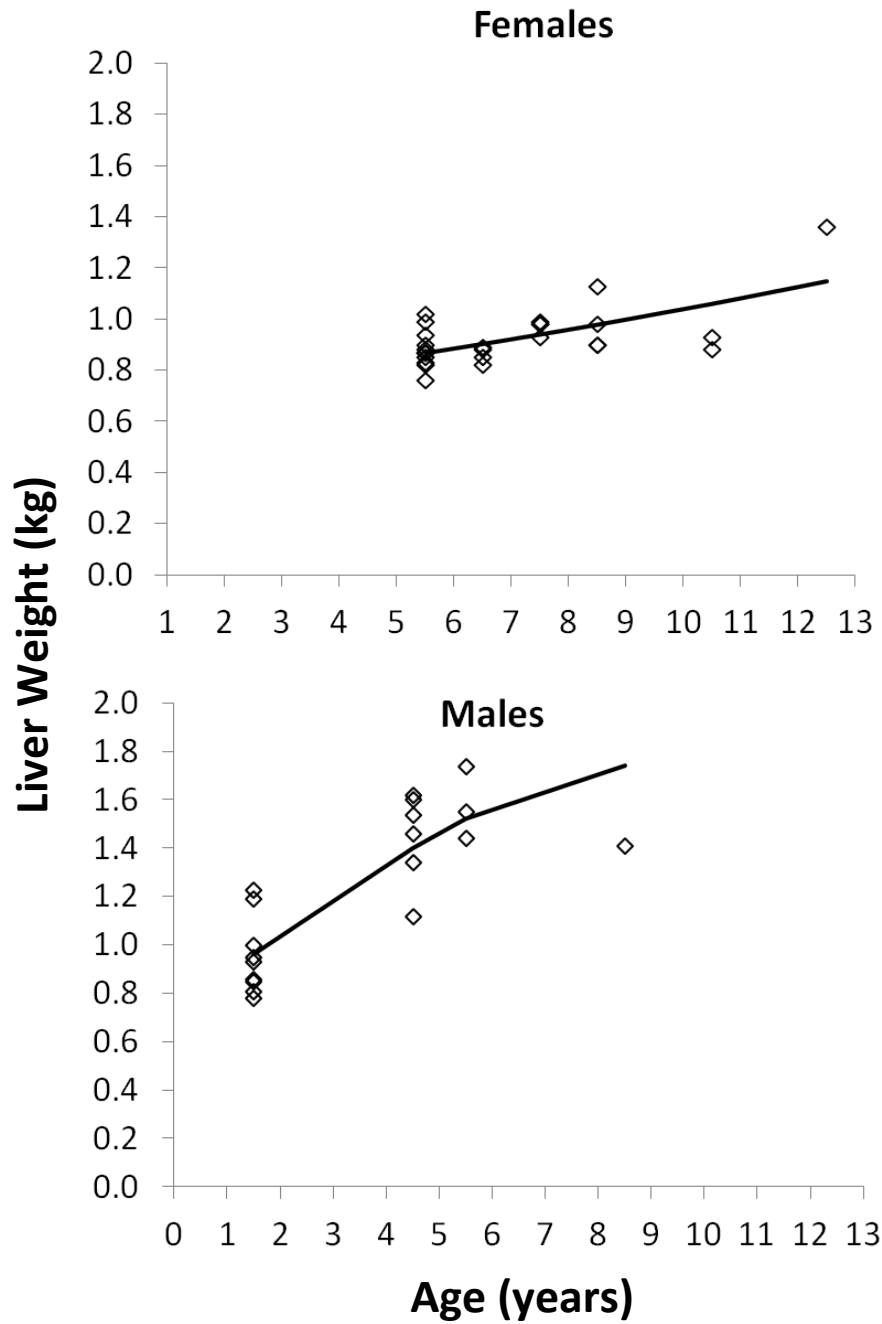




**Figure 1** Body weight (kg) and liver weight (kg) data with regressions for male and female white-tailed deer (*Odocoileus virginianus*) at Kerr WMA, Kerr County, Texas, USA, November, 2011. The mean age for each sex was used in the analysis.



**Figure 2** Body weight (kg) and liver weight (kg) with regressions for male and female white-tailed deer (*Odocoileus virginianus*) at the ranch, Jim Hogg County, Texas, USA, October, 2010.



**Figure 3** Liver weight (kg) and age (yrs) with regressions for male and female white-tailed deer (*Odocoileus virginianus*) at Kerr WMA, Kerr County, Texas, USA, November, 2011. The mean body weight was used for females and the mean body weight for each age was used for males.

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## **VITA**

Claire Parra (formerly Claire Larkin) was born and raised in Austin, Texas and has always shown an interest in science and a love for animals. She earned a B.S. in biology at Texas State University San Marcos in spring of 2010 and joined the Wildlife Ecology Program at Texas State in the fall of 2010. Areas of interest include birds and mammals with a focus in ecology and conservation. She hopes to continue working in central Texas in her fields of interest.

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