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# Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal

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## Summary

**1.** Body reserves of numerous taxa follow seasonal rhythms that are a function of temporal patterns in food availability and life-history events; however, tests of the theory underlying the allocation of somatic reserves for long-lived organisms are rare, especially for free-ranging mammals. We evaluated the hypothesis that allocation of somatic reserves to survival (i.e., metabolic processes) and reproduction should be sensitive to current nutritional state relative to seasonal thresholds in those reserves.

**2.** Our goal was to reveal the linkages between nutrition and life-history traits to understand how long-lived, iteroparous organisms balance the allocation of somatic reserves to reproduction, while retaining reserves as insurance for survival in unpredictable environments. Our evaluation was based on seasonal dynamics in fat (measured as ingesta-free body fat; IFBFat) and protein reserves (measured as ingesta-free, fat-free body mass; IFFFBMass) of 136 female mule deer (*Odocoileus hemionus*) over 8 years.

**3.** Although mean changes in fat and protein reserves were positive over summer and negative over winter, accretion and catabolism of those reserves was not consistent among individuals. Over winter, both lipid and protein stores available in autumn were catabolized in proportion to their availability above a post-winter threshold (5·8% IFBFat, 33 kg IFFFBMass); however, lean body tissue was spared at the expense of lipid reserves.

**4.** Female deer mostly synthesized lean body tissue over summer and committed post-winter fat reserves to reproduction relative to their availability above an autumn threshold (>8·6% IFBFat), which was lowered by 2·8 percentage points (pp) for each additional young recruited. Mothers reduced their autumn fat threshold to secure current reproductive investment and, thereby, endured a cost of reproduction at the expense of fat accumulation.

**5.** Allocation of somatic reserves occurred in a risk-sensitive framework; females allocated reserves relative to their availability above seasonal thresholds. In contrast to current notions of summer accretion and winter catabolism of body reserves, some individuals deposited reserves over winter and catabolized reserves over summer, mainly because regulation of individual condition was state-dependent. Consequently, behaviour and life-history strategies may be as much a function of nutritional contributions of the previous season as of the current one.

**Key-words:** California, carry-over effects, compensation, cost of reproduction, life-history strategies, mule deer, nutritional condition, recruitment, Sierra Nevada, trade-offs

## Introduction

Animals exhibit an array of behavioural and physiological strategies to survive and reproduce. Individuals may rely on internal stores or external sources of nutrients, or a combination thereof, to fuel seasonal demands for maintenance and reproduction (McNamara & Houston 1990; Jönsson 1997; Festa-Bianchet, Gaillard & Jorgenson 1998; Parker, Barboza & Gillingham 2009). Internal stores are composed of protein (skeletal muscle) and energy (lipids; Oftedal 2000). A central tenant of life-history theory, the cost of reproduction, concerns the manner that individuals

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*Correspondence author. E-mail: kmonteit@uwyo.edu allocate resources to current reproduction vs. reserving resources to insure future survival (Williams 1966; Stearns 1992). With few exceptions, theoretical and empirical evidence indicates that females of long-lived species should adopt a conservative strategy to favour their own survival and secure the potential for future reproduction—an over-investment in reproduction could jeopardize survival in seasonal and unpredictable environments (Gaillard *et al.* 2000; Ricklefs 2000; Bårdsen *et al.* 2008, 2011; Therrien *et al.* 2008).

In temperate and arctic regions, large terrestrial herbivores encounter marked variation in food availability and exhibit life-history tactics that differ among seasons, both of which determine metabolic demands and the resources available to meet those demands. Winter often is conceptualized as a nutritional bottleneck, resulting in the mobilization of somatic reserves and precipitating a decline in physical condition (Adamczewski *et al.* 1987; Hobbs 1989; Parker, Barboza & Stephenson 2005). In an unpredictable environment, individuals should ensure that they retain reserves during summer that are sufficient to survive a nutritionally demanding winter (Bender, Lomas & Browning 2007; Bårdsen *et al.* 2008; Bårdsen *et al.* 2010). Consequently, nutritional reserves may fluctuate around seasonal set points or thresholds that determine regulation of body reserves between seasons (Renecker & Samuel 1991); however, the mechanisms involved are not well understood.

In contrast to winter, summer is viewed as a period of nutritional abundance leading to the accretion of somatic reserves and is considered a critical period for replenishment of reserves lost during winter (Mautz 1978; Bårdsen & Tveraa 2012). Nevertheless, lactation is energetically expensive (Moen 1978), and somatic reserves available following winter are mobilized by mothers when energetic income cannot meet lactational demands (Landete-Castillejos *et al.* 2003; Tollefson *et al.* 2010). Consequently, somatic costs of reproduction may force a trade-off between current reproductive investment and future reproduction and survival for iteroparous animals (Therrien *et al.* 2008; Bårdsen & Tveraa 2012).

We investigated seasonal dynamics of fat and protein reserves of a large migratory mammal from a long-term, longitudinal study of mule deer (*Odocoileus hemionus*) in a highly variable environment, Sierra Nevada, California, USA (Monteith *et al.* 2011; Pierce *et al.* 2012). Our goal was to reveal the linkages between nutrition and life-history traits to understand how long-lived, iteroparous organisms balance the allocation of somatic reserves to reproduction with retaining reserves as insurance for survival in an unpredictable environment.

Adaptation to highly variable and seasonal environments may require animals to prepare for periods of food deprivation during winter by replenishing body reserves during summer and attaining a seasonal-specific level of fat stores (i.e., seasonal threshold; Schwartz, Hubbert & Franzmann 1988; Renecker & Samuel 1991). Ungulates in temperate and arctic climates are fat reserve obligates and can possess fat reserves that approach 25% of body mass, with levels <1% indicative of acute malnutrition (Parker, Barboza & Gillingham 2009; Cook *et al.* 2010). Bårdsen *et al.* (2008) proposed the hypothesis of risk-sensitive reproductive allocation, wherein long-lived organisms allocate resources to reproduction conservatively to enhance survival and secure the potential for future reproduction. Risk-sensitive reproductive allocation aligns with life-history theory and the selfish-mother hypothesis (Festa-Bianchet & Jorgenson 1998), whereby female ungulates favour their own survival over investment in their progeny. We extended the model of risk-sensitive reproductive allocation to encompass additional life-history traits. We hypothesized that allocation of fat and protein reserves to survival (i.e., metabolic processes) and reproduction occurs in a risk-sensitive framework, wherein seasonal synthesis and catabolism of somatic reserves should be most sensitive to current nutritional state relative to seasonal thresholds of fat and lean body tissue. Based on that overarching hypothesis, we tested three main predictions.

1. To avoid risk of malnutrition during winter, allocation of body reserves to gestation or survival should be low for individuals in relatively poor condition in autumn compared with individuals in better condition.
2. Allocation of body reserves to reproduction during summer should be higher for females that have greater fat and protein reserves post-winter; accordingly, summer accretion of fat and protein should be lower for those females with greater reproductive costs.
3. Maintenance of lean body tissue should be a priority during both summer and winter; females should conserve and replenish protein reserves during summer in precedence to fat, and abundance of fat reserves during winter should reduce the catabolism of protein.

## Materials and methods

### STUDY AREA

We studied a migratory population of mule deer that resided on winter range in Round Valley (37°24′N, 118°34′W), California, USA, during approximately November–April each year, and migrated to high elevation summer ranges in the Sierra Nevada (Monteith *et al.* 2011). The crest of the Sierra Nevada (hereafter Sierra crest) sharply delineates the western slope from the eastern slope of their summer range and causes a rain-shadow effect, resulting in >3× greater moisture deposition on the west side, and an arid landscape on the eastern slope where the Great Basin Desert begins.

Mule deer inhabiting winter range in Round Valley have been subjected to the vagaries of climate, coupled with influences of density dependence (Pierce *et al.* 2012). Within the region, 75% of the highly variable (CV = 57%) precipitation accumulates between November and March (Monteith *et al.* 2011). During a severe drought, the deer population declined by 85% between 1985 and 1991, which was driven mostly by poor annual adult survival (0·65; Pierce *et al.* 2012). In this Great Basin ecosystem, winter snowpack has a positive influence on growth of deer forage (Pierce *et al.* 2012). Winter severity is not a direct limiting factor, but population growth is linked to the proportion of primary winter forage (bitterbrush; *Purshia tridentata*) in deer diets in March, with concomitant effects on body condition of deer (Pierce, Bowyer & Bleich 2004; Pierce *et al.* 2012). During this study, the wintering population of mule deer rose from an estimated 2388 animals in 2002 to a high of 3100 individuals in 2005, and declined thereafter to 1864 individuals by 2009. The study area and population ecology of this mule deer population have been described in detail elsewhere (Kucera 1997; Pierce, Bowyer & Bleich 2004; Monteith *et al.* 2011; Pierce *et al.* 2012).

### DATA COLLECTION

To evaluate factors that influenced seasonal accretion and catabolism of somatic reserves, we obtained longitudinal data on nutritional status of female mule deer and linked those data with individual life-history characteristics and climate. During mid-March and mid-November 2002–2009, we captured adult (>1 year old) female mule deer on winter range in Round Valley using a hand-held net gun fired from a helicopter. Each animal was hobbled, blindfolded and transported via helicopter to a central processing station. We removed 1 incisiform canine (Bleich *et al.* 2003) to allow ageing by cementum annuli (Matson's Laboratory, Milltown, MT, USA). We measured body mass with an electronic scale (±1 kg) and fitted each animal with a VHF radiocollar. We attempted to capture every radiocollared female in March and >50% of the radiocollared females in November. Most females had migrated to winter range prior to our November capture and we selected radiocollared females at random; we believe our November sample was representative of the population (Monteith *et al.* 2011). We recaptured radiocollared females to obtain longitudinal data on individuals, and new, unmarked females were captured to attempt to maintain >75 radiocollared females. Our sample included 136 individual adult females that we captured an average of 4·3 times (range: 2–14), to yield 215 seasonal transitions from November to March (winter) and 233 seasonal transitions from March to November (summer).

We determined nutritional condition of female deer using standard protocols developed for mule deer, which combined measurements of subcutaneous rump fat using ultrasonography (Aloka 210; Aloka, Inc., Wallinford, CT, USA) and palpation to achieve a body-condition score (Stephenson *et al.* 2002; Cook *et al.* 2007). We estimated ingesta-free body fat (IFBFat) with a combination of body mass, body-condition score and maximum thickness of rump fat (Cook *et al.* 2010). IFBFat was weakly correlated with body mass in March ($r^2 = 0{\cdot}00$, $n = 822$, $P = 0{\cdot}06$) and November ($r^2 = 0{\cdot}12$, $n = 331$, $P < 0{\cdot}001$). We also estimated lean body mass by calculating body mass adjusted to an ingesta-free, fat-free basis (Cook *et al.* 2007, 2010). Ingesta-free, fat-free body mass (IFFFBMass) was correlated strongly with body mass in March ($r^2 = 0{\cdot}97$, $n = 822$, $P < 0{\cdot}001$) and November ($r^2 = 0{\cdot}92$, $n = 331$, $P < 0{\cdot}001$). We subtracted foetuses and other products of conceptus from estimates of body mass for March estimates (Cook *et al.* 2010). We determined pregnancy and number of foetuses by ultrasonography with transabdominal scanning using a 3-MHz transducer (Stephenson *et al.* 1995).

During autumn, when mother–infant bonds were still intact, we determined number of recruits (i.e., number of young-at-heel) for each marked female as they arrived on winter range in late-October through November (Monteith *et al.* 2011). Methods of research and animal capture were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (protocol: 650-0410) and followed guidelines of American Society of Mammalogists (Gannon, Sikes & the Animal Care and Use Committee of the American Society of Mammalogists 2007) and California Department of Fish and Game (CDFG).

### STATISTICAL ANALYSES

We evaluated seasonal transitions in deer condition based on two primary variables that were representative of the absolute change in fat and protein reserves. Therefore, change in IFBFat [based on percentage points (pp)] and change in IFFFBMass (kg) over winter and summer were our response variables in four separate analyses. We modelled response variables as a function of population- and individual-level covariates using linear mixed models (PROC MIXED; SAS Institute, Cary, NC, USA), with a repeated-measures structure to avoid inflating degrees of freedom, and account for potential autocorrelation from repeatedly sampling individual deer. We used Akaike's Information Criterion adjusted for small sample size ($AIC_c$) to select the best-fitting covariance structure for repeated measures (Ferron, Dailey & Yi 2002) from those deemed biologically appropriate (Verbeke & Molenberghs 2000; Yoccoz, Nichols & Boulinier 2001). We considered simple and variance components, compound symmetry, spatial power, spatial exponential, spatial Gaussian and heterogeneous autoregressive models (Littell *et al.* 1996). Variance component, which specifies similar within-individual covariance through time, was the most appropriate covariance structure for body fat, whereas the heterogeneous autoregressive, which specifies greater covariance between measurements closer in time, was the best structure for lean body mass.

We modelled factors that were related to seasonal transition in two steps by first evaluating population-level or environmental factors. Secondly, we retained those variables identified as influential at the population level (Arnold 2010; Monteith *et al.* 2011) for the same analysis with the incorporation of variables at the individual level. We conducted our analyses in that two-step approach because covariates at the individual level were not available for every animal, and population-level and individual-level factors can affect life-history characteristics differently (Monteith *et al.* 2011).

At each level of our analyses, we evaluated all possible combinations of predictor variables that we hypothesized would influence seasonal transition in condition of mule deer (Yoccoz, Nichols & Boulinier 2001; Whittingham *et al.* 2006; Arnold 2010; Monteith *et al.* 2011). For each model, we calculated $AIC_c$, $\Delta AIC_c$ and Akaike weight ($w_i$; Burnham & Anderson 2002). We calculated model-averaged parameter estimates, and the associated 90% CI, based on unconditional SEs. Model averaging minimized effects of uninformative parameters and, thereby, provided a conservative assessment of variable importance (Arnold 2010). We calculated importance weights as the sum of $w_i$ across all models that contained that particular variable (Burnham & Anderson 2002; Arnold 2010). We retained variables from the previous stage of an analysis if the 90% CI of the model-averaged parameter estimate did not overlap zero or had an importance weight >0·60 (sensu Arnold 2010).

### PREDICTOR VARIABLES

Growth of bitterbrush, the primary winter forage for mule deer in the Sierra Nevada (Pierce, Bowyer & Bleich 2004), was determined mostly by the water content of the snowpack from the preceding April measured in a drainage adjacent to Round Valley (Pierce *et al.* 2012). As in previous studies (Sinclair, Dublin & Borner 1985; Pierce *et al.* 2012), we calculated a density-dependent proxy to forage availability based on the quotient of the water content of the snowpack during the preceding April and the estimated number of females for that year (per capita snowpack; cm per female).

Predictor variables at the population level included seasonal temperature and precipitation, per capita snowpack and mean IFBFat of adult females from the preceding March. We obtained data on daily weather from a weather station immediately adjacent to the spring holding area for deer from Round Valley, and calculated average daily temperature and total precipitation during spring, summer, and autumn (May – October) and winter (November – April; Monteith *et al.* 2011). We included mean IFBFat from the previous March because that variable provides an additional representation of habitat conditions relative to deer density. At the population level, we also included summer residency (i.e., side of the Sierra crest occupied during summer) because conditions differed sufficiently to warrant considering them as two groups (Monteith *et al.* 2011). We included year as an alternative predictor variable in exchange for other annual variables to account for potential variation among years that was not explained by our other predictor variables. At the individual level, we included age (Gaillard *et al.* 2000), number of foetuses (Pekins, Smith & Mautz 1998), preseason IFBFat, preseason IFFFBMass (Bårdsen & Tveraa 2012) and number of recruits in autumn (summer transition only; Festa-Bianchet, Gaillard & Jorgenson 1998) that corresponded to each individual mule deer. We evaluated multicollinearity among all predictor variables in each stage of analysis (Table S1, Supporting information) and did not let highly correlated ($r > |0{\cdot}50|$) variables enter the same model (Neter *et al.* 1996).

We evaluated interactions between predictor variables that were biologically meaningful and followed from our predictions based on whether confidence intervals of the parameter estimate for the interaction term included zero and if the inclusion of the interaction term resulted in an improvement of model fit using the global model in each stage of the analysis ($< 2\ \Delta AIC_c$; Burnham & Anderson 2002). None of the interaction terms we investigated were significant or resulted in improved model fit and were thus, removed from analyses, because inclusion of interaction terms can alter model-averaged estimates of the independent counterpart of those terms. Similarly, for age-specific patterns, we retained the quadratic effect of age (age$^2$) in a model set only if its inclusion resulted in improved model fit. To best depict relationships between a specific predictor variable and a response variable in figures, we used the best model ($\Delta AIC_c = 0$) of all possible combinations of variables and modelled expected effects (*y*–axis) of the variable of interest (*x*–axis) within the observed range while holding other variables constant at their mean.

## Results

### WINTER DYNAMICS

Mean IFBFat and IFFFBMass (±SE) of adult females in March 2002–2009 was 6·38 ± 0·15% and 37·17 ± 0·39 kg, respectively. Mean change in absolute IFBFat over winter was −3·41 ± 0·16 percentage points (pp), but ranged from −16·7 to 6·7 pp among individuals. Mean change in IFFFBMass over winter was −2·17 ± 0·31 kg and ranged between −15·08 and 12·39 kg among individuals. Of the 215 individuals monitored over winter, 75·8% declined in IFBFat while 74·0% declined in IFFFBMass, indicating that some females accrued fat and protein over winter.

At the population level, overwinter change in IFBFat varied as a function primarily of summer residency and per capita snowpack and was positively related, albeit not significantly, to mean IFBFat of March$_{t-1}$ (Table 1).

**Table 1.** Model-averaged parameter estimates, confidence intervals and Akaike importance weights from an analysis to determine factors that affect change (percentage points) in ingesta-free body fat (IFBFat) of adult (>1 year of age) female mule deer over winter (Nov – Mar), evaluated at the population ($n$ = 215) and individual ($n$ = 201) levels, Sierra Nevada, California, USA, 2002–2009

| | | | 90% CI | | |
|---|---|---|---|---|---|
| Level | Parameter | Estimate | Lower | Upper | Importance weight |
| Population | Summer residency | 1·68$^a$ | 0·48 | 2·88 | 0·95 |
| | Per capita snowpack | −106·84$^a$ | −172·07 | −41·82 | 0·98 |
| | Winter temperature | −0·005 | −0·063 | 0·007 | 0·01 |
| | Winter precipitation | −0·006 | −0·015 | 0·004 | 0·01 |
| | Mean Mar IFBFat$_{t-1}$ | 0·13 | −0·33 | 0·59 | 0·57 |
| | Year | n/a | n/a | n/a | 0·00 |
| Individual | Summer residency | 0·041 | −0·20 | 0·28 | 0·45 |
| | Per capita snowpack | 36·30$^a$ | 7·03 | 65·53 | 1·00 |
| | Age | −0·16$^a$ | −0·24 | −0·072 | 0·94 |
| | Foetal number | 0·61$^a$ | 0·21 | 1·01 | 0·99 |
| | Nov IFBFat | −0·84$^a$ | −0·89 | −0·78 | 1·00 |

Variables identified as being influential were included in lower levels of analysis and were considered influential if their 90% CI did not overlap zero or if their importance weight was >0·60.

[a]Adjacent to parameter estimates indicate 90% CIs do not overlap zero.

Females that summered on the west side of the Sierra crest lost more fat over winter than those that resided on the east side. That relationship, however, waned at the individual level after we accounted for preseason IFBFat, because females residing on the west side were consistently fatter in autumn (Table 1). Similarly, but contrary to our expectations, per capita snowpack was related negatively to change in IFBFat during winter at the population level. Nevertheless, after accounting for IFBFat of individuals entering winter, per capita snowpack was related positively to over-winter change in IFBFat, indicating that greater per capita snowpack reduced loss of fat over winter. Although summer residency, per capita snowpack, and mean IFBFat in $\text{March}_{t-1}$ exhibited similar relationships with IFFFBMass (as they did with IFBFat), none had a significant effect at the population level (Table 2).

At the individual level, overwinter changes in IFBFat and IFFFBMass were most closely linked to their respective values prior to winter (Tables 1 and 2). Individual females with greater IFBFat in November lost more absolute body fat over winter than females entering winter in poor condition (Fig. 1a). Similarly, catabolism of lean body mass of females over winter was related directly to the amount of IFFFBMass entering winter (Fig. 1b). Catabolism and accretion in fat and lean tissue were both evident during winter, implying that individuals exhibited seasonal thresholds in those tissues. Model estimates indicated the mean post-winter threshold (no net change over winter) for IFBFat was 5·81% (90% CI, 5·32–6·25%). For an average year, models predicted a gain in 0·84 pp of IFBFat over winter for each percentage point decrease below 5·81% IFBFat in November. The post-winter threshold for IFFFBMass was 32·7 kg (90% CI, 29·2–35·2 kg), with predicted gains in 0·39 kg over winter for every 1 kg reduction in lean body mass from that threshold at the onset of winter (Table 2).

Winter change in IFBFat was related linearly to age, with older females losing greater amounts of fat over winter (Table 1; Fig. S1, Supporting information); however, change in IFFFBMass during winter exhibited a curvilinear relationship with age (Table 2), indicating that middle-aged individuals catabolized less lean body mass than did younger (<5 years old) or older females (>12 years old; Fig. S1, Supporting information). Contrary to costs presumed to be associated with gestation, loss of IFBFat and IFFFBMass over winter declined as foetal number increased (Tables 1 and 2). Even after accounting for preseason levels of IFBFat and IFFFBMass, maternal females catabolized 0·61 percentage points less IFBFat and 1·66 kg less IFFFBMass over winter with each additional foetus (Fig. 2).

### SUMMER DYNAMICS

Mean IFBFat and IFFFBMass (±SE) in November 2002–2008, was 9·73 ± 0·22% and 38·97 ± 0·33 kg, respectively. Mean change in absolute IFBFat over summer was positive (2·47 ± 0·27 pp), but ranged from a −9·4 to 16·5 pp. Average change (±SE) in IFFFBMass over summer also was positive (2·74 ± 0·29) and ranged between −9·9 and 19·3 kg among individuals. Of the 233 seasonal transitions we monitored over summer, 68·8% of individuals increased in fat, while 73·8% increased in lean body mass.

Deposition of fat over summer was related to population-level factors including summer residency, per capita snowpack, summer temperature and mean March IFBFat (Table 3). Females on the west side of the Sierra crest

**Table 2.** Model-averaged parameter estimates, confidence intervals and Akaike importance weights from an analysis to determine factors that affect change (kg) in ingesta-free, fat-free body mass (IFFFBMass) of adult (>1 year of age) female mule deer over winter (Nov – Mar), evaluated at the population (*n* = 215) and individual (*n* = 201) levels, Sierra Nevada, California, USA, 2002–2009

| Level | Parameter | Estimate | 90% CI Lower | 90% CI Upper | Importance weight |
|---|---|---|---|---|---|
| Population | Summer residency | 0·61 | −0·16 | 1·38 | 0·78 |
| | Per capita snowpack | −49·08 | −119·06 | 20·91 | 0·90 |
| | Winter temperature | 0·099 | −0·063 | 0·26 | 0·10 |
| | Winter precipitation | −0·011 | −0·033 | 0·011 | 0·05 |
| | Mean Mar $\text{IFBFat}_{t-1}$ | 0·15 | −0·24 | 0·55 | 0·55 |
| | Year | n/a | n/a | n/a | 0·00 |
| Individual | Summer residency | 0·087 | −0·51 | 0·68 | 0·61 |
| | Per capita snowpack | −58·63 | −123·51 | 5·25 | 1·00 |
| | Age | 0·64[a] | 0·011 | 1·28 | 0·58 |
| | $\text{Age}^2$ | −0·038[a] | −0·075 | −0·001 | 0·58 |
| | Foetal number | 1·66[a] | 0·97 | 2·34 | 1·00 |
| | Nov IFFFBMass | −0·39[a] | −0·47 | −0·31 | 1·00 |
| | Nov IFBFat | 0·090[a] | 0·014 | 0·17 | 0·68 |

IFBFat, ingesta-free body fat; IFFFBMass, ingesta-free, fat-free body mass.

Variables identified as being influential were included in lower levels of analysis and were considered influential if their 90% CI did not overlap zero or if their importance weight was >0·60.

[a] Adjacent to parameter estimates indicate 90% CIs do not overlap zero.

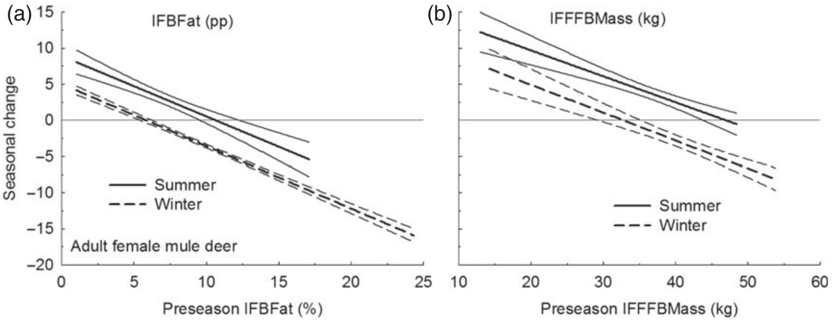

**Fig. 1.** Estimated effect (±90% CI) of preseason, ingesta-free body fat (IFBFat) on absolute change in IFBFat (a) and preseason lean body mass (IFFFBMass) on change in IFFFBMass (b) of adult (>1 year of age) female mule deer over summer (Mar – Nov) and winter (Nov – Mar), Sierra Nevada, California, USA, 2002–2009.

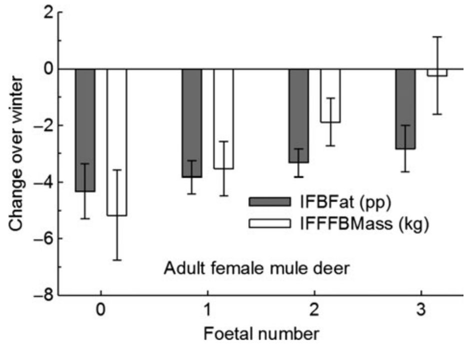

**Fig. 2.** Estimated effect (±90% CI) of foetal number on absolute change in ingesta-free body fat (IFBFat) and ingesta-free, fat-free body mass (IFFFBMass) of adult (>1 year of age) female mule deer over winter (Nov – Mar), Sierra Nevada, California, USA, 2002–2009.

($\bar{x}$ ± SE; 3·6 ± 0·34 pp) deposited more fat over summer than females on the east side (1·4 ± 0·33 pp). Higher per capita snowpack and cooler summer temperatures were associated with greater fat deposition over summer (Table 3). Development of lean body mass over summer also was associated with quality of summer range, and cooler and wetter summers (Table 4). Females that summered west of the Sierra crest accumulated more lean body mass (3·5 ± 0·39 kg) than females residing on the east side (2·1 ± 0·42 kg).

At the population level, mean IFBFat in March was related negatively to change in IFBFat over summer (Table 3). After individual-based covariates were incorporated, however, the effect of mean IFBFat in March switched sign, indicating that greater overall fat levels in March resulted in increased fat deposition over summer. The opposite held at the individual level (Table 3); higher

**Table 3.** Model-averaged parameter estimates, confidence intervals and Akaike importance weights from an analysis to determine factors that affect change (percentage points) in ingesta-free body fat (IFBFat) of adult (>1 year of age) female mule deer over summer (Mar – Nov), evaluated at the population (*n* = 233) and individual (*n* = 221) levels, Sierra Nevada, California, USA, 2002–2009

| | | | 90% CI | | |
|---|---|---|---|---|---|
| Level | Parameter | Estimate | Lower | Upper | Importance weight |
| Population | Summer residency | −2·24[a] | −3·13 | −1·30 | 1·00 |
| | Per capita snowpack | 106·30[a] | 30·39 | 182·21 | 1·00 |
| | Summer temperature | −0·35 | −0·063 | 0·086 | 0·70 |
| | Summer precipitation | 0·017 | −0·016 | 0·049 | 0·23 |
| | Mean Mar IFBFat | −0·62[a] | −1·16 | −0·071 | 0·85 |
| | Year | n/a | n/a | n/a | 0·00 |
| Individual | Summer residency | −1·86[a] | −2·69 | −0·94 | 1·00 |
| | Per capita snowpack | 125·36[a] | 61·67 | 189·05 | 1·00 |
| | Summer temperature | −0·10 | −0·39 | 0·18 | 0·50 |
| | Mean Mar IFBFat | 0·78[a] | 0·17 | 1·39 | 0·91 |
| | Age | −0·043 | −0·20 | 0·12 | 1·00 |
| | Foetal number | −0·43 | −1·13 | 0·27 | 1·00 |
| | Mar IFBFat | −0·76[a] | −0·96 | −0·56 | 1·00 |
| | Recruitment number | −2·75[a] | −3·38 | −2·12 | 1·00 |

Variables identified as being influential were included in lower levels of analysis and were considered influential if their 90% CI did not overlap zero or if their importance weight was >0·60.

[a]Adjacent to parameter estimates indicate 90% CIs do not overlap zero.

**Table 4.** Model-averaged parameter estimates, confidence intervals and Akaike importance weights from an analysis to determine factors that affect change (kg) in ingesta-free, fat-free body mass (IFFFBMass) of adult (>1 year of age) female mule deer over summer (Mar – Nov), evaluated at the population (*n* = 233) and individual (*n* = 221) levels, Sierra Nevada, California, USA, 2002–2009

| | | | 90% CI | | |
|---|---|---|---|---|---|
| Level | Parameter | Estimate | Lower | Upper | Importance weight |
| Population | Summer residency | −1·55$^{a}$ | −2·50 | −0·60 | 0·97 |
| | Per capita snowpack | −55·16 | −143·22 | 32·90 | 0·99 |
| | Summer temperature | −1·062$^{a}$ | −1·71 | −0·42 | 0·95 |
| | Summer precipitation | 0·13$^{a}$ | 0·16 | 0·23 | 0·68 |
| | Mean Mar IFBFat | −0·18 | −0·63 | 0·26 | 0·58 |
| | Year | n/a | n/a | n/a | 0·00 |
| Individual | Summer residency | −1·90$^{a}$ | −2·82 | −0·98 | 0·99 |
| | Per capita snowpack | −27·77 | −98·19 | 42·64 | 0·99 |
| | Summer temperature | −0·78$^{a}$ | −1·37 | −0·19 | 0·89 |
| | Summer precipitation | 0·20$^{a}$ | 0·096 | 0·31 | 0·93 |
| | Age | 0·034 | −0·13 | 0·20 | 1·00 |
| | Foetal number | −1·26$^{a}$ | −1·99 | −0·52 | 1·00 |
| | Mar IFFFBMass | −0·33$^{a}$ | −0·42 | −0·24 | 1·00 |
| | Recruitment number | −1·23$^{a}$ | −1·95 | −0·52 | 0·98 |
| | Mar IFBFat | −0·82 | −0·17 | 0·005 | 0·56 |

IFBFat, ingesta-free body fat; IFFFBMass, ingesta-free, fat-free body mass.
Variables identified as being influential were included in lower levels of analysis and were considered influential if their 90% CI did not overlap zero or if their importance weight was >0·60.
$^{a}$Adjacent to parameter estimates indicate 90% CIs do not overlap zero.

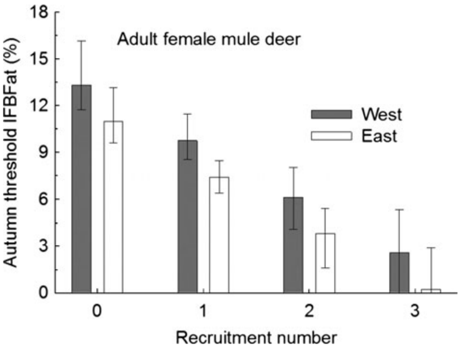

**Fig. 3.** Estimated effect (±90% CI) of recruitment of young on autumn threshold of ingesta-free body fat (IFBFat) for adult (>1 year of age) female mule deer, Sierra Nevada, California, USA, 2002–2009.

IFBFat in March resulted in lower fat deposition during summer (Fig. 1a). Deposition of fat and lean body mass over summer was associated strongly with the preseason nutritional state of individuals, but summer fat thresholds were altered by reproductive investment and habitat quality (Tables 3 and 4). Fat thresholds in autumn declined by 2·75 pp for each additional recruit, but were 1·86 pp higher for females that summered on the west side of the Sierra crest (Fig. 3). Individual females were predicted to gain 0·76 pp in autumn IFBFat for every 1 pp decrease in March fat below those thresholds. Similarly, autumn thresholds in lean body mass declined by 1·23 kg for each additional recruit from 48·6 kg (90% CI, 45·2–54·8 kg) for females residing on the west side and 43·7 kg (90% CI, 40·9–48·3 kg) for females on the east side. Gains of 0·33 kg in lean body mass were expected over summer for every 1-kg decrease in lean body mass in March below the aforementioned thresholds.

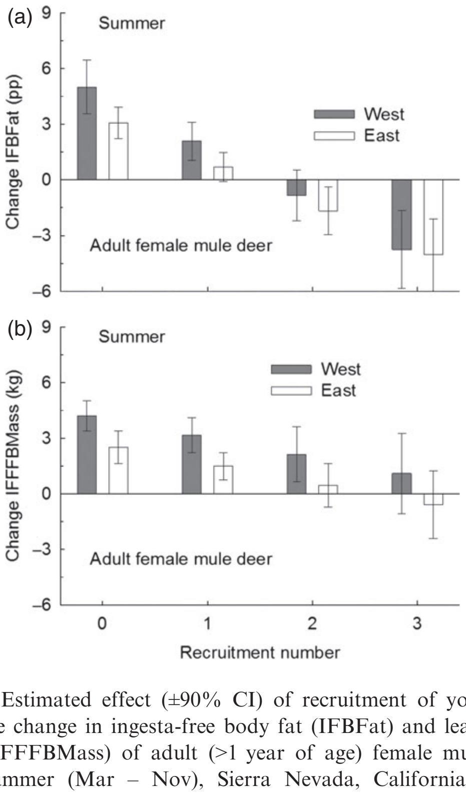

**Fig. 4.** Estimated effect (±90% CI) of recruitment of young on absolute change in ingesta-free body fat (IFBFat) and lean body mass (IFFFBMass) of adult (>1 year of age) female mule deer over summer (Mar – Nov), Sierra Nevada, California, USA, 2002–2009.

When losses in fat and lean body mass occurred over summer, they were mostly a result of reproductive costs (Tables 3 and 4), with greater autumn recruitment resulting in reduced deposition, or even catabolism, of fat and protein reserves (Fig. 4). Females from both sides of the Sierra crest deposited fat during summer when one or less young were recruited; however, recruiting two or more young resulted in a predicted loss of IFBFat over an average summer (Fig. 4a). Although development of lean body tissue over summer also declined as recruitment increased (Table 4), protein was either used more sparingly or was less limiting within diets because deposition in lean body tissue occurred when up to two young were recruited. Catabolism of lean body tissue was predicted only for females on the east side when three young were successfully recruited (Fig. 4b).

### FAT VS. PROTEIN

Fat and protein reserves were mobilized as a function of their respective preseason levels over winter and summer, but both fat and protein were readily catabolized over winter (Fig. 1); only fat was readily catabolized over summer (Fig. 1). In accordance with those observations, change in IFFFBMass over winter was positively related to preseason IFBFat (Fig. 5). During an average year, changes in IFFFBMass over summer were mostly positive regardless of preseason IFFFBMass, IFBFat or autumn recruitment (Fig. 1b).

## Discussion

Knowledge of seasonal dynamics in nutritional reserves, and how they are allocated for survival and reproduction, is important for understanding the interplay of life-history strategies and the nutritional adequacy of the environment (Parker, Barboza & Gillingham 2009). Nevertheless, empirical evidence for those relationships is rare because they require long-term and individual-based studies (Monteith *et al.* 2009; Clutton-Brock & Sheldon 2010). Our research offers empirical support for the hypothesis that allocation of body reserves to survival and reproduction occurs in a risk-sensitive framework for a long-lived mammal (Bårdsen *et al.* 2008), but that the risk and subsequent allocation of body reserves to fitness components differ between seasons and are altered by reproductive investment. Body fat was used preferentially over protein during winter, but lean body mass was readily catabolized to support overwinter survival as fat reserves were depleted. Conversely, lean body mass was spared during summer, while fat was catabolized to support reproductive costs. Overall, accretion and catabolism of body reserves during summer and winter largely was a function of the quantity of those body stores at the beginning of the season, indicating that regulation of individual condition was state-dependent. Individuals in poor condition partially compensated for reduced stores of fat and protein during both seasons; we documented gains in fat and protein reserves during winter and declines during summer for some individuals, which is antithetical to the dogma of summer accretion and winter catabolism of body reserves for temperate herbivores. Summer thresholds of fat and protein stores were affected by recruitment of young, which suggests that, although allocation of resources to reproduction was largely determined by available reserves (i.e., was risk sensitive), energetic costs associated with securing current reproductive investment altered resource allocation.

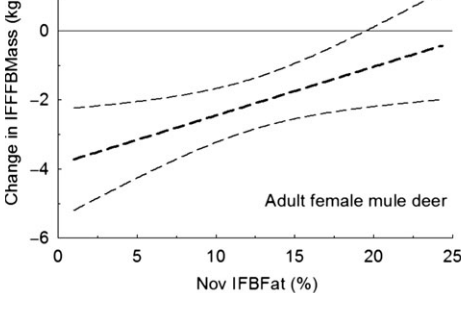

**Fig. 5.** Estimated effect (±90% CI) of preseason (Nov) ingesta-free body fat on absolute change in lean body mass (IFFFBMass) of adult (>1 year of age) female mule deer over winter (Nov – Mar), Sierra Nevada, California, USA, 2002–2009.

### WINTER DYNAMICS

Large herbivores exhibit seasonal variation in appetite and voluntary food intake, both of which are a function of metabolic demand, physiological changes and adaptations to living in environments with seasonal abundances and deficiencies in food availability (Moen 1978; Parker *et al.* 1996; Tyler *et al.* 1999; Rhind, Archer & Adam 2002). Yet, the regulation of voluntary intake and consequent dynamics of body condition are not rigid, but vary among individuals (Schwartz, Hubbert & Franzmann 1988; Sibbald 1997; Rhind, Archer & Adam 2002; Fauchald *et al.* 2004). On average, absolute fat and protein reserves declined over winter for female mule deer, which aligns with general perceptions of winter conditions for temperate ungulates (Mautz 1978); however, mobilization of fat and lean tissue occurred in accordance with preseason levels of those tissues (Fig. 1). Therefore, autumn levels of fat and protein reserves relative to post-winter thresholds regulated changes in those tissues as winter progressed (Renecker & Samuel 1991; Bårdsen & Tveraa 2012).

In a review of intake control of ruminants, Arnold (1985:82) suggested that energy balance is likely controlled by the size of fat stores. Catabolism of body reserves during winter occurred according to the size of those stores in mule deer (this study), black-tailed deer (*O. hemionus*; Parker *et al.* 1996), caribou (*Rangifer tarandus*; Fauchald *et al.* 2004; Dale *et al.* 2008; Bårdsen *et al.* 2010), North American elk (*Cervus elaphus*; Cook *et al.*

2004), muskoxen (*Ovibus mochatus*; Gustine, Barboza & Lawler 2010) and domestic ruminants (Chilliard *et al.* 2000). Notably, ~25% of female mule deer we monitored over seven winters were effective at halting winter catabolism and even depositing fat and lean body tissue. Individuals apparently regulated food intake and metabolism according to the proximity of their nutritional state to a post-winter threshold. Indeed, intake rates (Arnold 1985; Schwartz, Hubbert & Franzmann 1988; Sibbald 1997) and forage selection (Frost, Launchbaugh & Taylor 2008) by large herbivores are under strong endogenous control. The ability of individuals to halt winter catabolism of tissues, however, can be affected by environmental and habitat conditions (Table 1; Couturier *et al.* 2009). For example, young (<1·5 years old) mule deer in captivity are capable of growing throughout winter (Renecker & Samuel 1991), whereas, under severe conditions, young mule deer lost >26% of their body mass over winter (Doman & Rasmussen 1944).

Ample evidence indicates maternal stores of protein are used to support foetal growth (Adamczewski *et al.* 1987; Barboza & Parker 2008; Gustine, Barboza & Lawler 2010); however, changes in maternal protein and fat stores over winter were opposite of expected gestational costs (Fig. 2). We measured nutritional status at the onset of the third trimester of gestation, the period during which >90% of the energetic costs of gestation occur (Pekins, Smith & Mautz 1998). Therefore, gestating females apparently conserved protein reserves during winter to maintain body tissues in preparation for deposition of endogenous nitrogen in foetal tissues to enhance foetal growth while consuming a poor quality diet, which may be possible through recycling N when gestational costs are low (Parker, Barboza & Stephenson 2005; Barboza & Parker 2008; Gustine, Barboza & Lawler 2010). Alternatively, the contradictory relationship of foetal number with changes in body composition that we observed may have been caused by some unmeasured factor.

### SUMMER DYNAMICS

If mothers are unable to meet energetic and protein demands of lactation, they must reduce milk output, mobilize maternal tissues or use some combination of both strategies (Festa-Bianchet 1998; Chan-McLeod, White & Russell 1999; Oftedal 2000; Cook *et al.* 2004), which results in an immediate cost of reproduction (Landete-Castillejos *et al.* 2003; Tollefson *et al.* 2010). Consequently, investment in reproduction over summer is traded against accumulation of body reserves to improve overwinter survival (Fauchald *et al.* 2004). Indeed, summer accretion in fat and protein stores declined with increasing costs of reproduction relative to quality of summer range (Fig. 4).

In support of the theory that long-lived organisms should invest in reproduction within a risk-sensitive framework (Stearns 1992; Festa-Bianchet 1998; Bårdsen *et al.* 2008), allocation of fat and protein stores to reproduction was a function of the nutritional state of females following winter (Fig. 1). Nevertheless, the attainment of a threshold in nutritional stores over summer was modulated by reproductive costs (Fig. 3); females sought to secure reproductive investment by promoting survival of their young at the expense of autumn somatic reserves (Festa-Bianchet 1998; Festa-Bianchet & Jorgenson 1998; Landete-Castillejos *et al.* 2003). The autumn threshold of fat stores declined 2·75 pp with each additional recruit from ~12% IFBFat for females that failed to recruit any young. On average, females with >8·6% IFBFat following winter allocated fat reserves directly to reproduction when one young was raised. Reproductive females adopted a risk-sensitive reproductive strategy by investing in offspring according to both the fat stores and forage resources that were available, but the relationship between allocation and maternal condition was altered by the costs of successful reproduction (Fig. 3).

### SEASONAL CONTRIBUTIONS

Ecologists working in temperate and arctic landscapes often seek to identify which seasonal range limits or regulates population growth (Adamczewski *et al.* 1987; Christianson & Creel 2007). Our results and those from other studies suggest that nutritional carryover between seasons and the different life-history strategies occurring on each seasonal range diminish the value of separating their interactive and collective effects (Harrison *et al.* 2011; Bårdsen & Tveraa 2012). Nutritional limitation on summer ranges is less acute and less obvious than on winter range, partially because females adjust expenditures for reproduction according to their nutritional state. Females that successfully recruited young were consistently in poorer nutritional condition than those that were less successful (Fig. 4), because mobilization of lipid reserves was necessary to ensure success of current offspring (Landete-Castillejos *et al.* 2003; Bradford *et al.* 2012).

Entering winter in poor nutritional condition, mostly as a result of reproductive expenditures and quality of summer range, altered overwinter regulation of body reserves (Fig. 1), which highlights the role of summer nutrition on nutritional dynamics and behavioural decisions of individuals during winter. In other systems where food availability during winter may be equally challenging, but severe weather is more common (Sæther 1997), females that expend resources below autumn thresholds may not be able to compensate for their poor nutritional condition. Greater risk of winter malnutrition could result in a selective advantage for females that are more conservative towards reproductive investment (Fauchald *et al.* 2004; Bårdsen *et al.* 2008, 2010, 2011). Consequently, summer and winter contributions to nutrition are not independent; instead, they interact to affect life-history strategies, reproductive performance and survival.

### FAT VS. PROTEIN

Seasonal cycles of gains in body mass during spring and summer, followed by loss of mass over winter, typify seasonal patterns of body-mass development for temperate ungulates (Parker *et al.* 1996; Tyler *et al.* 1999). Body mass alone was a strong predictor of protein reserves, but was only weakly correlated with fat reserves. Indeed, underlying seasonal changes in body mass are fluctuations in body fat and protein (Torbit *et al.* 1985; Barboza & Parker 2008), which are important for different life-history components (Barboza, Parker & Hume 2009). Body fat provides a labile source of energy that is efficiently synthesized and catabolized, whereas body protein serves structural functions and can be a labile source of nitrogen for reproduction, but its conversion to a source of energy is less efficient than that of fat (Barboza, Parker & Hume 2009). Mobilization of lipid reserves to meet metabolic requirements is considered normal, whereas relying on lean body tissue to meet an energy deficit is a sign of heightened malnutrition (Torbit *et al.* 1985; Parker *et al.* 1996).

According to the risk-sensitive hypothesis, large herbivores should preferentially mobilize fat during winter (Torbit *et al.* 1985; Parker *et al.* 1996) and replenish and conserve protein reserves during summer. In support of that prediction, after accounting for lean body tissue prior to winter, females with greater fat reserves catabolized less lean body tissue during winter than those entering winter in poor nutritional condition (Fig. 5). Female mule deer did, however, readily catabolize lean body tissue (average change) over winter when it was available (Fig. 1b), presumably to support metabolic function.

As also evident among captive mule deer (Renecker & Samuel 1991), available protein for catabolism during winter was based on the quantity of lean body tissue above a post-winter threshold (33 kg). Below that threshold, female mule deer were capable of halting protein catabolism, and in some instances (26% of deer), synthesized protein over winter. In contrast, the autumn threshold for lean body tissue was rarely maintained over winter (7% of observations) indicating that, on average, lean body tissue was mostly synthesized and rarely allocated to reproduction during summer (Figs 1 and 4b). Indeed, ruminants first allocate energy to maintenance, then to protein deposition, and finally to lipogenesis (Chan-McLeod, White & Russell 1999).

The conservation of lean body tissue during reproduction and the more liberal use of protein to meet metabolic demands over winter support the conservative reproductive strategies proposed for long-lived herbivores (Festa-Bianchet & Jorgenson 1998; Bårdsen *et al.* 2008, 2010). These outcomes further indicate that lipid and protein reserves serve as different forms of currency. Protein reserves may be used to support foetal growth (Barboza & Parker 2008; Gustine, Barboza & Lawler 2010), but function mostly as insurance against winter malnutrition, whereas lipid reserves offer a universal source of energy for both survival and reproduction (Figs 1 and 4).

## Conclusions

Seasonal dynamics in body reserves of mule deer demonstrated that a number of suppositions regarding the nutritional ecology of large herbivores are at odds with empirical evidence. First, the long-held assumption that temperate ungulates cannot meet metabolic demands on winter ranges is misleading – death is not an imminent consequence of entering winter in poor condition (King & Murphy 1985). Although maintenance of nutritional condition and survival both depend upon severity of winter conditions (Christianson & Creel 2007; Couturier *et al.* 2009; Bårdsen & Tveraa 2012), forage intake is subject to strong endogenous controls, and individuals may be able to compensate for entering winter in poor nutritional condition. Second, in agreement with a growing body of literature (Cook *et al.* 2004; Dale *et al.* 2008; Couturier *et al.* 2009), limitation of nutritional quality of summer range is often, but erroneously, deemphasized, partially because female ungulates adjust their reproductive expenditures according to their nutritional state, and doing so conceals effects of summer nutrition. Third, nutritional contributions from seasonal ranges are not independent, because nutritional gains and deficits from one season affect the nutritional state of an individual entering the next season. In turn, nutritional state determines life-history decisions and regulation of body reserves; thus, many life-history traits may be as much a function of nutritional contributions of the previous season as of the current season.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Estimated effect (±95% CI) of age on absolute change in ingesta-free body fat (IFBFat) and lean body mass (IFFFBMass) of adult female mule deer over winter (Nov – Mar), Sierra Nevada, California, USA, 2002–2009.

**Table S1.** Correlation matrix between predictor variables for winter (A) and summer (B) transition in fat and protein reserves.