

Estimating the size of European rabbits consumed by predators: Relationship between body mass and tooth dimensions

Javier CALZADA¹, Daniel T. HAYDON² and Francisco PALOMARES³

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A method for estimating body mass of European rabbits *Oryctolagus cuniculus* (Linnaeus, 1758) based on tooth dimensions is proposed. Regression models identified significant relationships between the body mass of 87 rabbits and individual tooth length, breadth, product of tooth length and breadth, and whether or not the individual was infected with myxomatosis. Dimensions of 10 of 14 different teeth explained over 80% of variation in body mass, and those teeth were selected as adequate predictors of rabbit body mass. Models were tested using teeth from 16 additional rabbits of known body mass. Body mass, predicted on the basis of 9 of the 10 selected teeth, was statistically indistinguishable from the observed values for all 16 individuals. When myxomatosis infection status of the rabbit was included in the model, all 10 selected teeth yielded predictions statistically indistinguishable from those observed. Prediction errors can be computed permitting statistical comparison of the average predicted value of body mass from different samples of rabbits. The model is useful in estimating rabbit body masses from teeth recovered from feces of predators and it will facilitate testing of hypotheses on size-selective predation. The method was applied to rabbit teeth found in fecal samples from the Iberian lynx *Lynx pardinus* collected over a one-year period. Lynx preyed preferentially upon younger rabbits during the peak breeding period of this lagomorph.

Department of Applied Biology, Estación Biológica de Doñana, CSIC, Avda María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain, e-mail: ffpaloma@ebd.csic.es (JC, FP); Centre for Tropical Veterinary Medicine, Easter Bush, Roslin, Midlothian, Scotland EH25 9RG, United Kingdom (DTH)

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Present addresses:

¹ Departamento de Biología Ambiental y Salud Pública, Facultad de Ciencias Experimentales, Universidad de Huelva, Campus Universitario de La Rábida, 21819 Palos de la Frontera, Huelva, Spain, e-mail: javier.calzada@dbasp.uhu.es

² Department of Zoology, University of Guelph, Guelph, Ontario Canada N1G 2W1, e-mail: dhaydon@uoguelph.ca

³ To whom all correspondence should be addressed

Introduction

The European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) has spread from its center of origin in Spain to all continents except Antarctica and is present on more than 800 islands worldwide (Flux 1994). As a result, rabbits are prey of more than 80 vertebrate predators, (Delibes and Hiraldo 1981, Jaksic and Soriguer 1981, Soriguer 1981, Thompson and King 1994, Palomares and Delibes 1997). Because rabbits represent an important resource base for such a variety of predator species, the details of their occurrence in predator diet is of interest to ecologists and wildlife managers.

In this paper, we propose a method for estimating the body mass of European rabbits using dimensions of their teeth that can frequently be recovered intact from feces and pellets of predators. For instance, Calzada and Palomares (1996) found teeth in 69 and 64% of the feces with rabbit remains, of Iberian lynx *Lynx pardinus* and red fox *Vulpes vulpes*, respectively. Distinctive tooth morphology makes it relatively easy to distinguish one tooth from another (Popesko *et al.* 1990), so estimating body mass based on tooth dimensions could reduce the difficulty of fragment identification, and can allow identification of multiple prey items within a single scat or pellet (Carss and Elston 1996).

We constructed and parameterized a statistical model that allows estimation of the body mass of individual rabbits consumed as prey, and the average mass of groups of individual rabbits using individual tooth dimensions together with an associated prediction error. We also examined the effect of factors that could potentially influence the body mass of a rabbit (sex, seasonality, and myxomatosis infection status). We tested the accuracy and precision of the model with an independent sample of rabbits. Finally, we applied the technique to estimate the body mass of rabbits consumed by the endangered Iberian lynx over one year in the Doñana National Park.

Material and methods

We used 87 rabbits selected from the Mammal Collection of the Doñana Biological Station. They were collected over all seasons during the years 1995, 1996 and 1997 from an area of mediterranean scrubland called Coto del Rey, situated in the north of Doñana National Park (37°09'N 6°26'W), southwestern Spain. The area is flat with sandy soils and is covered with large shrubs comprised mostly of *Pistacia lentiscus* and *Halimium halimifolium* scrubs, pulse pastures, and scattered *Quercus suber* trees. The climate is mediterranean subhumid, with wet winters and hot, dry summers, with an annual rainfall between 500 and 600 mm.

Rabbits of Doñana generally weigh less than their European counterparts (Rogers *et al.* 1994). In our study area, mean adult body mass is 1100 g for males and non-pregnant females, whereas pregnant females are approximately 150 g heavier (Calzada 2000). Myxomatosis is prevalent within the Doñana populations to varying degrees (Rogers *et al.* 1994) and is associated with weight loss, among other pathological signs, in infected individuals (Calvete 1999).

Rabbits represented all sex, age, and reproductive classes, and included animals infected with myxomatosis (Table 1). Myxomatosis diagnosis was determined based on external clinical signs: facial skin lesions (especially patent in nose and ears), pus suppurating and swelling eyes and genital organs

Table 1. Rabbits used in the study. Rabbits were classified as adult if > 810 g for males, and > 750 g for females (minimum body mass of reproductive rabbits in Doñana, Villafuerte 1994). The presence or absence of myxomatosis signs determined disease status.

Health status	Young		Adult	
	Male	Female	Male	Female
Diseased	7	5	3	8
Healthy	9	6	28	21

(Calvete 1999). Rabbit body mass ranged from 105 g at first emergence from burrow to 1350 g, maximal adult body mass recorded in the population.

Rabbit teeth were extracted with laboratory forceps after soft boiling the skulls. Teeth were cleaned of any dirt with a toothbrush, and then maximal length and breadth of each tooth were measured by digital calliper with a precision of 0.01 mm. Teeth were defined as one of 14 anatomic types (Popesco *et al.* 1990; Table 2). To identify, which parameters affect rabbit body mass, a preliminary general linear model (GLM) was constructed examining the relationship between the natural logarithm of rabbit body mass and tooth dimensions, effect of sex, season, and myxomatosis infection. As there were 14 different tooth types, tooth dimensions were represented by the scores corresponding to the first 3 principal components obtained from a principal components analysis (Sharma 1996) of the dimensions of all 14 tooth types for all 87 rabbits.

The results of this analysis were used to guide the construction of an additional GLM for each tooth type which used the natural log of the *i*th rabbit body mass ($w_{i,obs}$) as the dependent variable, and

Table 2. Parameter values and their standard errors in brackets corresponding to eq. (1) for the 14 tooth types. I – incisor, P – premolar, M – molar. Non-zero values of the parameters are significantly different from zero.

Tooth	m_1 (tooth length)	m_2 (tooth breadth)	m_3 (interaction)	C (the constant)	Error mean square (\hat{s}^2)	R^2
I ¹	4.076 (0.794)	2.327 (0.531)	-1.067 (0.322)	-1.444 (1.086)	0.046	0.85
I ²	7.279 (1.352)	3.772 (1.240)	-3.657 (1.312)	-0.489 (1.232)	0.081	0.73
P ²	1.155 (0.320)	0.737 (0.176)	0	2.894 (0.228)	0.071	0.76
P ³	4.952 (0.810)	1.717 (0.405)	-0.878 (0.225)	-2.717 (1.259)	0.040	0.86
P ⁴	4.931 (0.729)	1.713 (0.423)	-0.892 (0.214)	-2.637 (1.218)	0.039	0.87
M ¹	7.152 (0.921)	3.149 (0.484)	-1.614 (0.273)	-6.987 (1.496)	0.041	0.86
M ²	6.022 (0.965)	2.920 (0.495)	-1.468 (0.305)	-4.836 (1.382)	0.043	0.86
M ³	2.816 (0.291)	0	0	4.670 (0.207)	0.110	0.53
I ₁	4.945 (0.875)	3.236 (0.634)	-1.479 (0.357)	-3.656 (1.412)	0.056	0.82
P ₃	0	2.835 (0.108)	0	-0.761 (0.258)	0.058	0.80
P ₄	4.734 (1.073)	3.901 (0.739)	-1.417 (0.368)	-5.825 (1.881)	0.048	0.84
M ₁	6.185 (1.076)	5.465 (0.894)	-2.036 (0.406)	-9.516 (2.112)	0.047	0.85
M ₂	4.593 (0.854)	3.954 (0.750)	-1.422 (0.346)	-5.493 (1.667)	0.044	0.85
M ₃	2.125 (0.573)	3.041 (0.988)	-1.016 (0.495)	1.268 (0.908)	0.074	0.76

tooth length ($x_{i,1}$), breadth ($x_{i,2}$), the product of tooth length and breadth ($x_{i,3}$), and disease status ($x_{i,4}$) as independent variables to model predicted log body mass (\hat{w}_i):

$$\hat{w}_i = x_{i,1} \cdot m_1 + x_{i,2} \cdot m_2 + x_{i,3} \cdot m_3 + x_{i,4} \cdot m_4 + c \quad (1)$$

Equation (1) is more conveniently expressed in matrix vector notation as $\hat{W} = XM$. Here X is a matrix of 87 rows and five columns, the first three columns are tooth length, breadth, and product of length and breadth, the fourth column is equal to 1 if the rabbit is disease free, and 0 if diseased, whereas the fifth column is equal to 1 and represents the constant in a regression model. M is a column vector containing the five model coefficients estimated using the least squares method (Sokal and Rohlf 1995). Using these models it is possible to estimate the $\ln(\text{mass})$ of any additional rabbit from any tooth and the disease status using the relationship $\hat{w}_i = x_i M$, where x_i is a row vector containing the independent variables ordered in the same way as a single row of X . The standard deviation of the i th individual prediction (s_i) made from these general linear models is given by:

$$s_i = \hat{s}^2 \cdot \sqrt{1 + x_i (XX^T)^{-1} x_i^T} \quad (2)$$

where \hat{s}^2 is the error mean square associated with the underlying general linear model (see Hocking 1985: 58).

Estimates of the mean (\hat{w}) and standard error (SE) of sets of teeth from a population of N rabbits can be made by averaging the predicted weights for each individual:

$$\hat{w} = \frac{1}{N} \sum_{i=1}^N \hat{w}_i \quad (3)$$

and adding the average of the variance of each prediction to the sample variance before proceeding with the calculation of the standard error in the usual way:

$$SE = \frac{1}{\sqrt{N}} \sqrt{\frac{1}{N^2} \sum_{i=1}^N s_i^2 + \sigma_{\hat{w}}^2} \quad (4)$$

where $\sigma_{\hat{w}}$ is the standard deviation of \hat{w} in the absence of uncertainty in the individual predictions.

All models were constructed using rabbit body mass transformed to the natural logs, but the non-transformed mass can be estimated using an approximate back transformation of \hat{w} where:

$$\text{estimated rabbit mass} = e^{\hat{w}} \left(1 + \frac{\sigma_{\hat{w}}^2}{2}\right) \quad (5)$$

Because it is often possible to identify several different teeth belonging to the same rabbit, we also calculated the variances and covariances between body mass predictions obtained for the same individual using different teeth, defined as:

$$E[(\hat{w}_{i,j} - w_{i,obs}) (\hat{w}_{i,k} - w_{i,obs})] \quad (6)$$

where $\hat{w}_{i,j}$ and $\hat{w}_{i,k}$ are estimates of the weight of the same individual obtained using the j th and k th teeth. These covariances are useful because they indicate the additional information about rabbit body mass that can be obtained from additional teeth found in feces.

The preliminary GLM indicated that length, breadth, their product, and the disease status have a significant influence in the models (see Results). However, at present myxomatosis infection status cannot be determined from remains found in feces or pellets, and therefore, a reduced model was constructed that excluded disease status (ie not fitting the parameter m_4).

We tested the accuracy and precision of the model for each tooth using a set of 16 different rabbits of known body mass, sex, and disease status (7 females, 9 males; one diseased), and evaluated both the reduced model (excluding disease status knowledge) and the full model (with disease status knowledge). We compared the observed and predicted body masses (based on each tooth) of the 16 rabbits with a paired t -test (using a Bonferroni corrected value of $\alpha = 0.05/10$ since we perform a separate test for each tooth).

To determine the accuracy and precision of the combined reduced models as a function of sample size, a computer program was developed to repeatedly sample different-sized sub-samples of randomly

selected teeth. Only those teeth, the measurements of which could predict over 80% variation in $\ln(\text{body mass})$, were used. The resulting pool of 870 teeth was randomly sub-sampled with replacement. Predicted mean $\ln(\text{body mass})$ from 100 randomly selected sub-samples was calculated for each of several different sample sizes and the predictions plotted as a function of sample size. The reduced model (ie the one omitting information about disease status) was used to predict each rabbit body mass from the tooth measurements.

In order to show a practical application of the models proposed here, we examined the monthly prey selection of Iberian lynx in the study area. Lynx feces were collected monthly between February and December 1995. Feces were washed on a 1.5-mm diameter sieve under running water, and their contents was separated and identified with the help of reference collections. From the rabbit remains, teeth were separated, cleaned, and measured with a digital caliper, and the reduced model was used to predict body mass. A one-way ANOVA was conducted to test for differences in the mean logarithmic body mass of prey eaten by lynx each month. Sequential monthly changes in body mass of prey selected by lynx was examined using pairwise multiple comparison Bonferroni corrected (0.05/10) for the 10 tests over the 11 months.

PCA analysis, GLMs, ANOVA, and associated post-hoc tests were performed using SPSS v.7.5 (SPSS 1989). The normality of the residuals in all models was checked by Kolmogorov-Smirnov tests, and homoscedasticity of variances by the test suggested by Glejser (1969).

Results

Residuals from all models were normally distributed, and their variances were homoscedastic. The first principal component (PCA1) explained 83% of variation in tooth dimensions, and was a good predictor of rabbit body mass (Fig. 1). The second and third principal component (PCA 2 and PCA3) only explained an additional 6%

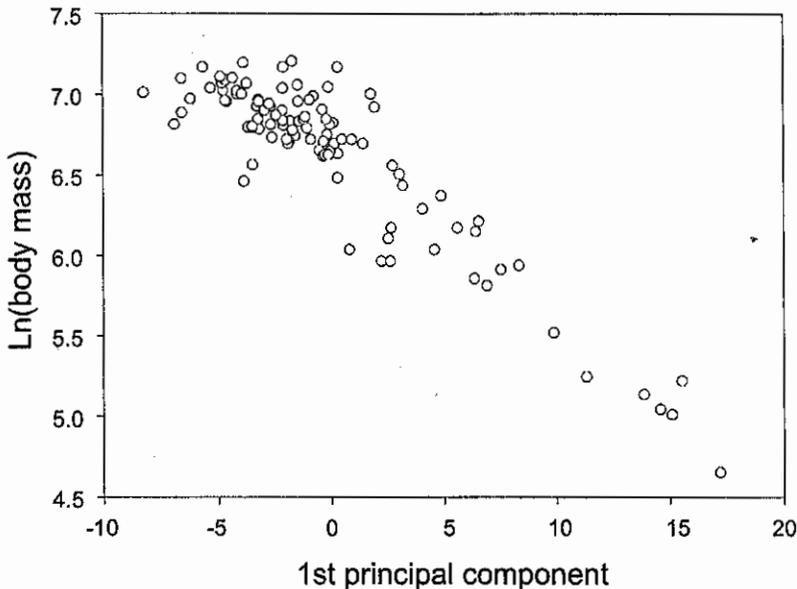


Fig. 1. Relationship between the first principal component and $\ln(\text{body mass})$ for 103 rabbits. The first principal component summarizes 83% of variation in tooth width, breadth, and product of width and breadth.

of the remaining variation, therefore only the scores corresponding to the first principal component were included in this preliminary analysis.

The results of the preliminary GLM analysis indicated that there were no significant interactions between any of the variables except tooth length and breadth, nor any detectable difference between male and female rabbits ($F_{1,68} = 1.422$, $p = 0.237$). Disease status explained a significant amount of variation in rabbit body mass, diseased individuals being an average of 162 g lighter than non diseased individuals ($F_{1,69} = 14.28$, $p < 0.001$). Season explained a significant amount of the variation in body mass only in the absence of knowledge about disease status. Together disease status and season explained only an additional 6% of variation over that explained by PCA1 alone.

Regression models that excluded disease status as a parameter, explained over 80% of variation for 10 of the 14 individual teeth (Table 2). The 4 teeth that explained the least variation (I^2 , P^2 , M^3 , and M_3) were excluded from subsequent analyses. The 45 covariances for the 10 selected teeth were all positive, remarkably uniform, and averaged 80% of the value of the variances.

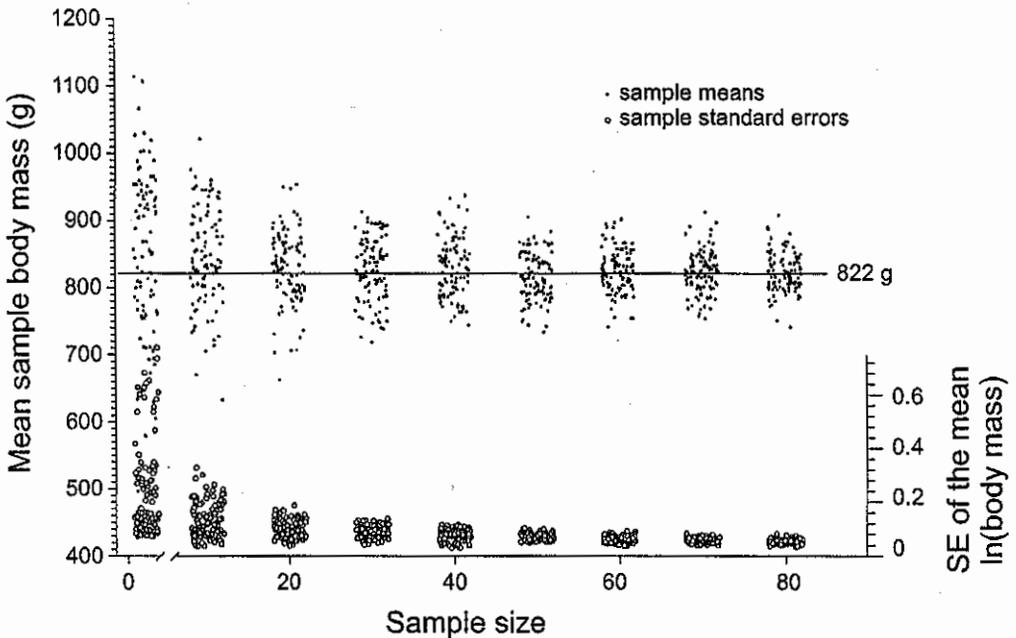


Fig. 2. Reliability of estimates of averaged body mass of rabbits, obtained from samples of different numbers of individuals. Each dot is the averaged prediction from a sample of N individuals sub-sampled with replacement from the dataset of 87 rabbits and their 870 teeth. Sample sizes were 3, 10, 20, ... 80. One hundred resamplings were performed for each sample size category. Some random 'jiggle' has been added to the x -axis to allow different sub-samples to be distinguished. The observed mean body mass of 822 g for the 87 rabbits is indicated. The right-hand axis indicates the standard error of each sub-sample mean.

Predictions of the average body mass of the 16 rabbits based on the reduced model using each of the 10 selected teeth separately indicated that 9 of the 10 teeth predicted average body masses statistically indistinguishable from those observed (paired t -tests: $1.606 \leq t \leq 2.694$, all $p \geq 0.017$). The exception was the P_3 tooth ($t = 5.174$, $p < 0.001$), which significantly underestimated rabbit body mass. Estimations of each individual rabbit $\ln(\text{body mass})$ differed by an average of 0.138 (SD = 0.116) from the observed value, ie by 104 g (SD = 87), using the back transformation proposed in equation (5). Use of the full model including disease status resulted in all 10 paired t -tests indicating no significant differences between predicted and observed body masses ($-0.384 \leq t \leq 2.823$, all $p < 0.0127$). Estimations of each individual rabbit $\ln(\text{body mass})$ differed by an average of 0.128 (SD = 0.116) from the observed value, ie 103 g (SD = 84).

Using the standard deviations obtained from the resampling procedure, and assuming the distribution of resampled means to be normal, the probability of obtaining estimates of average body masses within 100 g of the true mean with sample sizes of 3, 10, and 20 was 46, 83, and 94% respectively. The probability of obtaining estimates of average body masses within 50 g of the true mean with samples of 20, 40, 60, and 80 was 65, 75, 86, and 91% (Fig. 2).

For the prey selection study, we collected 556 lynx feces. Rabbit remains were found in 99% of the samples. Intact rabbit teeth were recovered from 81% of the

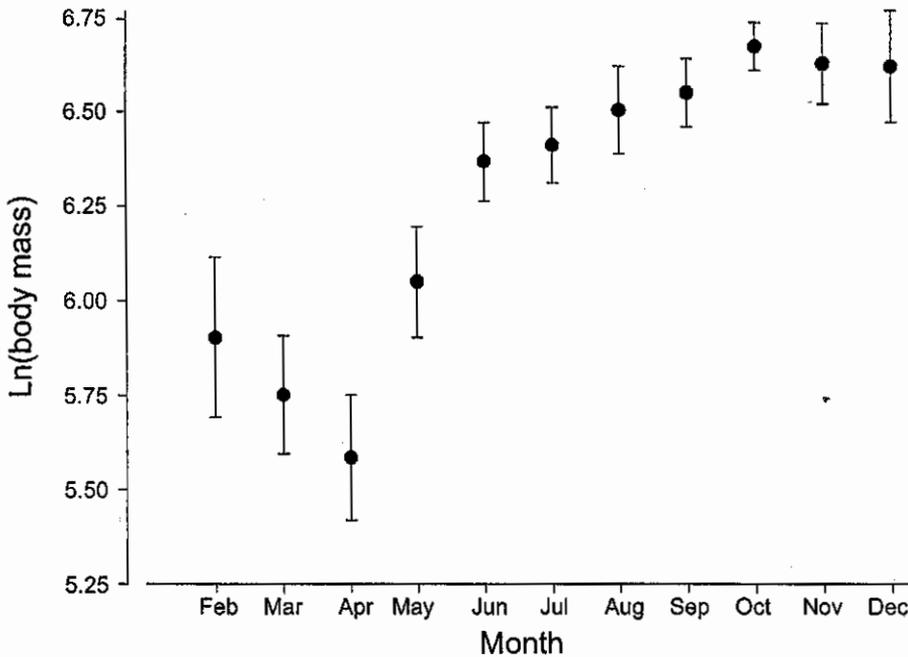


Fig. 3. Monthly rabbit size selection by lynx. Dots and error bars indicate mean $\ln(\text{body mass})$ and 95% confidence interval of rabbits predated by lynx each month.

feces with rabbit remains. A total of 516 body masses of rabbits consumed by lynx were estimated. ANOVA showed that differences in body masses of rabbits consumed monthly were significantly different ($F_{10,505} = 28.270$, $p < 0.001$). Pairwise multiple comparison among months indicated that rabbits consumed between February and April were significantly smaller than those consumed over the rest of the year (Fig. 3).

Discussion

Our models allow rabbit body mass to be predicted from tooth dimensions. Prediction errors can be computed and combined with standard errors of sample means, so that averaged predictions from different samples can be statistically compared. Taken individually, 10 out of 14 teeth explain over 80% of the variation in the observed rabbit body masses, and 9 of these teeth successfully predicted the mean mass of additional independently acquired rabbits. Knowledge of myxomatosis infection increased the percentage of variation explained by ca 6%. Resampling simulations suggested that with sample sizes of 20 individual weight estimates, the estimate of the sub-sample mean has over a 90% chance of falling within 100 g of the overall sample mean. Sample sizes 40 should place the estimated sample mean within 50 g of the overall sample mean with probability at least 0.75.

Covariances between predictions of individual body masses obtained from multiple teeth of the same individual (possibly extracted from the same jaw bone for example) were positive and were typically 80% of the variance of estimates obtained from single teeth. This observation suggests that little additional information is likely to be available from measurements of multiple teeth, and effort expended in collecting data on multiple teeth from a single individual is likely to go largely unrewarded. Our models suggest that it will be only slightly less efficient to estimate mass from a single tooth. Furthermore, when teeth occur separately in the feces, attempting to use more than one tooth could result in the mixing up of teeth of multiple prey items of similar body mass. Our study indicated that any of the following 9 teeth can be used to estimate rabbit body mass: I^1 , P^3 , P^4 , M^1 , M^2 , I_1 , P_4 , M_1 or M_2 . The P_3 tooth is more problematic, and the teeth I^2 , P^2 , M^3 , and M_3 should be regarded as last choices (Table 2). Furthermore, the small size of I^2 , M^3 , and M_3 (never exceeding 1.95 mm) will likely increase measurement error.

Individuals free of myxomatosis infection were typically ~20% heavier than infected ones in our studied population. Myxomatosis prevalence in the 87 rabbits from which these models were constructed was 26.4%. It is not currently possible to determine infection status from rabbit remains found in feces and pellets, however if some idea of myxomatosis prevalence amongst sampled rabbits is known these figures suggest a crude multiplicative correction to the mean (unlogged) weights of groups of rabbits predicted by the model. Let p be the disease prevalence.

Multiplying $e^{\hat{\mu}} (1 + \frac{\sigma_{\hat{\mu}}^2}{2})$ by the quantity $1.045 - 0.174p$ will approximately correct for myxomatosis prevalences other than the 26% inbuilt in the model.

The model can be used to test for differences between the average body mass of different groups of rabbits. In the example of lynx prey selection, the rabbits predated during the first months of the year were significantly lighter than those killed from June to December. The predicted average body mass of the rabbits collected from April to September differs significantly (with 95% confidence) from the observed mean body mass for the October to March using all of the selected teeth except P_3 . Differences observed in the mean body masses of rabbits consumed by lynx are congruent with rabbit biology in our study area. In Doñana, the breeding period usually lasts from October to May, reaching peak in March, April and May (Delibes and Calderón 1979). On the other hand, rabbit growth is fast, reaching adult size in 3.5 months (Villafuerte 1994). The Iberian lynx is a rabbit specialist (Delibes 1980), that preys upon the most available rabbit age and size classes (Calzada 2000). During the first months of the year, the most abundant rabbit size classes in the field are the lighter ones, and lynx prey more heavily upon them. Reproduction is finished in May, and lighter rabbits become rare in the field until the next breeding period. Therefore, lynx prey upon heavier rabbits from June until the beginning of the next reproduction period of rabbits.

Obtaining information about size-selective predation of rabbits, as with most small prey items, is difficult. Hunting events are rarely observed and, even when witnessed, size of selected prey items is difficult to determine. One approach is to capture and mark rabbits with radio transmitters and record when are they killed, but the costs of materials and labour used in rabbit radio tracking studies renders collaring and monitoring of large numbers of rabbits prohibitively expensive. Another approach is to analyze prey remains left by predators at carcasses, skeletons, or big osseous structures of ingested prey that can be found in pile remains and in bigger raptor pellets (Janes and Barss 1985, Donazar and Ceballos 1989, Dickman *et al.* 1991, Rohner *et al.* 1995, Barry and Barry 1996). In carnivore feces, long osseous structures are more fragmented because carnivores crush the bones before swallowing, and only the smallest hard remains of prey can be recovered intact (Calzada and Palomares 1996). So size selection studies have been based on small hard pieces of prey such as otoliths, scales, nails, vertebral centrums or teeth, among others (Wise 1980, Feltham and Marquiss 1989, Heggberget and Moseid 1994, Zalewski 1996). The accurate identification of remains such as distal phalanxes or vertebral centrums can pose severe difficulties. As a result, when such remains are used it is usually only possible to estimate rabbit weight as belonging to one of a small number of size categories (Palomares and Delibes 1991, Goszczyński and Wasilewski 1992).

While it may be difficult or even impossible to study size-selective predation from the remains of many types of small or medium size prey, it is possible to

examine it using rabbit tooth remains. Accurate estimates of rabbit size composition in predator diets is possible using the methods we described.

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