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Estimation of the age or age class of harvested animals is often necessary to interpret the condition and dynamics of wildlife populations. The mammalian eye lens continues to grow until death and hence the dry mass of the eye lens has commonly been used to estimate the age of mammals. The method requires the relationship between eye lens mass and age to be parameterized using individuals of known age. However, predicting age is complicated by the curvilinear relationship between eye lens mass and age. We used frequentist and Bayesian methods to predict the ages and age classes of harvested hog deer *Axis porcinus* from eye lens mass. Deer were tagged as calves and harvested 4–177 months later in southeastern Australia. Lenses were extracted, fixed and oven-dried. Of the five growth models evaluated, the Lord model best described the relationship between age and eye lens dry mass ($R^2 = 95\%$). The precision of age predictions obtained using the Lord model in a Bayesian mode of inference decreased with increasing eye lens dry mass, with the size of the 95% CI equaling or exceeding predicted age for hog deer > 6 years. However, most predictions of hog deer age will have reasonable precision because few animals > 6 years are harvested. Linear discriminant analysis had high predictive power for classifying hog deer to four widely-used age classes (juvenile, yearling, prime-age and senescent). The Bayesian method is recommended for inverse non-linear prediction of age and the frequentist linear discriminant analysis method is recommended for estimating age class. We provide tables of correspondence between hog deer eye lens dry mass and predicted age and age class. Our statistical methods can be used to estimate age and age class for other mammalian species, including from other ageing techniques such as tooth eruption-wear criteria.

Accurate estimation of the age of harvested animals is required for understanding the condition (e.g. age-sex specific body mass; Bonenfant et al. 2009) and dynamics (e.g. age-sex class composition; Gaillard et al. 2000, Williams et al. 2002) of wildlife populations. The mammalian eye lens continues to grow until death (Smith 1883, Krause 1934, Augusteyn 2007a) and hence the dry mass of the eye lens has commonly been used to estimate the age of mammalian species (Lord 1959, Dudzinski and Mykytowycz 1961, Dapson 1980, Mysterud and Østbye 2006, Augusteyn 2007b). The form of the relationship between age and the eye lens mass is similar for all mammal species studied, with an early rapid increase followed by slower increase throughout the life span that approaches an asymptotic maximum (Augusteyn 2008, 2014). In contrast to tooth wear (Hamlin et al. 2000), the growth of the eye lens is unaffected by nutritional factors and gender (Augusteyn 2014). Because the mass of the lens may

change post-mortem, the dry mass of fixed lenses is used to predict age (Augusteyn and Cake 2005).

Predicting the age of an individual from eye lens dry mass requires the species-specific relationship to be estimated, and this must be done using known-age animals (Dapson 1980). The prediction of age from eye-lens dry mass is problematic because uncertainty in the relationship used for prediction increases as the asymptotic maximum is approached (i.e. uncertainty increases with age). The frequentist methods commonly used to estimate age from eye lens dry mass were reviewed by Dapson (1980). He noted that key assumptions of least-squares regression, a method widely used to estimate age from eye lens dry mass, may often be violated. The issue of properly accounting for uncertainties in predicted ages (e.g. as 95% confidence intervals) from non-linear inverse prediction was also highlighted. Recent computational advances mean that Bayesian methods can now be applied to the challenging task of age estimation. A key advantage of Bayesian methods is that they provide a natural framework to properly account for uncertainties in the relationship between eye lens dry mass and the age of known-age animals when predicting

the age of an individual using non-linear inverse prediction (Gelman et al. 2004).

Knowing age class rather than age may be sufficient for the study and management of many harvested populations (Williams et al. 2002, Mysterud and Østbye 2006). In ungulate populations, the strong age-dependent variation in demographic variables (e.g. survival and reproduction) is usually assessed by discriminating among four age classes: juvenile, yearling, prime-age, and senescent (reviewed by Gaillard et al. 2000). Frequentist classification methods such as linear discriminant analysis (Fisher 1936, Lee et al. 2005) could be used to assign harvested animals to age classes according to eye lens mass, but to our knowledge these methods have not been applied to this problem.

Here we use Bayesian and frequentist methods to predict the ages and age classes of hog deer *Axis porcinus* harvested in southeast Australia. We first parameterize the relationship between eye lens dry mass and age using known-age individuals. We next use non-linear inverse prediction in a Bayesian mode of inference to predict the ages of harvested deer from their eye lens dry mass. Finally, we use frequentist linear discriminant analysis to predict the age classes of harvested deer from their eye lens dry mass. Tables of correspondence between hog deer eye lens dry mass and predicted age and age class are provided for management purposes.

Methods

Study area

We conducted the study on the 1620-ha Sunday Island, in Corner Inlet, Victoria, southeast Australia (38°42′S, 146°37′E). The island is approximately 1 km from mainland Australia and consists of a series of east–west sand dunes up to 15 m a.s.l. (Mayze and Moore 1990). The island's vegetation is dominated by forest, primarily *Melaleuca ericifolia*, manna gum *Eucalyptus viminalis*, coast banksia *Banksia integrifolia*, coast wattle *Acacia longifolia*, coastal tree tree *Leptospermum laevigatum,* with an understory of bracken fern *Pteridium esculentum* (Mayze and Moore 1990).

Hog deer are native to the floodplain grasslands and forests of the major Asian river systems (Mayze and Moore 1990, Dhungel and O'Gara 1996). The southeast Australian hog deer population is descended from 10 animals released at Corner Inlet in 1865 (Mayze and Moore 1990). For further information on the study area and species see Mayze and Moore (1990).

Sunday Island has been managed for the hunting of hog deer since it was purchased by the Parapark Co-operative Game Reserve Ltd in 1965. From 1985–2009, approximately 30 calves were captured, ear-tagged and released annually. Calves were caught at night with the aid of a spotlight and hand-held net during October–January (see Mayze and Moore 1990 for further information). The sex and age of each calf was recorded, with the latter always estimated by the same observer from the width of the annular ridge that commenced from the hairline of the hooves and progressed downwards as the hoof grew and the tips were worn away (Mayze and Moore 1990). Based on information from calves born in captivity on Sunday Island the ages are assumed

to be correct to within two weeks (R. J. Mayze, Parapark Co-operative Game Reserve Ltd, pers. comm.). A uniquely numbered yellow sheep tag (Allflex FlockTags, <www.allflex.com.au/flexiflocktags.htm>) was placed in both ears. Antiseptic spray was applied to each ear and the calf immediately released.

Sunday Island has an autumn hunting season (Para Park Co-Operative Game Reserve 2014) and harvested deer are registered with the State Government (Department of Sustainability and Environment 2009). The date of harvest is recorded for each deer.

Eye lens sampling protocol

We collected eyeballs from 111 tagged deer of known age harvested in the 2007–2010 hunting seasons (Table 1). Both eyeballs were removed as soon as possible after harvesting (always within 12 h), although two intact lenses could not always be recovered from each deer. Each eyeball was placed in a uniquely labeled vial and covered with 95% ethanol for ≥ 14 days. Lenses were subsequently extracted with a scalpel and placed on glass petri dishes and kept at room temperature for 24 h before being placed into an oven at 100°C. Lenses were weighed (g; to four decimal places) at 24-h intervals for five days with professionally calibrated Mettler AE260 scales. We used eye lens dry mass obtained at the fifth drying stage as the response variable in our analyses.

Statistical analyses

There was no significant difference between the mass of the left and right eye lens for the sub-sample of animals for which both lenses were available (n = 96; paired t-test p ≥ 0.24 at all five drying stages). We therefore included individuals with only one eye lens in our analyses. For individuals with two eye lenses we used the lens with the largest mass in our analyses because the other lens likely had a lower mass due to a problem occurring during the drying process (e.g. cracking). We did not expect differences in lens development between sexes (Augusteyn 2014) and therefore pooled data from males and females for all analyses.

We first evaluated the functional relationship between eye lens dry mass and age of animals harvested using five non-linear models previously used for describing asymptotic

Table 1. Numbers of known-age hog deer (males and females pooled) harvested at Sunday Island, southeast Australia, 2007 − 2010, that were included in our study.

Age class (years)	n
0	23
1	20
2	12
3	10
4	19
5	9
6	5
7	3
8	3
9	2
≥ 10[a]	5
Total	111

[a]The oldest individual was a female aged 14 years.

growth: Lord, Richards, monomolecular, Gompertz, and logistic growth models (Winsor 1932, Lord 1959, Richards 1959, Dudzinski and Mykytowycz 1961, France et al. 1996; Table 2). We used Akaike's information criterion with second-order adjustment (AIC_c) to correct for small-sample bias, and Akaike weights (w_i) to identify the relative support for each of the five models (Burnham and Anderson 2002).

We next fitted the most parsimonious model (i.e. Lord model) using Bayesian methods. A Bayesian model provides a natural and flexible way to account for uncertainty when computing inverse predictions of age from a given eye lens dry mass, which is problematic using frequentist methods (reviewed by Dapson 1980). The Lord model was formulated as a non-linear model linking expectation μ of the lens mass y to age x, with y a random variable following a normal distribution $N(\mu, \sigma)$:

$$y = \mu + \epsilon,$$
$$\epsilon \sim N(0, \sigma)$$
$$\mu = \gamma e^{\left(\frac{-\beta}{x+\alpha}\right)}$$

Bayesian methods assume prior distributions for model parameters and use Bayes' theorem to derive the posterior distributions of parameters (Gelman et al. 2004). The four values to be estimated for the Lord model are γ, β, α and the residual standard deviation σ. An estimated α value greater than the gestation period in hog deer (approximately 230 days or 0.62 years; Mayze and Moore 1990) would indicate that pre-natal growth of the lens was faster than post-natal growth and that another growth model should be used for the pre-natal period. In the absence of data for the pre-natal period we estimated α rather than fixing it (Augusteyn 2007b), thus imposing the same growth function pre- and post-birth. This procedure enabled the best fit of the model to be obtained with available data, the purpose of which was to optimize the prediction of animal age from lens dry mass. We used numerical methods based on Markov chain Monte Carlo (MCMC) simulations to derive posterior distributions of α, β, γ and σ. The following uninformative prior

Table 2. The five growth models fitted to the relationship between age and lens mass in hog deer harvested at Sunday Island, southeast Australia, 2007–2010. K, number of estimated parameters; AIC_c, Akaikes information criterion; w_i, Akaike weight. In each of the five models, γ is the asymptotic eye lens dry mass, α is the natal eye lens dry mass (except for the Lord model in which it corresponds to the length in years of the pre-natal growth period), and β is the relative growth rate of the eye lens dry mass. The Richards model includes an additional shape-determining parameter, m, that locates the inflection point. Note that when $m = -1$ the Richards model is the monomolecular model, when $m = 0$ it is the Gompertz model and when $m = 1$ it is the logistic model. For further information on these models see Winsor (1932), Lord (1959), Richards (1959), Dudzinski and Mykytowycz (1961), and France et al. (1996).

Model name	Structure[a]	K	ΔAIC_c	w_i
Lord	$\gamma e^{(-\beta/age + \alpha)}$	4	0.00	0.91
Richards	$\gamma\alpha/(\alpha^m + (\gamma^m - \alpha^m)(e^{-\beta \times age}))^{1/m}$	5	4.60	0.09
Monomolecular	$\gamma - (\gamma - \alpha)e^{-\beta \times age}$	4	12.18	0.00
Gompertz	$\gamma e^{(-\ln(\gamma/\alpha)e^{-\beta \times age})}$	4	22.15	0.00
Logistic	$\gamma\alpha/\alpha + (\gamma - \alpha)e^{-\beta \times age}$	4	32.42	0.00

[a]Age is the postnatal age.

distributions were used: normal for β with a mean of 0 and a variance of 1000, and uniform for α, γ and σ with values ranging between 0 and 100. An initial burn-in of 50 000 iterations was used, and posterior distributions of parameters were based on 50 000 more iterations. We used three chains to check for the stability of posterior distribution estimates using Gelman and Rubin's convergence diagnostic (Gelman and Rubin 1992).

For the following, consider θ the vector of model parameters and residual variance, and D the data. The Bayesian approach allows computation of:

$$[\theta | D] \propto [D | \theta][\theta]$$

We were interested in computing probability x_n (age) given y_n (eye lens dry mass) and θ. Therefore:

$$[x_n | y_n, \theta, D] \propto [y_n | x_n, \theta, D][x_n | \theta, D]$$

We assumed that neither the data nor the parameter estimates influence the probability of x_n and that x_n has uniform distribution between 0 and 20 years (i.e. maximum age observed in captive populations; Mayze and Moore 1990):

$$[x_n | \theta, D] = [x_n]$$

$$x_n \sim U(0, 20)$$

We also consider that $[y_n | x_n, \theta, D]$ followed a normal distribution with expectation $\mu_n = \gamma e(-\beta / (x_n + \alpha))$ and standard deviation σ so that:

$$[x_n | y_n, \theta, D] \propto e\{-0.5((y_n - \gamma e(-\beta / (x_n + \alpha))) / \sigma)^2\}$$

We did not know θ but were able to obtain its posterior probability distribution (i.e. $[\theta | D]$). Hence,

$$[x_n | y_n, D] \propto \int_\theta [x_n | y_n, \theta, D][\theta | D]$$

We estimated $[x_n | y_n, D]$ as follows. For each θ^* generated by the MCMC, and given y_n, we randomly sampled x_n^* in the probability distribution of $[x_n | y_n, \theta^*, D]$ by using the ratio-of-uniform method (Gilks 1996). We repeated this approach for each value of θ^* generated by MCMC. Finally, we computed for the distribution of x_n, for a given y_n, the median and 95% credible interval (i.e. the 2.5% and 97.5% quantiles).

We next used linear discriminant analysis (Fisher 1936, Lee et al. 2005) to predict the probability that a harvested hog deer is from an age class using their eye lens dry mass. We distinguished four biologically important age classes (reviewed by Gaillard et al. 2000) for age estimation: juvenile (<1 year), yearling (1–2 years), prime-age (2–7 years) and senescent (>7 years). We assessed the predictive power of the linear discriminant model using 2:1 cross-validation (i.e. two-thirds of the data were used for building the linear discriminant model and one third was used for testing the predictive power of the model). Using leave-one-out cross-validation to assess the predictive power of our linear discriminant model provided similar results. We performed bootstrap simulations to estimate mean success rate based on 50 000 linear discriminant functions built from 50 000 random samples using two-thirds of the data set. Lower and upper 95% bounds were computed from the 2.5% and

97.5% quantiles of the distribution of the error rates. The same priors for being in a given age class were used during analyses and corresponded to the class proportions for the overall dataset. These priors should therefore represent a typical sample of harvested animals.

We performed all analyses using R 3.0.2 (<www.r-project.org>). AIC_c values and non-linear least-squares estimates of model parameters were obtained using the Gauss–Newton algorithm (Bates and Watts 1988). Bayesian model fitting and model diagnostics such as the convergence of MCMC chains (Gelman and Hill 2007) were performed using the libraries rjags, coda and Runuran (Plummer et al. 2006, Leydold and Hörman 2012, Plummer 2014). Linear discriminant analysis was performed using the lda function in the MASS library (Venables and Ripley 2002).

Computer code and data availability

The R script for implementing all models is provided in Supplementary material Appendix 1. All supplements are available online at <www.wildlifebiology.org/appendix/wlb-00185>. Data associated with this paper ("hog.txt" in Appendix 1) have been deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.0r31r>. (Forsyth et al. 2016).

Results

Of the five growth models (Table 2, 3) considered, the Lord model best described the relationship between age and eye lens dry mass ($w_i = 0.91$). The next best model was the Richards model ($w_i = 0.09$). The monomolecular, Gompertz and logistic models all had negligible support ($w_i = 0.00$). The Lord model provided a good fit to the data ($R^2 = 0.953$, Fig. 1), with no systematic departure of observed and fitted values (Supplementary material Appendix 2 Fig. A1).

The precision of age predictions obtained using the Lord model in a Bayesian framework decreased with increasing eye lens dry mass (Fig. 2, 3), with the size of the 95% credible interval equaling or exceeding predicted age for hog deer > 6 years. A table of correspondence between eye lens dry mass and predicted age (with 95% credible intervals) is provided for management purposes (Supplementary material Appendix 3 Table A1).

A linear discriminant model based on age classes had high predictive power (mean error rate [95% CI] = 2.8% [0.0–8.3%]). Juvenile (0.0% [0.0%–0.0%]) and senescent classes (0.0% [0.0%–0.0%]) were discriminated without error, whereas yearling (5.4% [0.0–20.0%]) and prime-age (5.9%
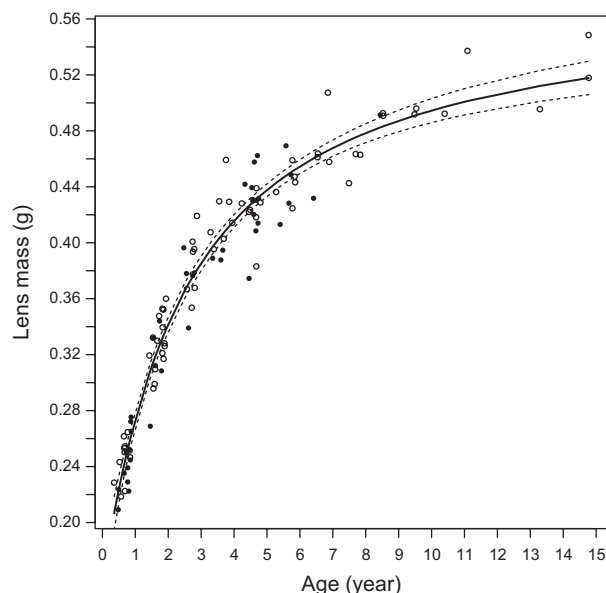

Figure 1. Growth of lens mass (g) in male (filled circles) and female (open circles) hog deer of known ages harvested at Sunday Island, southeast Australia, 2007–2010. The solid line is the fitted Lord model, and the dashed lines are the upper and lower 95% confidence bounds.

[0.0–17.6%]) classes had low error rates. This linear discriminant model enables biologists to obtain the posterior probability that a harvested animal is from a given age class from its eye lens dry mass (Supplementary material Appendix 4 Table A2). For example, hog deer with an eye lens dry mass of 0.520 g had a posterior probability of 0.99 of being in the senescent age class and a posterior probability of 0.01 of being in the prime-age class. A hog deer with an eye lens dry mass of 0.365 g had almost the same posterior probability of being in the yearling (0.48) or prime-age (0.52) class, and the Bayesian–Lord model predicted that the animal was 2.57 years old (95% CI = 1.8–3.7; Supplementary material Appendix 3 Table A1). A deer with an eye lens dry mass of 0.370 g had posterior probabilities of 0.33 and 0.67 of being in the yearling and prime-age classes, respectively. A deer with an eye lens dry mass of 0.360 had posterior probabilities of 0.63 and 0.37 of being in the yearling and prime-age classes, respectively. This example indicates how a small change in lens mass (0.05 g) substantially changes the posterior probabilities in favor of one class or the other due to the high discriminatory power of the function.

Table 3. Parameter estimates (SE) for the five growth models fitted to assess the relationship between age (years) and lens mass (g) in hog deer harvested at Sunday Island, southeast Australia, 2007–2010. For model structures see Table 2. In all models, γ is the asymptotic eye lens dry mass, α is the natal eye lens dry mass (except for the Lord model in which it corresponds to the length in years of the pre-natal growth period), and β is the relative growth rate of the eye lens dry mass. The Richards model includes an additional shape-determining parameter, m, that locates the inflection point.

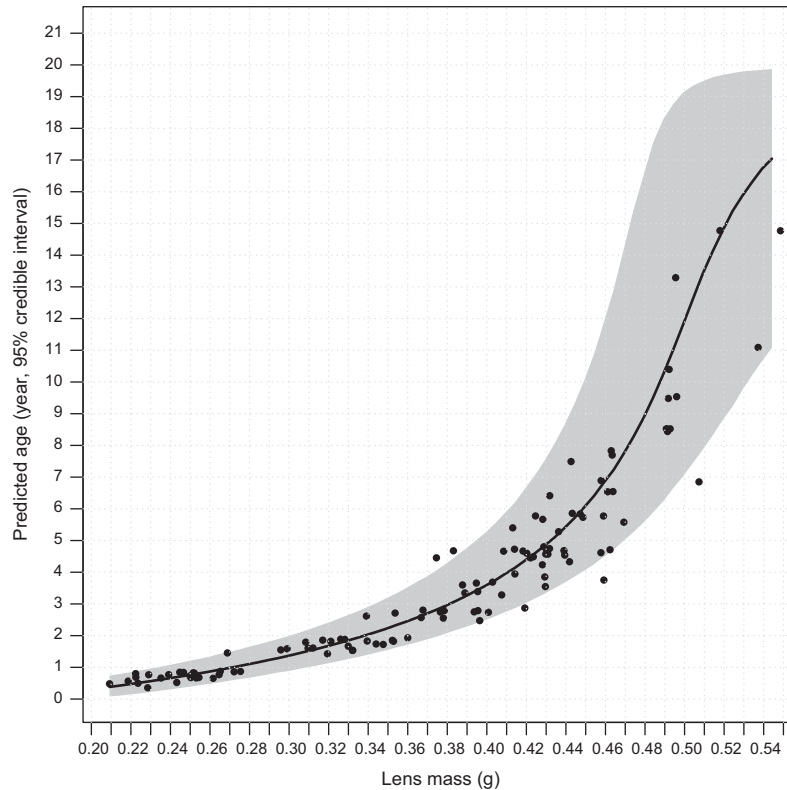| Model name	γ	α	β	m
Lord	0.578 (0.012)	1.362 (0.178)	1.767 (0.177)	
Richards	0.537 (0.019)	0.097 (0.106)	0.165 (0.049)	−2.754 (0.548)
Monomolecular	0.504 (0.007)	0.182 (0.007)	0.326 (0.023)	
Gompertz	0.495 (0.007)	0.197 (0.006)	0.425 (0.027)	
Logistic	0.488 (0.006)	0.207 (0.006)	0.530 (0.032)	

Figure 2. Ages of hog deer predicted from their eye lens dry mass using the Lord model in a Bayesian mode of inference. The filled circles are the data and the shaded area is the 95% credible interval.

Discussion

Our analyses have advanced the many previous attempts to estimate the age of individual mammals from eye lens dry mass in three main ways. First, we used information theoretic methods (Burnham and Anderson 2002) to identify the growth model that best explained the relationship between age and eye lens dry mass (i.e. the Lord model) using a large sample of known-age hog deer. Second, we fitted the Lord model in a Bayesian framework to properly account for uncertainty (Gilks 1996, Gelman et al. 2004) when using inverse prediction to estimate the age of harvested animals from their eye lens dry mass. Third, we used linear discriminant analysis (Fisher 1936, Lee et al. 2005) to estimate the probability that a harvested animal is from each of four age classes (i.e. juvenile, yearling, prime-age or senescent) used for deer population management (Gaillard et al. 2000).

The eye lens grows throughout the life of a mammal, but the rate of growth declines with increasing age (Augusteyn 2008, 2014). Hence, many models could potentially explain the curvilinear relationship between age and eye lens dry mass (reviewed by France et al. 1996). Our information theoretic approach showed that the Lord model (Lord 1959, Dudzinski and Mykytowycz 1961) best explained the relationship between age and eye lens dry mass in hog deer, although there was some support for the Richards model. Further work is required to determine if the Lord model is the most parsimonious explanation of the curvilinear relationship between age and eye lens dry mass for other mammalian species.

A Bayesian approach is particularly suited to the estimation of age from eye lens mass because it allows for coherent expressions of uncertainty about all known quantities and does not rely on large samples for validity of inference, with prediction made using the posterior predictive distribution (Gelman et al. 2004). The Bayesian approach provides a 95% credible interval for the predicted age for any eye lens mass, uncertainty that should be incorporated in population modeling (Williams et al. 2002). The precision of age predictions obtained using inverse prediction from the Lord model decreased with increasing eye lens dry mass. The increasingly poor precision for heavier eye lenses was due to the curvilinear relationship between age and eye lens dry mass (Dapson 1980, Mysterud and Østbye 2006). However, most estimates of hog deer age will have reasonable precision because few animals > 6 years are harvested in southeast Australia (< 12%; Table 1).

Given the poor precision of estimated ages for heavier eye lens dry masses, in some situations it may be more relevant to use classification methods to assign individuals to age classes that have biological and/or management relevance (e.g. when constructing stage-based matrix models; Williams et al. 2002). Linear discriminant analysis assigned hog deer to the oldest (i.e. senescent) age class without error, a major advance over the imprecise predictions for older animals from the Lord model. Many classification methods could potentially be applied to the estimation of age class from eye lens dry mass (reviewed by Lee et al. 2005). Preliminary analyses not reported here revealed that linear discriminant analysis performed better than quadratic discriminant analysis, mixture discriminant analysis, support vector machine and
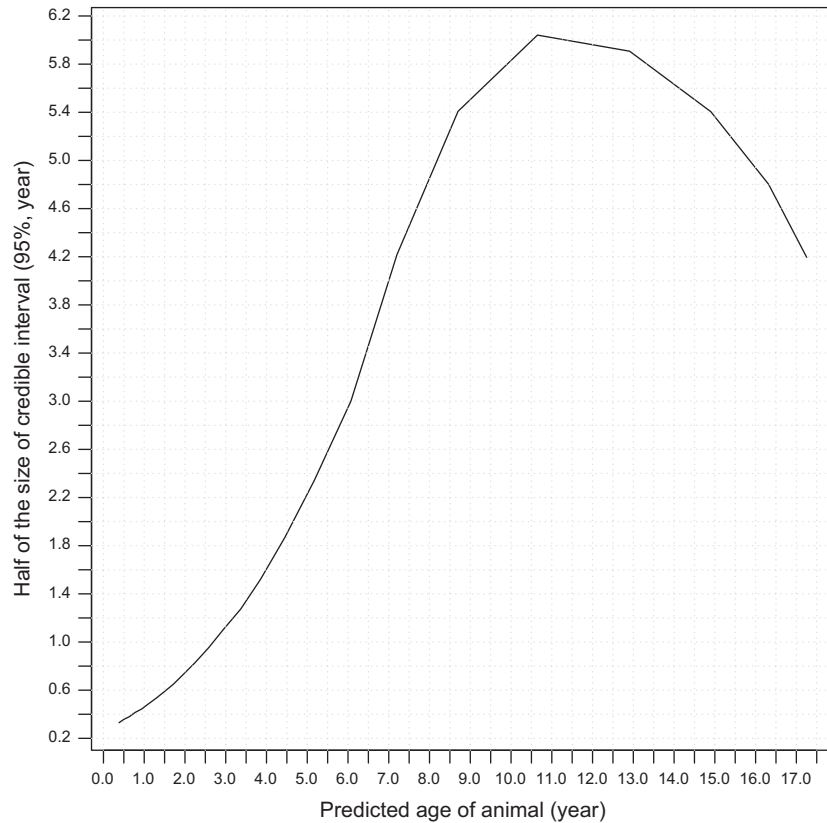
Figure 3. Relationship between ages of hog deer predicted from their eye lens dry mass and the uncertainty of the prediction using the Lord model in a Bayesian mode of inference.

random forest methods. This result likely arose because: 1) we only had one discriminant variable, 2) eye lens dry masses were approximately normally distributed within age classes, and 3) interclass variances were similar. Classification methods could be used to assign individuals to age classes using other aging techniques (e.g. tooth eruption-wear criteria; Hamlin et al. 2000).

Knowing the age classes of harvested hog deer is important for setting harvest quotas for this species in southeast Australia (Mayze and Moore 1990) because the harvest of yearling and prime-age females is likely to have the most significant impacts on population size and age structure (Gaillard et al. 2000). The field and statistical methods reported here enable managers and researchers to estimate the age and age class of harvested hog deer from the eye lens dry mass (Supplementary material Appendix 1, 3, 4). The procedure for extracting, fixing and drying the eye lens is straightforward for management agency staff and volunteers to use. There were sometimes substantial differences between the weights of eye lenses extracted from the same deer, most likely due to material being lost from the lens during drying and weighing. We recommend that both eye lenses be extracted and dried to a constant mass, and that the heaviest of the two lenses (rather than the mean of the two lenses) is used for predicting age and/or age class.

Conclusion

The problem of mammalian age estimation can be addressed using two methods, one 'new' and one 'old'. If the age in years is required then a Bayesian mode of inference is recommended because it provides a natural and flexible means of obtaining inverse, non-linear predictions (Gilks 1996, Gelman et al. 2004), overcoming the issues associated with frequentist solutions (Dapson 1980) to this problem. However, if only the age class (e.g. juvenile, yearling, prime-age or senescent) is required then frequentist linear discriminant analysis (Fisher 1936) is recommended because it has high predictive power and is straightforward to implement. These methods can be used to estimate age and age class for other mammalian species, and could be applied to other mammalian ageing techniques such as tooth eruption-wear criteria.

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Supplementary material (available online as Appendix wlb-00185 at <www.wildlifebiology.org/appendix/wlb-00185>). Appendix 1–4.