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Aude Verwilghen, Marie-Agnès Rabillard, Yannick Chaval, Dominique Rieffel, Martua Hasiholan Sinaga, et al.. Relative age determination of *Rattus tiomanicus* using allometric measurements. *Mammalia*, 2015, 79 (1), pp.81-90. 10.1515/mammalia-2013-0113 . hal-01114386

HAL Id: hal-01114386

<https://hal.science/hal-01114386>

Submitted on 27 May 2020

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Relative age determination of *Rattus tiomanicus* using allometric measurements

Abstract: For sustainable oil palm production, barn owl (*Tyto alba*) predation should be enhanced and monitored to better understand its impact on rodent population dynamics, notably for selective predation based on age or size. Our aim was to assess the best combination of osteometric variables that predict eye lens weight and thus the relative age of an individual *Rattus tiomanicus* based on pellet remains. We captured 161 individuals in an oil palm plantation in Indonesia and measured 15 osteometric variables for the jaw, skull, and femur. We investigated the variables' correlations with eye lens weight and estimated the measurement errors. In addition, 120 pellets were collected to assess the frequency of different types of bones. Predictive modelling was then used. We suggest that the model using the femur length would be more appropriate, even if it is slightly less precise than the models that consider the skull and jaw variables. The femur was well represented in the pellet sample, its length highly correlated with the eye lens weight, with a low measurement error. Our study demonstrates the utility of femur length for age prediction in prey from macroremains in oil palm plantations, wherein most pellets are headless and *R. tiomanicus* is the dominant prey.

Keywords: allometry; barn owl pellet; eye lens weight; oil palm plantation; rodent.

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Introduction

Oil palm is one of the world's most rapidly expanding crops; the main producer countries are Indonesia and Malaysia (Oil World 2012). Expanding oil palm plantations (OPPs) over large areas support rodent population outbreaks, and certain rodents are considered invasive pests that cause significant damage to production (Liau 1990, Turner and Gillbanks 2003). Pest control typically includes treating a field using anticoagulant rodenticides and/or reinforcing barn owl predation (*Tyto alba*, Scopoli) in the plantation by providing nest boxes (Wood and Fee 2003). For more sustainable oil palm production, natural predation by barn owls should be enhanced, which requires that we better understand its impact on rodent population dynamics (Hafidzi 1994), notably for selective predation based on rodent age or size (Saint Girons 1973, Kittlein 1997).

In Southeast Asian OPPs, barn owls primarily feed on rats (Lenton 1984, Small 1990, Puan et al. 2011); their prey spectrum is almost entirely confined to the three species, which are the major pests for oil palm crop: *Rattus tiomanicus* Miller, the Malaysian field rat; *Rattus argentiventer* Robinson and Kloss, the ricefield rat; and *Rattus tanezumi* Temminck (synonym: *Rattus rattus diardii* Jentink), the oriental house rat (Liau et al. 1993, Corley and Tinker 2003, Wood and Fee 2003). In most mature estates, *R. tiomanicus* predominates (Hafidzi and Saayon 2001, Wood and Fee 2003, Chia 2005), wherein it composes most of the barn owl prey (Lenton 1984). Although barn owl predation on

rats on oil palm estates is widely used and has been primarily studied in Malaysia for a long time (Duckett 1976, 2008, Lenton 1980, Small 1990), the real effect of barn owl predation on the rat population is inconclusive (Chia et al. 1995, Wood and Fee 2003). In addition, there is no clear pattern for selective predation based on size, weight, or age (Small 1990, Lim et al. 1993, Hafidzi and Naim 2003, Puan et al. 2011), and certain authors suggest that differential barn owl predation may be site specific (Trejo and Guthmann 2003, Leveau et al. 2006). Therefore, predation must be locally investigated to adapt pest control strategies to each plantation/site.

Thus, as suggested by Sherfy et al. (2006), prediction models based on morphometrics are valuable for reconstructing the prey population age structure, which is a useful tool for monitoring the demographic consequences of population control. Eye lens weight (ELW) is considered to be the most accurate age indicator for mammals because it varies much less with environmental conditions than other body measurements (Lord 1959, Friend 1967, Morris 1972, Pucek and Lowe 1975, Leirs 1994, Gliwicz and Jancewicz 2001, Lalis et al. 2006, Augusteyn 2008). ELW is widely used to estimate rodents' exact or relative age (Le Louarn 1971, Poulet 1980, Barnett and Dutton 1995, Burllet et al. 2010). Eye lens growth patterns from known-age individuals bred in a laboratory have primarily been investigated using vole and mice (Rowe et al. 1985, Yabe and Arakawa 2009). A few *Rattus* species also exhibit a quantitative relationship between age and ELW (Williams 1976, Hardy et al. 1983, Tanikawa 1993, Shrestha et al. 2002); however, *Rattus tiomanicus* has not been studied. The eye lens cannot be retrieved from raptor pellets; however, other macroremains can be collected, such as skulls and bones. Therefore, models have been developed to predict the ELW from osteometric measurements. Variables related to skull and jaw dimensions are typically considered most appropriate for small-mammal age estimations using macroremains (Quééré et al. 1994, Granjon and Traoré 2007). However, because of prey decapitation, the absence of skull was frequently reported for barn owl pellets from Southeast Asian OPPs (Medway and Yong 1970 in Lenton 1984, Lim et al. 1993, Hafidzi and Naim 2003, Puan et al. 2011); thus, it was necessary to use variables other than cranial and dental variables. Very few authors have investigated the allometric relationships between osteometric measurements and age or size/body weight for *R. tiomanicus* (Small 1990, Lim et al. 1991, 1993), although this species is the most studied rodent pest in OPPs (Wood 1984, Wood and Liau 1984a,b, Buckle et al. 1997, Chia 2005). Moreover, only two authors, Lim et al. (1993) and Puan et al. (2011), have explored

the relationship between femur length and relative age, respectively, for *R. tiomanicus* and *Rattus tanezumi*, to overcome the absence of skull elements in pellets.

In this study, we investigated the correlations between ELW and a range of osteometric measurements for *Rattus tiomanicus* trapped in a Sumatran (Indonesia) OPP. Our objectives were to assess the following: (i) the frequency of different types of bones and their physical integrity in barn owl pellets and (ii) the best combination of osteometric variables to predict *R. tiomanicus* lens weights theoretically (i.e., considering all variables) and practically (i.e., considering the bones most often observed in owl pellets).

Materials and methods

Study site and sampling design

The research was conducted at the Libo Estate, which is a large-scale OPP (approximately 4370 ha) in the Riau Province, Sumatra. The climate is typically humid equatorial, with an average temperature of 28°C, a mean annual rainfall of 2500 mm, and two dry seasons in February and June through August. The palm plantation is old (it was planted between 1986 and 1990) and has not been treated using rodenticide for >10 years after the introduction of barn owls for rodent pest control in the 1990s. The rodents were trapped in May 2011. Nine trap lines with 25 cage traps were set up approximately every 9 m at the base of palm trees. The traps were set for two or three consecutive nights (seven trap lines were only set for two consecutive nights) and controlled each morning. We used locally constructed cage traps (32×12×15 cm) that were baited with freshly cut half of a palm fruit. The traps were located in the plantation core at a minimum distance of 600 m from human settlements to minimise trapping species other than *Rattus tiomanicus*.

Species identification and osteometric measurements

The rats were euthanised using chloroform (outdoors with safety precautions for the operator's health) and then sexed, and classic external body measurements were collected (weight, head/body, and tail length; see Herbreteau et al. 2011). The head and left leg were severed for further dissection, boiled in an autoclave at 121°C for 30 min, and then submerged in water for 1 week to ease bone and flesh separation. For eye lens processing, various similar

techniques are described in the literature (Poulet 1980, Rowe et al. 1985, Shrestha et al. 2002, Jánová et al. 2007), and as noted by Lalis et al. (2006), the accuracy is rarely assessed. We adapted the protocol to tropical conditions. The eyeballs were removed and fixed in 4% formalin for at least 2 weeks in a refrigerator. The lenses were then excised, washed with distilled water, and oven dried at 40°C in two batches for 9 and 7 days (given the humid conditions, a preliminary trial was used for the first batch to estimate the drying duration necessary for weight stabilisation). Once out of the oven, the eyeballs were immediately weighed in pairs to the nearest 0.1 mg. The mean weight of each pair was used for analysis.

One hundred and sixty-one presumably *Rattus tiomanicus* individuals (identified according to external morphology; Corbett and Hill 1992, Aplin et al. 2003) were used as the reference collection for our measurements. A subsample composed of 120 individuals was selected using the following process. A principal component analysis with log-transformed osteometric measurements (see below) was used to select three variables that were least correlated between each other and least correlated for animal size (BP, CML1-3, and JawL1; see Figure 1). The

animals were then selected at the periphery and centre of the data cloud from a triangular graph, wherein the axes were the three variables. The animals were then identified using a molecular barcoding method, with species assignment using the RodentSEA reference database available at http://www.ceropath.org/barcoding_tool/rodentsea (Clairon et al. 2010).

The following 15 osteometric variables (Figure 1) were measured to the nearest 0.1 mm for each specimen by the same person using digital calipers: (i) in accordance with Dickman et al. (1991) and Quéré et al. (1994), 11 variables for the skull and jaw that relate well to age and are typically collected intact from bones and easily found in pellets; (ii) two femur variables, one composing the entire length of the bone, and the other excluding the distal epiphysis cartilage that is often absent (hereafter, the “short length”); the femur was used because certain authors note that heads are frequently absent from the pellets in OPPs, likely because barn owls decapitate their prey before carrying them to the nest (Lenton 1984, Lim et al. 1991); and (iii) two incisor variables were measured to use small-carnivore scat in the model because incisors are typically the only intact rat remnant in a scat (Bonnaud et al. 2008).

Material used for measurement (skull, femur, and eye lenses of each of the 161 specimens) is available at the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), Montpellier, France. Specimens are labelled LI1105XXxx (xx being the number of the individual trapped on the line XX; traplines are labelled AA, AB, AC, AD, AE, AR, AS, AT, AU).

The final aim of this study was to propose a model with a combination of variables (osteometric measurements) that best predicts the ELW and thus the relative rat age based on pellet remains. Therefore, concurrent with trapping, we collected the intact barn owl pellets inside nest boxes in our study area and the vicinity. One hundred pellets were collected in 57 nest boxes, covering an area of approximately 1600 ha (typically, one nest box in each block of 30 ha). It has been suggested that the presence or absence of skulls in pellets is associated with an owl's breeding cycle (Lenton 1984, Hafidzi and Naim 2003). Subsequently, 20 additional pellets were retrieved in August 2010, during the barn owl breeding peak, to encompass a potential behavioural change in prey consumption. We examined the occurrence and integrity of the rodent skull, jaw, and femur in pellets to assess which of the 15 variables were most likely to be collected from the pellets. We also estimated the imprecision for measurements from the same observer over two measurement sessions; the 15 variables from a sample composed of 30 rats were measured twice by the same person.

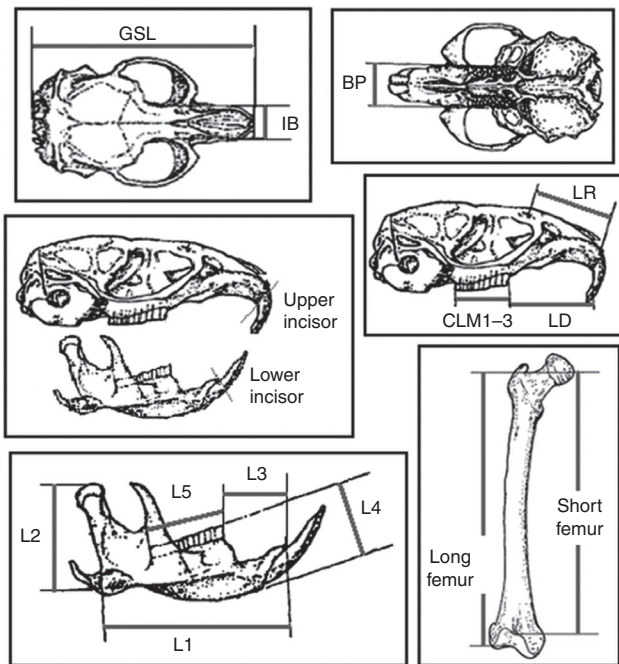


Figure 1 Skull, jaw, and femur variables.

Adapted from Quéré et al. (1994).

Skull: GSL, greater skull length; IB, interorbital breadth; LR, length of rostrum; CLM1–3, molar row length; LD, length of diastema; BP, breadth of palate; and upper incisor. Jaw: L1, mandible length; L2, mandible height; L3, diastema height; L4, jaw height; L5, molar row length; and lower incisor. Femur, short femur and long femur.

Statistical analysis

The percentage of measurement error (%ME; i.e., the percentage of sample variation due to measurer imprecision) can be defined as “the ratio of the within-measurement component of variance to the sum of the within- and among-measurement component” (Bailey and Byrnes 1990):

$$\%ME = [s^2_{\text{within}} / (s^2_{\text{within}} + s^2_{\text{among}})] \times 100.$$

The mean squares of the one-way ANOVA were calculated to determine the components of variance:

$$s^2_{\text{within}} = \text{MSS}_{\text{within}}$$

and

$$s^2_{\text{among}} = (\text{MSS}_{\text{among}} - \text{MSS}_{\text{within}}) / m,$$

where m is the number of repeated measurements (Yezeriac et al. 1992, Claude 2008).

Two sets of models were computed based on two sets of variables: (i) all osteometric variables without considering whether they can be frequently collected from the pellets (“theoretical” model) and (ii) variables most commonly found in pellets due to high bone integrity (i.e., likely to be most useful for researchers and practitioners working with pellets; “practical” models). The practical models were constructed using the osteometric variables selected on the basis of three criteria: (i) the frequency in pellets is >10%; (ii) the Pearson correlation coefficient for the given variable with an ELW is ≥ 0.8 ; and (iii) the ME percentage is <10%. Because we did not have a biological *a priori* for the order of variables in the model, a stepwise procedure (backward and forward) was used to select the best set of predictors based on the Akaike information criterion (AIC) (Burnham and Anderson 2002). Visual analyses of bivariate graphs among the ELW and osteometric measurements suggested that linear modelling was an acceptable option. The normality of model residuals was determined using the Kolmogorov-Smirnov goodness of fit test. We used a 10-fold cross-validation procedure to estimate the coefficient of determination (R^2) and the root mean squared error (Rmse), which is a good measure of model fit and accuracy.

The prey’s sex cannot be defined in pellets using our measurements. However, we investigated a potential difference in ELW between sexes from our trapped sample using a linear model. In addition, we also investigated the performance of models, including the variable sex as a covariate, to assess whether a bias was induced by using only one equation for both sexes.

The data were statistically analysed using the R software (version 2.15.0; R Foundation for Statistical

Computing, Vienna, Austria) and the packages *ade4*, *bootstrap*, *DAAG*, *epicalc*, *lattice*, *pgirmess*, *plotrix*, and *ipred*.

Results

Rattus tiomanicus characteristics

Among the 120 individuals that were subsampled for molecular identification, 110 were successfully sequenced, 100% of which were confirmed as *Rattus tiomanicus*. Summary statistics on the body and bone measurements (Table 1) as well as ELW distribution (Figure 2) suggest that both juvenile and adult specimens were sampled with minimum and maximum body weights at 17 and 139 g, respectively. The sex ratio of our sample was 1.36 males per female. We did not detect a significant difference in ELW between males and females (F-value=0.0723, $p=0.7883$; Kolmogorov-Smirnov test of

Table 1 Summary statistics for *Rattus tiomanicus* body and bone measurements (n=161).

Variable	Mean±standard deviation	Minimum	Maximum
Body weight (g)	72.73±23.27	17.00	139.00
Body length (mm)	139.9±15.1	90.00	183.00
Tail length (mm)	144.4±14.6	85.00	189.00
Eye lens weight (mg)	35.98±7.02	13.20	64.00
Jaw (mm)			
L1	16.82±1.24	11.77	21.02
L2	8.97±0.97	4.77	12.18
L3	5.27±0.43	3.51	7.08
L4	5.19±0.55	3.21	7.52
L5	6.16±0.15	4.23	6.86
Lower incisor	1.62±0.20	0.87	2.35
Skull (mm)			
GSL	36.27±2.62	25.67	41.92
IB	5.68±0.45	4.30	7.10
LR	12.74±1.24	8.21	17.30
CLM1–3	6.40±0.19	5.21	7.12
LD	9.87±1.01	6.51	12.92
BP	4.49±0.40	2.60	6.49
Upper incisor	1.97±0.20	1.18	2.71
Femur (mm)			
Long femur	23.57±3.00	12.62	30.40
Short femur	20.20±2.63	10.97	26.45

L1, mandible length; L2, mandible height; L3, diastema length; L4, jaw height; L5, molar row length; GSL, greater skull length; IB, interorbital breadth; LR, length of rostrum; CLM1–3, molar row length; LD, length of diastema; and BP, breadth of palate.

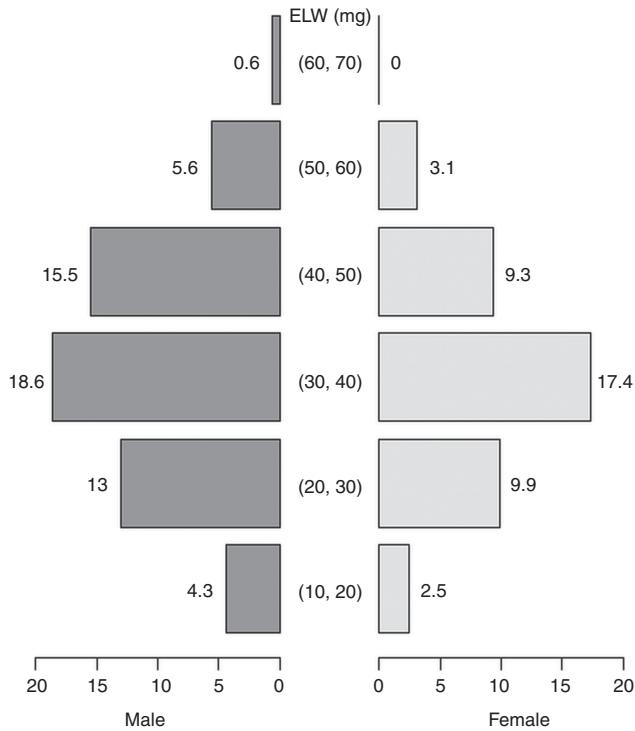


Figure 2 Population eye lens weight pyramid-stratified using sex for a *Rattus tiomanicus* sample (n=161) trapped on an oil palm plantation in Riau (Indonesia).

The numbers at the bar tops are percentages of the total.

residuals normality: $p=0.9747$; Bartlett test of homogeneity of residuals variance: $p=0.2532$).

Bone frequency in pellets and measurement errors

As reported in Table 2, full osteometric measurements were impossible in at least 70% of pellets because of the low integrity of the skull and jaw bones in barn owl pellets. However, we measured the short femur in 80.8% of pellets. Between the two different sessions of measurements (by the same person), the percentage of measurement errors was low for the short femur (%ME=0.23). The L1 and L2 values were also among the lowest at 1.8% and 1.4%, respectively. Seven variables, L3, L4, L5, Lower incisor, IB, CLM1–3, and Upper incisor, were >10% ME.

Predictive models for the relative age estimation

The Pearson correlation coefficients (r) between the ELW and the variables CLM1–3 and L5 were <0.4 (Table 2).

Table 2 Frequency in barn owl pellets (n=120), measurement errors, and correlation with eye lens weight for each *Rattus tiomanicus* osteometric variable (n=161).

Osteometric variable	Frequency in pellets (%)	Measurement error (%)	Correlation with eye lens weight	
			Pearson coef. r	p-Value
Jaw				
L1***	30.0*	1.8*	0.85*	<0.001
L2***	30.8*	1.4*	0.89*	<0.001
L3	32.5*	11	0.83*	<0.001
L4	32.5*	10.8	0.87*	<0.001
L5	32.5*	10.6	0.37	<0.001
Lower incisor	32.5*	14.5	0.86*	<0.001
Skull				
GSL	2.5	0.2*	0.87*	<0.001
IB	21.7*	26.4	0.79*	<0.001
LR	8.3	4.9*	0.89*	<0.001
CLM1–3	25.8*	26.8	0.27	<0.001
LD***	23.3*	1.9*	0.86*	<0.001
BP***	23.3*	4*	0.83*	<0.001
Upper incisor	22.5*	12.7	0.83*	<0.001
Femur				
Long femur***	25.0*	1.2*	0.92*	<0.001
Short femur***	80.8*	0.2*	0.92*	<0.001

L1, mandible length; L2, mandible height; L3, diastema length; L4, jaw height; L5, molar row length; GSL, greater skull length; IB, inter-orbital breadth; LR, length of rostrum; CLM1–3, molar row length; LD, length of diastema; and BP, breadth of palate. The values that fit with the pre-selection criteria (see Material and methods) are marked with an asterisk; the variables pre-selected for “practical” predictive modelling are indicated with three asterisks.

Other variables were strongly correlated with lens weight; r ranged from 0.79 to 0.92, and the most correlated variables were the short and long femur. Using criteria based on frequency in pellets (>10%), the measurement errors (<10%) and correlation with lens weight ($r \geq 0.8$), only six variables, namely, L1, L2, LD, and BP, as well as the short and long femur, were selected for the first predictive model (see Table 2). The model that best predicted the ELW was the model that included L2, LD, BP, and the short femur with an AIC=435.62 and $R^2=0.847$ (model 1, Table 3). Because most pellets are headless, we investigated a model based on the short femur measurement only; the AIC for this model (model 2, Table 3) was greater than model 1 (458.04 vs. 435.62). The accuracy evaluation for the two “practical” models through cross validation showed that model 1 was slightly more accurate at estimating ELW than the model that only included the femur (Rmse=3.86 vs. Rmse=4.14, only considering the femur). A “theoretical” model was constructed on

Table 3 Comparison of predictive model fitness and accuracy for *Rattus tiomanicus* eye lens weight estimation using a stepwise procedure and cross validation.

Pre-selection of variables	Model	Best combination of variables and associated equation	AIC	R ²	Rmse
L1, L2, LD, BP, short and long femur	1	ELW=(1.5060 L2+0.8413 LD+2.7511 BP+1.4777 Short femur)-28.0396	435.62	0.847	3.86
L1, L2, LD, BP, short and long femur, sex	1sex	ELW=(-1.542 Sex+1.601 L2+0.909 LD+2.560 BP+1.276 Long femur)-28.278	431	0.851	3.83
Short femur	2	ELW=(2.806 Short femur)-20.705	458.04	0.859	4.14
Short femur, sex	2sex	ELW=(-1.186 Sex+2.813 Short femur)-20.3405	456.72	0.851	4.16
All variables	3	ELW=(0.8263 L2-2.4834 L5+0.7125 LD+2.6186 BP+4.4933 Upper incisor+5.5058 Lower incisor+1.2114 Short femur)-17.1739	422.05	0.865	3.78
All variables, including sex	3sex	ELW=(-1.260 Sex+1.101 L2-1.603 L3-2.425 L5+1.030 LD+2.502 BP+4.146 Upper incisor+6.126 Lower incisor+1.245 Short femur)-14.637	419.1	0.851	3.71

Models 1 and 2 are “practical” models, and model 3 is the “theoretical” model.

ELW, eye lens weight; L1, mandible length; L2, mandible height; L3, diastema length; L5, molar row length; LD, length of diastema; and BP, breadth of palate.

the basis of all of the jaw, skull, and femur variables. The seven-variable combination that best predicted the ELW is shown in Table 3 (model 3). This model performed better than both of the best “practical” models (AIC=422.05 and R²=0.865); however, we only detected a slight improvement in the prediction precision (Rmse=3.78). The standard errors for the parameter estimates in the three models are presented in Table 4. Including the variable sex as a covariate slightly improved the performance of the models

(models 1sex, 2sex, and 3sex; Table 3). Our assumptions on the homogeneity of variance, independence, linearity, and normality of error were examined for each model. The normality of residuals was confirmed for each model (Kolmogorov-Smirnov test, p=0.843 for model 3, p=0.426 for model 1, and p=0.331 for model 2).

Discussion

We presented a set of best equations for the prediction of *Rattus tiomanicus*’ ELW, based on various skull, jaw, and femur measurements. We demonstrate here that, because rodent heads are frequently absent from barn owl pellets in Malaysian and Indonesian OPPs, the predictive model based only on the femur was the most useful, although slightly less precise than the models based on skull and jaw variables. We also argue that we can confidently attribute most, if not all, femurs in the pellets studied herein to *R. tiomanicus*.

Table 4 Parameter estimates and associated standard error (SE) for the *Rattus tiomanicus* eye lens weight prediction models.

Variable	Estimate	SE
Model 1		
Constant	-28.0396	2.4500
L2	1.5060	0.5760
LD	0.8413	0.5351
BP	2.7511	0.9358
Short femur	1.4777	0.2697
Model 2		
Constant	-20.705	1.9790
Short femur	2.806	0.0966
Model 3		
Constant	-17.1739	6.6529
L2	0.8263	0.5763
L5	-2.4834	1.1539
LD	0.7125	0.5094
BP	2.6186	0.8939
Upper incisor	4.4933	2.3100
Lower incisor	5.5058	2.3749
Short femur	1.2114	0.2710

L1, mandible length; L2, mandible height; L3, diastema length; L5, molar row length; LD, length of diastema; and BP, breadth of palate.

Species identification

As has been reported since the 1970s, *Rattus tiomanicus* is still the dominant species in mature OPPs in Southeast Asia; however, it has progressively been replaced by *Rattus tanezumi* (previously *Rattus rattus diardii*) in several localities, notably the Malaysian peninsula (Wood and Fee 2003). The *R. tiomanicus* predominance in our study area was confirmed through our trapping experiments. The specimens successfully sequenced herein (n=110)

were confirmed as *R. tiomanicus*. Additional investigations at the same estate confirmed that *R. tiomanicus* was predominant; the 19 specimens identified using the same molecular barcoding method were *R. tiomanicus* (Andru et al. 2013). Therefore, although we cannot completely exclude sibling species (Wilson and Reeder 2005, Pagès et al. 2010), we can assume that virtually all of the 161 specimens were *R. tiomanicus*.

Predictive modelling, a compromise between parsimony, accuracy, and practicability

Except for the upper and lower molar row length (CLM1–3 and L5), the monivariate correlations ($r \geq 0.80$) between the jaw or skull variables and ELW were strong; length of rostrum (LR) and L2 yielded the best correlations (both $r = 0.89$). We could not find similar investigations on *Rattus* species in the international literature, which precludes a comparison. Our results differ from the *Microtus* results. Shi et al. (2006) found that the length of the *Microtus ilaeus* Thomas upper molar row correlated best with age, and Quéré et al. (1994) found that the *Microtus arvalis* Pallas great skull length, LR, and molar row length (CLM1–3) correlated best with age. Moreover, the breadth of palate yielded one of the lowest correlations for *M. arvalis*, whereas in our results, it correlated well with ELW and was included in the final equation. We found a high measurement error for certain variables, such as CLM1–3 (26.9%), which may be due to the difficulty in finding precise landmarks on bones; therefore, these measurements were discarded from “practical” modelling.

We did not detect a significant difference in ELW between males and females. These data are consistent with Williams (1976) and Shrestha et al. (2002), who did not detect a difference in ELW based on sex for other *Rattus* species, such as *Rattus exulans* Peale and *Rattus brunneus* Hodgs, respectively. The latter species is currently regarded as a *Rattus tanezumi* synonym (Wilson and Reeder 2005). Certain authors have reported that males have slightly heavier lenses than females, such as for *Rattus norvegicus* Berkenhout (Hardy et al. 1983) and other rodents (Rowe et al. 1985, Yabe and Arakawa 2009). Our results indicate that the models perform only slightly better when the variable sex is used as a covariate. Therefore, using models 1–3 to predict age may produce a minor sex-related bias. However, Hardy et al. (1983) noted that considering the sex variable in modelling may not be justified because the improvement therefrom is slight.

Many studies aimed at estimating the age, size, or body mass of prey from pellets prefer only lower jaw variables

because this organ is highly frequent and well preserved in macroremains (Morris 1979, Trejo and Guthmann 2003, Granjon and Traoré 2007, Bueno and Motta-Junior 2008). However, we found that approximately 70% of pellets were headless. This result is consistent with other reports (Medway and Yong 1970 in Lenton 1984, Lim et al. 1993, Hafidzi and Naim 2003, Puan et al. 2011). Considering the frequent absence of heads in barn owl pellets on OPPs, we focused on elements other than the skull, jaw, and teeth for modelling. In addition, the tendency of the barn owl to decapitate larger prey may yield a bias if the skull or jaw is used to estimate the age or size distribution and further assess the impact of barn owl predation (Lim et al. 1993). The femur was a good candidate for ELW prediction because it was well represented in our pellet sample, and the variable short femur highly correlated with the ELW. Moreover, the femur measurement error was the lowest compared with the other variables used in the final equations. Thus, the final equation with only the short femur would be more accurate, even if the prediction precision was not greatly improved by considering all the variables.

Model limits and extrapolation

Age prediction is more accurate in younger animals (Tanikawa 1993, Shrestha et al. 2002). Williams (1976) found that the ELW was only a useful indicator of *Rattus exulans* age for up to 3 or 4 months. Myers et al. (1977, in Hardy et al. 1983) studied indigenous rats in Australia and found a similar lack of precision at this threshold, which clearly limits age determination using the ELW.

Our measurements are consistent with the maximum weight of adult rats reported in the literature (Corbett and Hill 1992, Aplin et al. 2003). However, according to Wood (1984), young rats up to approximately 10 g cannot be trapped by the cage traps used in our study. As the body weight of our specimens ranged from 14 to 139 g, we may not have included certain juvenile individuals in our models.

Because the rats' food supply does not vary greatly month to month owing to a relatively constant temperature and continuous oil palm fruiting throughout the year (Lenton 1984), an effect from rat nutritional status or season on ELW and, thus, age estimations is unlikely.

The equations proposed here are theoretically only applicable for comparing the population structure in the same area during the same period (Quéré et al. 1994). However, even if the rats were trapped in May, extrapolating to another season or year should not be a problem in the tropics and specifically in OPPs without

chemical control. Indeed, the rat population dynamics do not change markedly with the seasons (due to continuous oil palm tree fruiting; Lenton 1984), the population demography fluctuates slowly, and the weight spectrum is approximately constant (Wood 1984, Wood and Liao 1984b). In contrast, the location is important because population-based genetic variations cannot be excluded.

Owing to the lack of skulls or presence of broken skulls, it is difficult to identify prey species in pellets, which may be an issue for attributing the femur to the correct species. However, the barn owl diet generally reflects the abundance of prey species in the hunting territories (Bunn et al. 1982, Figueroa et al. 2009), as demonstrated for OPPs by Lenton (1984) and Puan et al. (2011). Therefore, because *Rattus tiomanicus* is the predominant species in our study area, we confidently assume that this species is the major, if not the only, prey in the barn owl pellets studied. In areas where several rat species are sympatric and abundant, new-generation molecular methods can be used to ensure that femurs from the pellets are from *R. tiomanicus* (Galan et al. 2012).

Conclusion

Our study demonstrates that the femur length is relevant to ELW predictions for prey from macroremains, specifically in OPPs, wherein most pellets are headless. Our models represent a preliminary step to establish a relative age structure for *Rattus tiomanicus* consumed by the barn owl and to compare it to the population structure in the field, with a view to further assessing the impact of barn owl predation and improving ecologically based pest control.

Acknowledgments: We thank the technicians from SMARTRI who helped with the fieldwork as well as PTSmart Tbk for their accommodation and for providing access to the facilities and plantation. We are grateful to the State Ministry of Research and Technology of Indonesia, which supported this research (0131/SIP:FRP/SM/V/2011).

Received July 18, 2013; accepted January 30, 2014; previously published online March 5, 2014

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