

**Synergy between wild and commercial
- Bio-economic modelling of Python farming -**

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Abstract

Bio-economic models have been proven to be a useful tool in dealing with situations where proper management is crucial to set up stable industries. The python farming industry has yet to emerge, despite the high demand for reptile products. This demand has increased, with the pursuit of alternative protein sources to cope with an increasing human population and higher meat consumption habits. Reptile farming or ranching provides a way of making a sustainable use of these animals, with either minimal or positive impact on wild populations. This industry holds great potential as, when provided with the ideal environmental conditions, reptiles can potentially outcompete traditional agricultural species in terms of growth and fecundity. Pythons in particular are able to cope with less than ideal conditions, and show an exceptional use of space. Nevertheless, limited studies have been made on the remarkable features of these animals, both in their biology and economic potential. In this study a group of Indian rock pythons (*Python molurus molurus*) were used to develop a python growth model and a bio-economic model. The bio-economic model integrates the python growth model within a population model, to which an economic analysis is applied. The study aims to determine whether python farming is profitable, and if so, in which conditions. The main findings show that python farming is profitable for an initial investment of setting up a farm. The python growth model predicts growth for a set of initial conditions and also shows the amount of feed intake which maximizes profitability for a given group of pythons. The bio-economic model calculates the profitability of the farming operations, for a given number of individuals being farmed. Hence these models provide a framework for producers to make management decisions which maximize profitability of the farming operations, taking into account the fluctuations typically associated with the demand for reptile products. The model requires further validation by being applied to an operating farm. With the proper adjustments it is possible to apply the model to other reptile species such as crocodiles, providing a new approach in managing these populations.

Contents

Abstract.....	3
Introduction.....	6
Methods.....	9
Results.....	24
Discussion.....	39
Conclusion.....	44
References.....	44
Appendix.....	55

Tables and Figures List

Figures

Figure 1: Population dynamics within a farm setup.....	17
Figure 2: Model fit for time series analysis for skin.....	26
Figure 3: Model fit for time series analysis for weight.....	26
Figure 4: Profitability for different feed intake values.....	27
Figure 5: Profitability for different percentages of individuals sold.....	28
Figure 6: Population dynamics for different percentages of individuals sold.....	30
Figure 7: Population dynamics for 100% of individuals sold.....	32
Figure 8: Impact of starting population in profitability values.....	34
Figure 9: Breakeven point analysis.....	36
Figure 10: Profitability values for different skin price scenarios.....	37
Figure 11: Profitability values for different meat price scenarios.....	38

Tables

Table 1: Values of non-estimated parameters.....	22
Table 2: Values for estimated parameters for the growth kernel model for skin.....	24
Table 3: Values for estimated parameters for the growth kernel model for weight.....	25
Table 4: Slope values for changes in profitability for different starting populations.....	35
Table 5: Slope values for changes in profitability for different price scenarios.....	38

Introduction

Sustainable use of wildlife has been shown to be a profitable business in many parts of the world, which has allowed for the development of important industries with conservation advantages. Examples include kangaroo harvesting, crocodile ranching, emu farming and vicuna farming¹. Problem animals such as crocodiles benefit much from this approach, as do the local communities who live alongside them⁹⁷. For instance, crocodile ranching in Zimbabwe has been shown to have a positive contribution towards local economies whilst enabling the restocking of depleted wild populations of crocodiles, as reported by the humanitarian news and analysis service, IRIN.

Python meat and skins have yet to emerge as a mainstream global industry, although these animals are traded in large numbers. According to CITES Asian Snake Trade Workshop 2011 (Guangzhou, CHINA)⁵⁰ there are approximately 2 million snake skins being traded annually, with a value of approximately 50 million dollars. Nevertheless the reptile skin market is subject to exorbitant fluctuations in demand, which depend mostly on the economic situation of the consumer nations and fashion trends⁸⁸. These boom and bust cycles have a tremendous impact on wild populations⁹⁵. This does not need to be the case if the market supply is managed in a regulated way through farming or ranching¹. In a farm setup all the animals are bred in captivity, whereas in a ranch setup there is some dependence on the wild population¹⁰. Reptiles have energy saving lifestyles based on the utilization of external heat sources to maintain optimal physiology and the avoidance of behaviours that are not directly related to growth and reproduction². Their low energy consumption does not necessarily affect their biomass production, which may equal that of birds and mammals⁷³. Because they are cold blooded animals, reptile physiology is directly linked to environmental conditions. Maintaining optimal environmental conditions is thus crucial to any form of commercial reptile rearing. With the relatively recent development of cost efficient and effective climate control techniques in production sectors such as poultry, aquaculture and horticulture it is now possible to provide these animals with such optimal conditions at an affordable cost. Furthermore, pythons and other snake species are able to buffer

surrounding temperature variation, to a certain extent, by aggregating^{63,66}, which makes these animals ideal to rear in a high density but humane and sustainable manner. For the reasons stated above python farming and ranching shows great potential to be established not only in marketing skins, but also for meat trade.

It is estimated that growth in human population will occur mostly in developing countries, with associated changes in feeding habits to higher energy diets such as meat^{12,31}. The current sources of protein for human consumption are not all sustainably produced, given the daily energy requirements of endothermic animals, which can be 25 to a 100 times higher than the requirements of a similar sized reptile³⁸. The efficient protein producing qualities of reptiles provide a low cost and environmentally friendly alternative for a growing human population with higher meat demands^{12,31,49}.

Traditionally reptile meat has been an important food resource for many human communities in the tropics⁵². However, population growth in developing countries and associated change in dietary habits has increased the demand for reptile meat, which has resulted in the development of mostly informal and ad hoc rearing facilities in more than 30 countries in North, Central and South America, Africa, Asia and Australia⁵¹. Nevertheless, reptile farming, such as crocodile farming, has seen many drawbacks⁸⁸, mainly due to mismanagement and empirical use of the animals. The recent improvements in captive reptile husbandry coupled with proper management can make this industry competitive alongside other agricultural industries.

Bio-economic models provide good tools to assess the viability of setting up these industries and have a vast range of applications. These go from wildlife and natural resource management^{13,58,59} to livestock management⁴⁴ and fisheries^{60,80}. Sophisticated models have been developed to assist farmers and livestock producers in decision making, such as CVDS^{30,87}, BEFMs⁴⁴, DGM⁶⁷. Several approaches are available to build these models, and these are still improving, alongside with developments in computer software. Nevertheless, all of them link biological processes with an economic framework. The way these processes are integrated falls within a gradient, where at one end there are biological models which include an economic analysis

component (SAVANNA¹⁴, HILLPLAN⁵⁵, CDFU⁹⁰, CENTURY⁴⁸, WaNuLCAS⁹¹, IBIEHM^{41,42,43}), while at the other end of the continuum there are economic optimization models in which the description of biological processes remains at a more basic level (SOLUS^{7,78}). Both of these extremes can be coupled in integrated bio-economic models, which stand at the centre of the above mentioned continuum (Carchi integrated simulation model¹⁶, FLORES³², GRAZPLAN^{19,61}).⁸

The way in which biological processes are incorporated can be either empirical or mechanistic, depending on if the model extrapolates from patterns observed in time series data or is built on existing theory and knowledge^{8,44}. Bio economic models may include temporal and/or spatial scales⁸, depending on the extent to which they are relevant to the study subject. The way time is incorporated can translate into dynamic or static models, if time is included explicitly or not, respectively. Furthermore, dynamic models can be either inter-temporal, optimizing a function over a certain period of time, or recursive, in which case the model runs for several periods using the end values of one period as starting values of the following period⁴⁴. Bio-economic models can behave in a deterministic or stochastic way, with a normative or positive approach, which reflects either an attempt to model the actual farm situation or an optimization procedure for a given farm setup, respectively. Stochastic models allow the incorporation of risk, which can be classified either as non-embedded risk (variation from biological processes or price fluctuations), for which the farmer has no control of or embed risk, which the farmer can reduce beforehand⁴⁴.

However, regardless of the approach used to build these models, the main reasoning behind bio-economic modelling is to link a biological production function with an economic analysis.

Few studies have been made both in the growth/production function^{28,75} and economics of snake species, despite their remarkable potential. It is of the uttermost importance to do so before the populations are depleted to a point where they cannot be further utilised. In this study, a set of Indian Rock Pythons (*Python molurus molurus*), reared at the Madras Crocodile Bank, were used to develop a mathematical model of growth for the average individual. This python growth model was integrated into a population model based on a farm set up, and an exploratory economic analysis of

python farming was applied. The main goals are to understand to what extent python farming is profitable and if so, under which conditions.

Methods

1. Data

Data were collected from 11 Indian rock pythons (*Python molurus molurus*) reared at the Madras Crocodile Bank Trust-MCBT (Chennai, India), between the 26th of September, 2009 (hatch date) and the 23rd of May 2011, according to the MCBT standard husbandry procedures. The feeding regime applied to the pythons consisted of suitably sized rodents (estimated 65% protein dry weight), provided once a week, which is considered the standard feeding procedure. Feeding intervals were constant.

Each python's weight and length was measured at six different times: hatch date, 5 months, 10 months, 14 months, 18 months and 21 months. Weight was measured in grams with a portable scale, whereas measurements on length were measured in cm with a standard measuring tape. Length was recorded for each python as total body length (*TBL*), snout-vent length (*SVL*) and tail length (*TL*) at the ages listed above. To calculate the total skin of the python, values for the python's surface area were determined. The pythons were assumed to have a cylinder shape between the base of the tail and the neck; hence a standard surface area (*SA*) formula for cylinders was applied.

$$SA = 2 * \pi * lng * r$$

The length (*lng*) of the python was considered to be between the rear of the skull and the vent, which corresponds approximately to the section of the python processed for commercial purposes. Therefore, both head length (*HL*) and tail length (*TL*) were subtracted from total body length (*TBL*) in each python. Such a procedure also approximates the python's shape to a cylinder shape.

$$lng = TBL - HL - TL$$

Growth in snakes follows proportion laws²², therefore both head and tail grow proportionally to total body length. In this manner it was possible to calculate a set of

ratios that allow the calculation of both head length and tail length for a particular *SVL*. *SVL* was used in detriment to *TBL*, since females and males show sexual dimorphism in tail length (*TL*). To obtain the head ratio, pythons of different sizes were used including the eleven in this study plus a number that were not included. The ratio is a function of body size rather than age to account for different feeding regimes within one age class, which may translate into different sizes among pythons of the same age.

$$HL = \text{head ratio} * SVL$$

Regarding the radius (*r*) component of the surface area formula, it is assumed that the growth in diameter will also follow a proportional law, which is a function of the python's *SVL*, for pythons with the standard feeding regime. Therefore, in this situation ratios can also be used to calculate the radius of a python for a given *SVL*.

$$r = (\text{diameter ratio} * SVL) / 2$$

The same set of pythons used to calculate the head ratio, were also used to calculate the diameter ratio. The measure of diameter used was taken at $0.4 * TBL$ in each python, since it corresponded approximately to the middle of the python's body and therefore was the most representative measure to use in calculating the surface area, taking into account that length (*lng*) does not take into account head and tail length.

The pythons were measured without any food in their stomach, in order not to influence measurements.

The measures of weight were straightforward, hence did not need any adjustments besides taking into account the weight of the bag in which the pythons were placed to be measured.

2. Models

The main aim of the modelling exercise is to predict the optimum conditions for python farming. The optimum conditions are the ones that provide the most profit for a given cost. Profit is measured in terms of the python's surface area and the python's weight, for skin and meat sales, respectively. Costs have three main components. The first is costs related to setting up the python farm. The values used are based on the

costs of setting up a crocodile farm with a maximal production of 1800 cull animals per year. The second component is costs related to operating the farm, which include costs of feeding the animals, staff salary and processing costs of meat and skin. These costs depend on the number of pythons being reared. Finally, there are fixed costs, which do not depend on the amount of skin and meat yield; these costs only depend on the farm size, hence on the maximal number of individuals which can be produced, and are related to water and electricity bills, and transport. In the model presented, water was assumed to be the only fixed cost, since this is the most relevant cost at MCBT. Electricity bills can be very high if the environmental temperature is not optimum, in which case enclosures require heating for optimal growth. This is not the case at MCBT, since its location together with enclosure aspect and design are able to provide an average daily range which always includes the optimal preference for pythons. For this reason electricity costs are not accounted for, since their value is not significant.

To calculate profitability and assist producers in decision making to maximize this quantity, two models were developed. The first model is a python growth model which predicts the surface area and weight for the average python per month, given a certain feed input and an initial surface area and weight. The model also allows determining which feed intake values for each age class translate into the most profitable scenario. Age is considered in months and each time step corresponds to a different age. Besides being a dynamic and discrete time model, the way in which time is incorporated makes it also recursive. The model is also classified as an empirical model since it is developed from time series data and it models at the individual level.

The python growth model is integrated into a bio-economic model. This second model takes into account the population dynamics within a farm setup. Therefore, the population was assumed to have the dynamics of a self-sustained closed cycle system, where there is a breeding population that restocks the total population. The bio-economic model couples the farm population dynamics and an economic framework which restrains these dynamics in the form of decision making to reach maximum profitability. The model runs on a yearly time step to account for the fact that pythons reproduce once a year⁷⁶, and therefore it is also a discrete time model. Furthermore, it is also a dynamical and recursive model.

Both models have at their base the theory of Net Present Value (NPV), through which a discount rate is applied. A discount rate is a value used to portray accurately the future value of money in the profits obtained within the desired time span. The value used is based on discount rates for reptile farming found in the literature³⁴.

All models and analysis were conducted using the statistical software R, version 2.11.1 (R Development Core Team (2011))⁷⁴.

2.1 Python growth model

The python growth model predicts the surface area (cm²) and weight (g) for the average python per month, for a time span of 36 months, which is the estimated time required for a python to be ready to be sold and also to be sexually mature.

The model is based on a growth kernel, which is defined as the amount of surface area and the amount of weight gained between two time steps as a function of both the amount of food intake at each time step and age. The growth kernel is incorporated into a time series analysis, to account for surface area and weight in the previous age class. The amount of weight and surface area gained are predicted by the growth kernel and summed to the weight and surface area of the previous time step, in order to determine these quantities in the current time step.

2.1.1 Growth kernel

To build the growth kernel the measurements taken for each python over 21 months were used. Given that these quantities were recorded for the same set of 11 pythons at each time step, the data shows temporal pseudoreplication. Therefore, there will be amplification of the residual error, if python identity (ID) is not accounted for as explaining a portion of the variation. Mixed effects models were used to correct for the above mentioned correlation between measurements in each individual, using ID as a random effect. Linear mixed effects models (lme), from the nlme package⁷¹ in R, were used since the model fitted was linear in its parameters and by having only one random effect (ID), there were no crossed random effects, so there was no requirement to use lmer.

The growth kernel predicts the amount of weight gained and the amount of skin gained for the average python between each age class. Two growth kernels were developed, one for gain in weight and another for gain in skin.

Both age and feed intakes seem to be important factors in determining growth in either case. Therefore, both were fitted as explanatory variables in the two models.

Feed intake in itself is also dependent on age. So the first step was to develop a function which allows the prediction of feed intake for each age class.

$$F = -1149.7761 + 444.8428 A_i - 16.6520 (A_i^2) + e$$

$$e \sim N(\text{mean}=0, \text{sd} = 138.3119)$$

The above function was developed using linear mixed effects models, accounting for ID as a random effect and it allows extrapolating feed intake for time steps over 21 months, by assuming it will be approximately the same as the feed intake at 21 months, as explained on page 14.

F represents feed intake in grams, A represents age in months, e represents a random number taken from a normal distribution, with a mean of zero and a standard deviation of 138.3119, which is the value of the standard deviation of the random effect ID. i represents the time step of the model.

The feed intakes predicted by the above described model were used as input in the growth kernel model.

The growth kernel model was developed by fitting the collected data on feed intake, age and gain in weight and skin, with lme. Through model simplification the following minimal adequate model was obtained for each situation:

Growth kernel for weight

$$Gw_i = -386.9516 + 14.3981 A_i + 0.8085 F_i - 0.0001 (F_i^2)$$

Growth kernel for skin

$$Gs_i = -991.1706 - 48.6509 A_i + 4.2412 F_i - 0.0011 (F_i^2)$$

G_w and G_s , stand for gain in weight in grams and gain in surface area of skin in cm^2 , respectively.

Goodness of model fit was examined using AIC and graphical analysis.

The data collected covers a time span of 21 months. During this time growth is fairly linear both in terms of weight and skin. At 36 months pythons are at the optimum size for commercial use and are also reaching sexual maturity. Given that pythons will only be sold or breed at this stage, the python growth model needs to be extrapolated to predict weight and surface area for the 36 month age class. In order to extrapolate for 36 months, the average amount a food a python will consume by that stage and the growth rates for this period of the python's life need to be established. In order to do so, some assumptions had to be made. It is observed that between 10 and approximately 14 months, feed intake starts to decline (Figure 1 in Appendix). The model for feed weight previously developed predicts feed intake between 5 and 21 months with high accuracy. However, when this model is used to extrapolate beyond 21 months of age, it predicts negative feed intake values, since it assumed that feed intake continues to decline. The aforementioned does not make biological sense; neither does it make sense to have a feed intake of zero in the long run. Therefore we assumed that feed intake for ages greater than 21 months, will be similar to feed intake at 21 months. This type of assumption has been made in other studies³.

Concerning growth rates for these age classes, they were also assumed to be roughly the same as the growth rate the model predicts for the 21 months age class. This means that the predictions of weight gained and surface area of skin gained between each time step after 21 months will be similar. The assumption seems reasonable, given that feed intake is assumed to remain constant after 21 months, which means that growth rates both in terms of length and weight should plateau as well. This is in accordance with previous studies made on snake's growth patterns⁵³.

2.1.2 Time series analysis

The growth kernel is used to estimate the python weight and surface area at a particular time step. A time series analysis was used to predict these quantities as a function of the values in the previous age class.

$$Pw_{t+1} = Gw_t + Pw_t$$

$$Ps_{t+1} = Gs_t + Ps_t$$

Pw stands for python weight in grams, and Ps stands for python surface area of skin, in cm^2 .

The above models predict python weight and skin surface area for a time span of 36 months on a per month time step, given an initial weight and an initial surface area, which in this case were the ones measured at hatch date.

2.1.3 Food optimum values analysis

Food intake values represent a trade off within an economic framework. There is a balance between how much a python can grow for certain feed values, and how much the feed costs.

The above mentioned equation allows the calculation of the average feed intake per month, for a particular time span:

$$F = -1149.7761 + 444.8428 A_i - 16.6520 (A_i^2) + e$$

$$e \sim N(\text{mean}=0, \text{sd} = 138.3119)$$

However the feed intake calculated might not be the optimal feed intake, since this formula is based on the values from the collected data. Therefore, the feeding regime was changed by certain percentages to see the impact it had on the growth predictions for skin and weight, given by the python growth model. Nine different feeding regimes were tested, and used as an input in the python growth model. The difference between each feeding regime was a 10% increase in the food input for all age classes, starting with the feed input calculated from the above formula. The same percentage was

applied to all age classes, for each feeding regime, in order to maintain the proportions that distinguish feed intake at each age class.

The main aim of this analysis is to understand how profitability changes with different feeding regimes. Therefore, a cost was assigned for feed, and profit was assigned to the respective final weight and surface area obtained from the python growth model, at each feeding regime.

The feed input correspondent to the maximum profit was determined through graphical analysis. A simulation was carried out to depict if these profit values converge to a constant maximal value, which will correspond to a particular feeding regime, which will be assumed to be the optimal feed input values for each age class.

The optimum values of feed input at each age class, and the correspondent yield in weight and surface area of skin at 36 months were used as input in the population model.

2.2 Bio-economic model

The bio-economic model integrates the biology of one average individual into a population framework. The population dynamics are dictated by economic decisions regarding profitability maximization. The main aim is to determine python farming profitability and in which conditions it is maximized.

2.2.1 Population dynamics

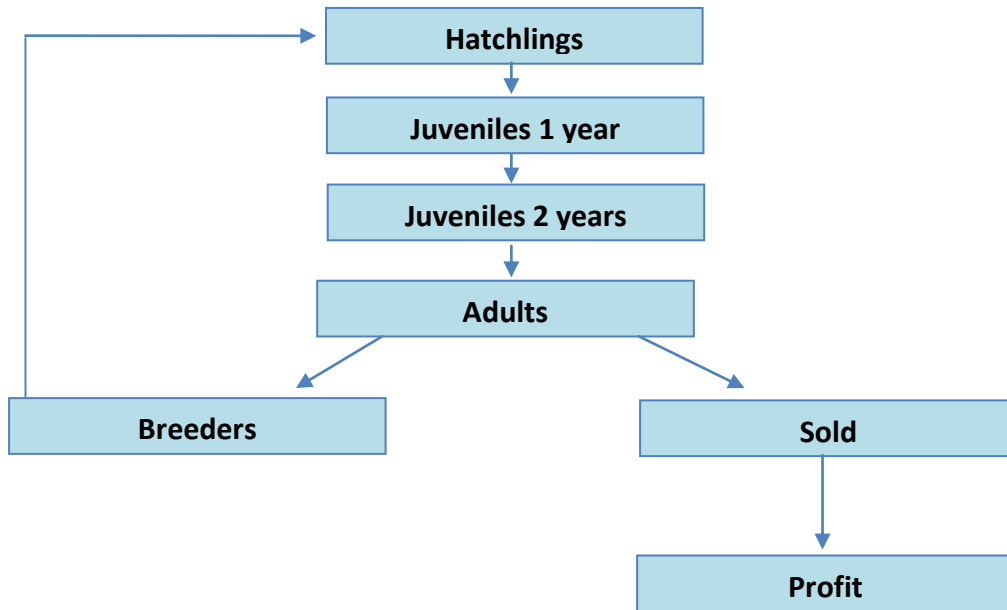


Figure 1. *Population dynamics within a farm setup.*

The farm setup is a closed cycle system, which means that the population has to be self sustainable. For this reason, a breeder population is required to restock the total population numbers between each time step. Taking the above mentioned into account, it was assumed that four population stages occur within the farm: a hatchling population, a one year old juvenile population, a two year old juvenile population and an adult population. These four populations were designated given that the model operates on a yearly time step and hatchlings take 3 years to grow into adults. The adult population is further subdivided into breeders and non breeders. Eggs are considered to be equivalent to hatchlings, since the model runs on a yearly time step, and python eggs hatch within approximately one month of being laid⁷⁶. Additionally, the costs of buying the eggs are considered negligible, compared to the costs of buying hatchlings, juveniles and adults.

The bio-economic model operates under two basic conditions:

- 1) There is a minimum number of adults which has to be allocated for breeding purposes, in order for the population not to decrease between each time step and ultimately go to zero.
- 2) There is a minimum number of adults which has to be sold in order for the costs of operating the farm to be paid for at each time step.

Profit can only be attained when both of these conditions are met and there are still available adults to be sold. The model takes as an input the number of individuals in the starting population, which can be either hatchlings, juveniles or/and adults.

Given the situation previously described, the population dynamics has to be modelled in two different ways, depending if the costs of setting up a farm have to be taken into account or not. This might be the case if the farm is being set up or if it is already operating, respectively. In this study it was assumed that the farm is being set up, in which case, the first time step of the model has to take into account costs of setting up the python farm and costs of buying the starting population. Unless there are enough adults in the starting population to be sold in order to cover these costs, there will be a negative balance in the first year. This value represents how much has to be invested on a farm for it to start operating. These costs are not taken into account in the following time steps; however it is possible to calculate the number of years it will take to have the farm's initial investment paid for (breakeven point) (section 3.3 of Results). All profit values and costs are given in US dollars.

Time step 1

The number of available adults to be sold, once conditions 1 and 2 are met, can be represented in the following way:

$$Re_{t=1} = T_{t=1} - ((oc + Hc * H_{t=1} + Jc * (J_{t=1} + Jj_{t=1}) + Ac * T_{t=1}) / Va) - rb * T_{t=1} * (1 + pm)$$

$H_{t=1}$, $J_{t=1}$, $Jj_{t=1}$ and $T_{t=1}$ correspond to the number of hatchlings, 1 year old juveniles, two year old juveniles and adults in the starting population, respectively.

Re stands for remaining adults, which are calculated by subtracting the total number of adults (T) by the costs of operating the farm per year (oc) and the costs of buying the starting population (Hc represents the costs of buying each hatchling, Jc are the costs of buying each juvenile and Ac the costs of buying each adult), all divided by the value of one python (Va). This first subtraction represents the number of pythons required for condition 2 to be met. Additionally, the number of individuals required to be allocated for breeding purposes is also subtracted, in order to meet condition 1. This value is calculated using a percentage (rb) that defines the number of females required to breed to maintain the current population (T) in the next time step. Furthermore, a percentage of males (pm) required to fertilize these females is also included.

The costs of operating the farm (oc) are represented as follows:

$$oc_i = w + lbr_i + prc_i$$

$$lbr_i = slr * ((H_i + J_{t-1} + J_j + T_i) / 225)$$

$$prc_i = lbr_i + w + 2 * ((lbr_i + w) / 4)$$

Labour costs (lbr) depend on total population number, with each member of staff allocated for a set of 225 pythons, whereas water (w) is a fixed cost for the farm size assumed. Processing costs of meat and skin (prc) are considered to be $\frac{1}{4}$ of the labour and water costs for the current time step. slr represents salary for one member of staff.

Value of one python corresponds to the amount of profit obtained from selling one python:

$$Va = Pw_{t=36} * mpr + Ps_{t=36} * spr$$

Both meat yield (Pw) and skin yield (Ps) are the output values from the python growth model. They represent the python's final length and weight at the 36 month stage for the optimal feed intake calculated previously. spr and mpr are the skin and meat prices, respectively, currently in the market.

The amount of profit (Pr) obtained in the first time step may be calculated as follows:

$$Pr_{t=1} = (p * Re_{t=1} * Va - frm_c) / ((1+dr)^d)$$

p represents percentage of the remaining pythons a producer wishes to sell and $frmc$ represents the costs of setting up the python farm. The costs of setting up the farm will be proportional to the number of pythons a producer wishes to produce. In this case, it was assumed that the costs would be the same as the costs of setting up a crocodile farm with a maximum production of 1800 cull animals per year. dr represents the discount rate. In order for discount rate to represent accurately the value of money, a variable s is included to specify in which moment in time the farm starts operating. For example, if the study is being made for a farm to be set up in 3 years, for example, s will be equal to 3. In this study it was assumed that the farm becomes operational in the current year.

Adult breeders (Ab) correspond to the remaining number of pythons which were not sold in the current time step, plus the individuals that had been allocated for breeding to meet condition 1. It is assumed that the individuals allocated for breeding cannot be sold, since they lose condition⁷⁶. The percentage of individuals designated for breeding depends on if the producer wishes to increase, maintain or decrease the total population number (explained further in pages 30 and 31).

$$rb = 1/(eggs*frt*htch)$$

$$Ab_{t=1} = (1-p)*Re_{t=1} + rb*T_{t=1}*(1+pm)$$

$$Fm_{t=1} = ((1-p)*Re_{t=1}) / (1+pm) + rb*T_{t=1}$$

$$Ml_{t=1} = pm*((1-p)*Re_{t=1}) + rb*T_{t=1}$$

The formulas above ensure that the number of female breeders is maximized, in order to obtain as many offspring as possible, for a reasonable number of males.

Following time steps

$$J_{t+1} = survh*H_t$$

$$Jj_{t+1} = survj2*J_t$$

$$T_{t+1} = survjj*Jj_t + surva*(Fm_t + Ml_t)$$

$$Re_{t+1} = T_{t+1} - surva*(Fm_t + Ml_t) - (((hf*H_t + jj*J_t + jjj*Jj_t + af*T_t)*fc + oc_t) / Va) - (1-surva)*Fm_t - (1-surva)*Ml_t$$

$$Pr_{t+1} = (p * Re_{t+1} * Va) / ((1+dr)^{s+t+1})$$

$$Ml_{t+1} = surva4 * Ml_t + (1-surva4) * Ml_t + pm * (1-p) * Re_{t+1}$$

$$Fm_{t+1} = surva * Fm_t + (1-surva4) * Fm_t + (1-p) * Re_{t+1} - pm * (1-p) * Re_{t+1}$$

$$Ab_{t+1} = Fm_{t+1} + Ml_{t+1}$$

$$H_{t+1} = Fm_{t+1} * eggs * frt * htch$$

survh, *survj*, *survjj* and *surva* are the survival rates of hatchlings (*H*), 1 year old juveniles (*J*), 2 year old juveniles (*Jj*) and adults which remain in the population for the next time step, which are both the female and male breeders (*Fm* and *Ml*), respectively.

Condition 2, in a time step different than one, also incorporates annual costs of feeding the animals produced in captivity. This is taken into account by a set of values which represent the optimal feed intake at a certain stage, for one individual. These values are *hf* for hatchlings feed intake, *jf* for one year old juveniles feed intake, *jff* for two year old juveniles feed intake and *af* for adults feed intake. These values are calculated from the feed intake formula (section 2.1.3) and multiplied for the number of individuals at each stage in the current time step and the cost of feed per gram (*fc*).

Model analysis allows calculating the optimum percentage of individuals to sell (*p*) at each time step for profits to be maximized. It also determines the number of years required to reach a breakeven point in terms of the initial investment used to setup a farm. Additionally, the model shows the population with the highest impact in profitability, which allows the producer to know in which population to invest.

Additionally, profitability was determined under different price scenarios for skin and meat, given the variability that these quantities show for longer time spans.

The non-estimated parameters used in the model were assumed to have the values shown in Table 1.

Non-estimated parameters

Parameter	Value	Reference
Food cost (<i>fc</i>)	0.002 US \$ per gram	65 % protein fish meal trade price, July 2011 value*
Water cost (<i>w</i>)	0.135 US \$ per year	Madras crocodile bank values
Staff cost (<i>slr</i>)	1048.5 US \$ per year per employee	Madras crocodile bank values
Processing equipment (<i>prc</i>)	$0.25*(w + lbr)$	Patrick Aust, personal communication
Cost of buying hatchlings (<i>Hc</i>)	20 US \$ per unit	http://www.eublahexotics.com/reptiles.html
Cost of buying juveniles (<i>Jc</i>)	60 US \$ per unit	http://www.eublahexotics.com/reptiles.html
Cost of buying adults (<i>Ac</i>)	400 US \$ per unit	Patrick Aust, personal communication
Skin price (<i>spr</i>)	0.006 US \$ per cm ²	Wholesale, air dried from Dago International
Meat Price (<i>mpr</i>)	0.03 US \$ per gram	Wholesale, air dried from Dago International
Discount rate (<i>dr</i>)	0.1	Heykoop, J. & Frechette, D. (2001)
Farm cost (<i>frmc</i>)	200,000 US \$	Spencer Creek Crocodile Farm, Victoria Falls, Zimbabwe
Percentage of females fertilized by one male	1 male to 3 females (1:3)	Patrick Aust, personal communication

(*pm*)

Survival rate of hatchlings (*survh*) 0.85 Patrick Aust, personal communication

Survival rate of one year old juveniles (*survj*) 0.90 Patrick Aust, personal communication

Survival rate of two year old juveniles (*survjj*) 0.95 Patrick Aust, personal communication

Survival rate of adults (*surva*) 0.99 Patrick Aust, personal communication

Number of eggs per female (*eggs*) 36 Reed, R. N. & Rodda, G. H. (2009)

Fertility rate of eggs (*frt*) 0.9 Patrick Aust, personal communication

Hatching rate of eggs (*htch*) 0.9 Patrick Aust, personal communication

*This quantity is equivalent in nutritional content of the rodents fed to the pythons used in this study; hence it is a good measure of feed costs.

Table 1. *Value of non-estimated parameters and source*

Results

1. Python growth model

1.1 Growth kernel: Model Diagnosis and parameter estimates

To assess the validity of the linear mixed effects model for the data collected, the model's assumptions were tested. Linear mixed effects models make the following assumptions⁷⁰:

- 1) The within group residuals are independent and their distribution is normal. Furthermore, the within group residuals are independent of the random effects.
- 2) The random effects are normally distributed.

The validity of these assumptions and goodness of fit was analyzed via graphical analysis (Figures 2, 3,4,5,6 and 7 in Appendix). The assumptions made were shown to be valid. R^2 values are also provided (Table 1 in Appendix) for the fit of the growth kernel models. These are in accordance with the graphical analysis.

Parameter estimates for growth kernel of skin

	Estimate	CI lower	CI upper	Std. Error	DF	p-value
(Intercept)	-9.91e+02	-2.17e+03	1.91e+02	5.85e+02	41	9.80e-02
Age (months)	-4.86e+01	-8.85e+01	-8.81e+00	1.97e+01	41	1.79e-02
Feed weight (grams)	4.24e+00	2.50e+00	5.98e+00	8.63e-01	41	1.49e-05
Feed weight ² (grams)	-1.12e-03	-1.72e-03	-5.10e-04	3.00e-04	41	6.04e-04

Table 2. Estimates of the parameters for the growth kernel of skin model, with the respective confidence intervals, standard errors and p-values.

Parameter estimates for growth kernel of weight

	Estimate	CI lower	CI upper	Std. Error	DF	p-value
(Intercept)	-3.87e+02	-6.31e+02	-1.43e+02	1.21e+02	41	2.67e-03
Age (months)	1.44e+01	6.16e+00	2.26e+01	4.08e+00	41	1.04e-03
Feed weight (grams)	8.08e-01	4.48e-01	1.17e+00	1.78e-01	41	5.00e-05
Feed weight ² (grams)	-1.31e-04	-2.57e-04	-6.04e-06	6.21e-05	41	4.04e-02

Table 3. *Estimates of the parameters for the growth kernel of weight model, with the respective confidence intervals, standard errors and p-values.*

In tables 2 and 3, both the confidence intervals (CI upper and CI lower) show the accuracy of the parameter estimates. All estimates seem reasonably accurate.

1.2 Time series analysis

Goodness of fit of the time series analysis component of the python growth model was analyzed via graphical analysis (Figures 2 and 3). The results presented are for a time span of 21 months, which corresponds to the time span covered by the data collected. The model is shown to predict accurately total surface area of skin and weight, for the average python.

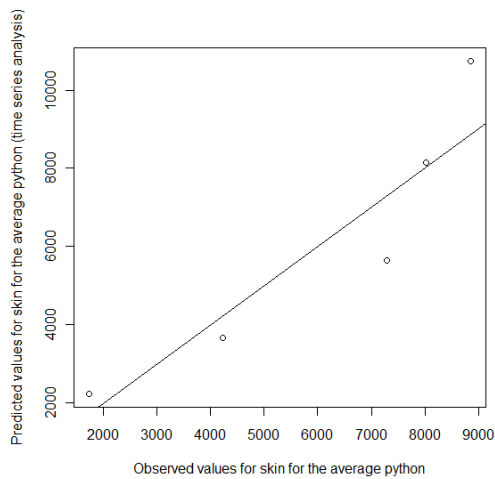


Figure 2. Assessment of model fit for time series analysis for surface area of skin.

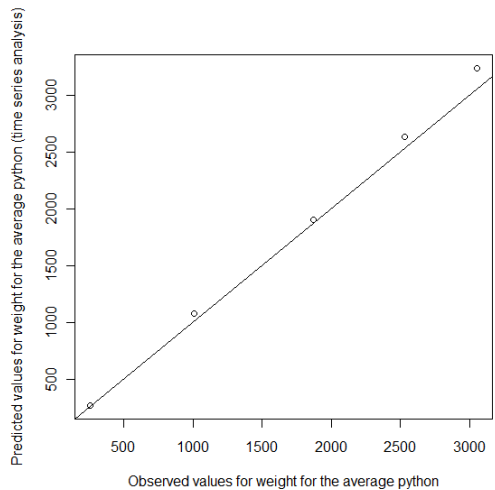


Figure 3. Assessment of model fit for time series analysis for weight.

2. Food optimum intakes

Profitability was tested for different feeding regimes, which means that different food values are used as an input for the python growth model. The bio-economic model was run for a 100 simulations, and the same pattern of profitability was obtained for each simulation (Figure 4). Therefore, it is possible to depict that there is a feed regime which consistently provides the most profitability. This is the case because this feeding regime will correspond to the situation where the animals show the most growth. The

model allowed to determine which was this feeding regime, which was found to be the total food input of 61542.42 g. This value corresponds to the food summed from the vector which had the reference feeding regime increased by 60%.

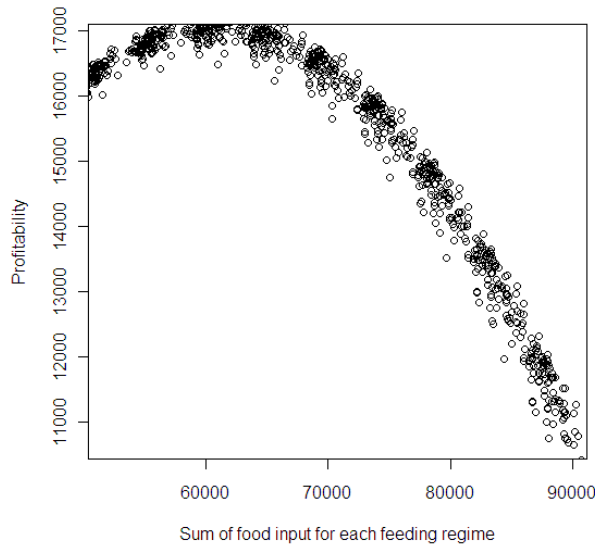


Figure 4. *Simulation of profitability for different feed intakes.*

3. Bio-economic model

The bio-economic model is a discrete time model and runs on a yearly time step. For the results shown, the model was simulated for 15 years. The number of simulations does not affect the patterns in the results shown, except in section 3.1, in which this is clearly pointed out.

3.1 Optimum percentage to sell

The following analysis was carried out to determine the number of individuals to sell at each time step which maximizes profitability. The starting population was assumed to have 10 hatchlings, 20 one year old juveniles, 30 two year old juveniles and 100 adults. The numbers for the starting population were chosen at random, since changing their values only influences the values of profitability, not the pattern observed in optimum

percentage to sell values. The only requirement is to have a value attributed to at least one stage of the population, otherwise the starting population is zero.

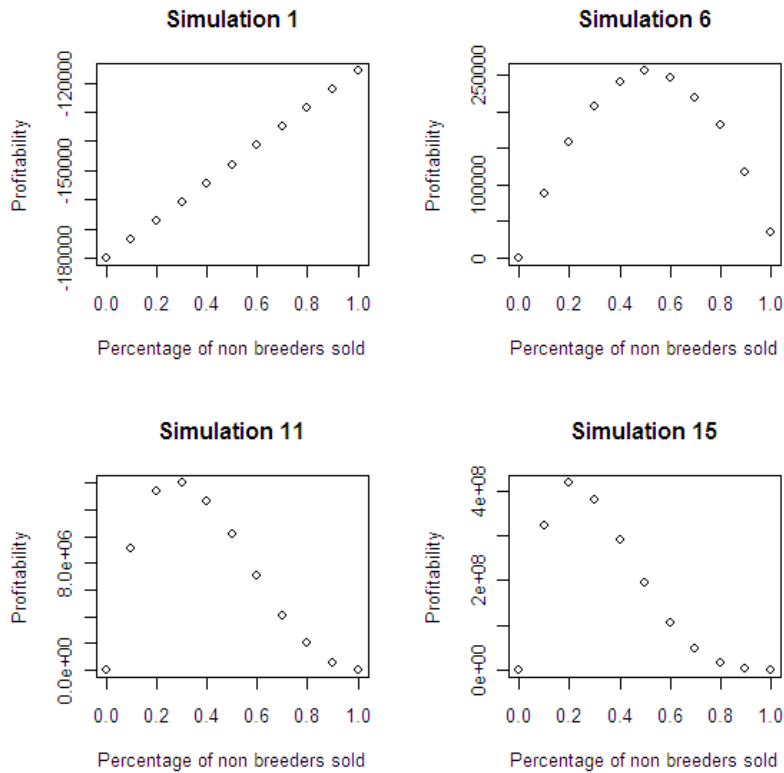


Figure 5. Change in profitability values as a function of changes in percentage to sell.

Figure 5 shows how the optimal percentage of remaining individuals to sell changes for different time steps (simulations). This occurs because the number of individuals in the total population changes through the model simulations. There are three main scenarios occurring in Figure 5.

Scenario 1

Simulation 1 (Figure 5) shows the impact of percentage to sell on profitability in the model's first time step. In the first time step the costs of setting up a python farm are taken into account. Therefore, unless the starting population has enough individuals to be sold to cover these initial costs, the balance will be negative. This value allows us to determine how much investment is required to set up a farm for the number of individuals in the starting population, or how much needs to be sold to invest a certain amount.

Another issue to take into account is that in this first scenario percentage to sell does not show a trade off. This is the case because the adult population in the starting population is independent of the number of breeders, since it is supplied from an external source; therefore it is expected for the graph to show that the more individuals sold the better. If the starting population also contains hatchlings and juveniles, this same pattern will show for the next three simulations, since a portion of the adults will still be not dependent on the number of breeders in the population.

Scenario 2

For simulations 6, 11 and 15 (Figure 5) no individuals are supplied from outside the farm, and the starting population has already been sold or allocated for breeding, hence the farm is operating in a closed cycle system. The remaining individuals available to be sold depend on conditions 1 and 2 being met. Within this framework, a trade off exists between percentage to sell and profitability. Figure 6 shows the relationship between total adults and total costs for different percentages of remaining individuals being sold. Total costs in this situation correspond to the total number of individuals required to meet conditions 1 and 2, in order to maintain the total population number between time steps and to cover both fixed and variable costs, and costs of setting up the farm in the first time step. Both variables decline in a parallel fashion with an increase in the initial values of percentage to sell. However, after a certain point these slopes start to converge, which in the present situation means that total costs are decreasing at a lower rate than the total adult population. This occurs given that the number of individuals required for conditions 1 and 2 to be met remains considerably high, for a decreasing total population, which translates in less individuals being available to be sold, hence less profit attainable. For this reason, selling a higher percentage of remaining individuals, shows to be less profitable, hence the optimal percentage to sell occurs at a point just before the slopes start to converge (Figures 5 and 6).

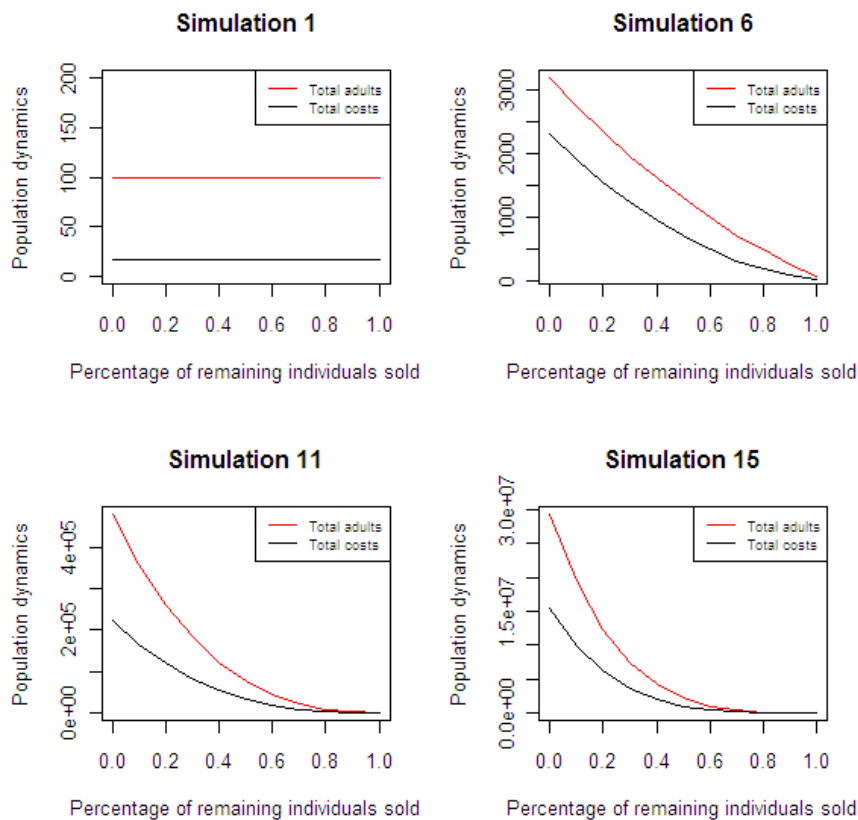


Figure 6. Population dynamics for different percentages of individuals being sold.

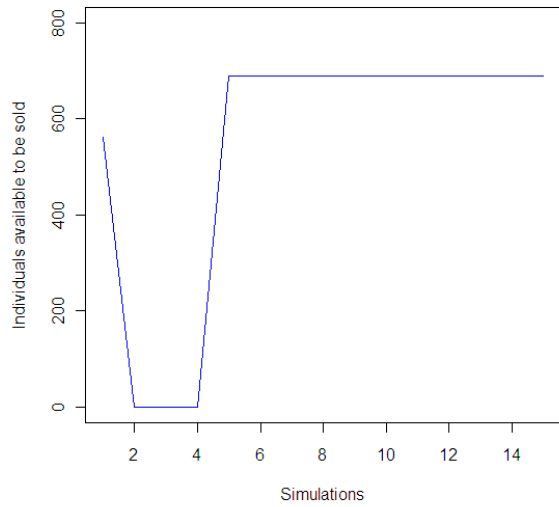
The trade-off present in percentage to sell means that in order to increase the total population, either to meet the market demand or to operate the farm at its maximum capacity, some of the remaining individuals, once conditions 1 and 2 are met, have to be allocated for breeding. These individuals cannot be sold, since they lose condition⁷⁶, as already mentioned. This means that less profit will be made in the current time step, since fewer individuals are being sold. However, breeding individuals represents an investment, since more individuals will be available to be sold in the next time step, if they are bred in the current time step, hence more profit will be made in the next time step, than if the individuals bred in the current time step were sold instead.

On the other hand, selling more of the remaining individuals in the current time step means that fewer individuals are allocated for breeding and therefore more time is required to increase the population.

In the case that all remaining individuals are allocated for breeding, there will be no profit in the current time step, however the population will increase more, and therefore there will be more individuals available to be sold in the next time step.

In the case all the remaining individuals are sold at each time step (percentage to sell = 100%), the population does not grow between time steps. It is maintained, since condition 1 is still valid. This situation may occur either when the number of remaining individuals meets market demand, or the farm is operating at maximum capacity. Figure 7 shows an example of such a situation for an initial population of 1000 adults. The initial population of remaining individuals declines to zero in the initial simulations because all of these individuals are sold between each time step. Given that the starting population did not have any hatchlings or juveniles, 3 years are required to have adults to be sold. For this reason, remaining individuals are equal to zero between simulations 2 and 4, and afterwards increase, since adults are produced. The maximum profit attainable will be constant, since the population is not increasing with time; hence the number of individuals to be sold also remains constant.

A



B

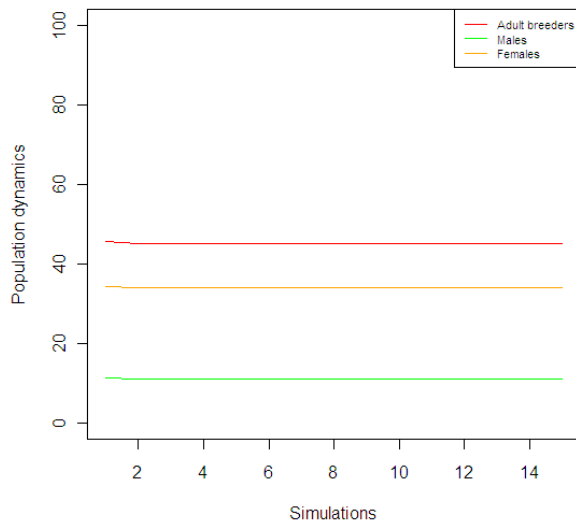


Figure 7. Population dynamics when all remaining individuals are sold between each time step. A. Population dynamics of the individuals available to be sold at each time step, when in the previous time step all remaining individuals were sold. B. Population dynamics of adult breeders, males and females, when all remaining individuals are sold.

The optimum values of percentage to sell maximize profitability for a particular population size in the current time step, without compromising profitability for the

following time steps. Investment in breeding is a sensible choice, however only until the point where the number of individuals being sold equals the market demand for them. Beyond this point we will be producing more individuals than what can be sold, and therefore having the costs of raising and maintaining these animals without profit. In the case the producer wishes to decrease the total population number, in order to avoid this situation, population size may be changed by changing the number of females breeding, in situations where there is not enough demand to sell more individuals. Therefore, in order to decrease the population, the number of females breeding should also be decreased. Regardless of the changes desired, there has to be a reasonable number of breeding males to fertilize the females.

Scenario 3

The optimum values of percentage of remaining individuals to sell decreases with time (Figure 5). This occurs because the population increases. As this happens, more individuals are required to meet conditions 1 and 2, therefore less are available to be sold without impacting the population growth. By impacting population growth, fewer individuals are available to be sold in the next time step, therefore the profit attainable decreases with time.

3.2 Impact of population stage on profitability

The following analysis was carried out to understand how changing the number of individuals at each population stage impacts profitability (Figure 8). This allows a producer to know in which population stage it is more profitable to invest. The analysis assumed that the stage analyzed would vary in population numbers from 10 to a 100, with all the remaining population stages having zero individuals in the starting population. This assumption is made to be able to compare the impacts of each stage without “noise” from other stages. It is also taken into account that hatchlings require three years to grow to adults, therefore in the situation where hatchling numbers are being analyzed, profit will only be made within 3 years, whereas with the adult analysis, profit will be made in the current time step. Hence, to make populations comparable, a time lag was incorporated in this analysis, since hatchlings will take more time to produce profit than juveniles, and the same applies for both cases compared to adults,

which is not an intrinsic property of the population stage. However, it has also to be taken into account that a starting population of adults bears the costs of setting up the farm in the first time step, whereas a starting population of hatchlings and juveniles does not.

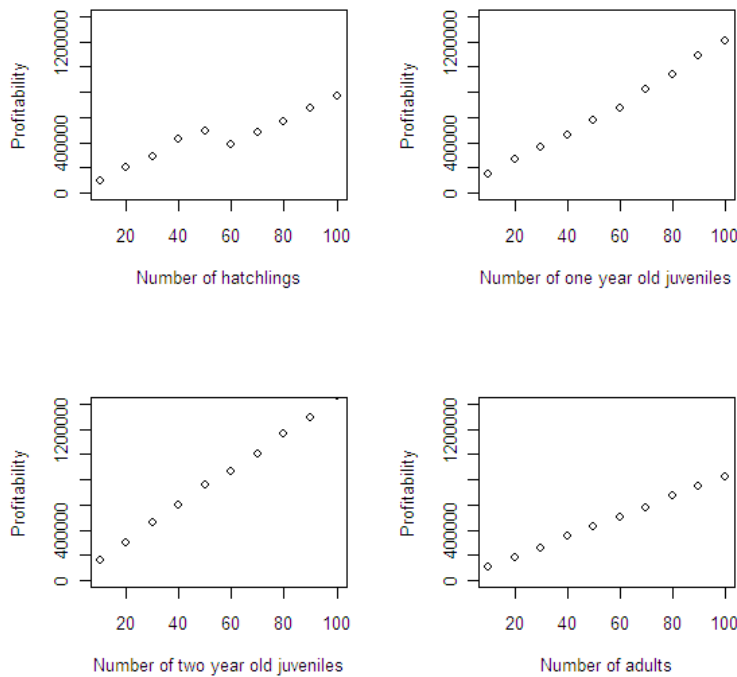


Figure 8. *Impact of initial number of individuals, in different population stages, in the farm's profitability per year.*

Figure 8 shows that the more individuals there are in the starting population, the more profit will be attainable. However the way profit increases in each stage of the population is different. Since the relationship between profit and number of individuals of a particular stage in the starting population is linear, the slopes were estimated using linear regression. The steepest slope corresponded to the population stage which had most impact in profitability (Table 4).

Slope analysis for impact of population stage

Population stage	Slope value
Hatchlings	6,557.419
Juveniles 1 year old	11,769.314
Juveniles 2 years old	14,264.037
Adults	8,027.333

Table 4. *Slope estimates for population stage impact on profitability*

The two year old juvenile population is shown to have the greatest impact on profitability.

3.3 Number of years to reach breakeven point

The following analysis was carried out to determine how the number of years required to reach a breakeven point for the farm investment varies with different population sizes at different stages. It was assumed a starting population for each stage, with number variation for the stage being analyzed and the remaining stages with zero individuals in the starting population. This analysis also assumed a time lag for profitability at different population stages.

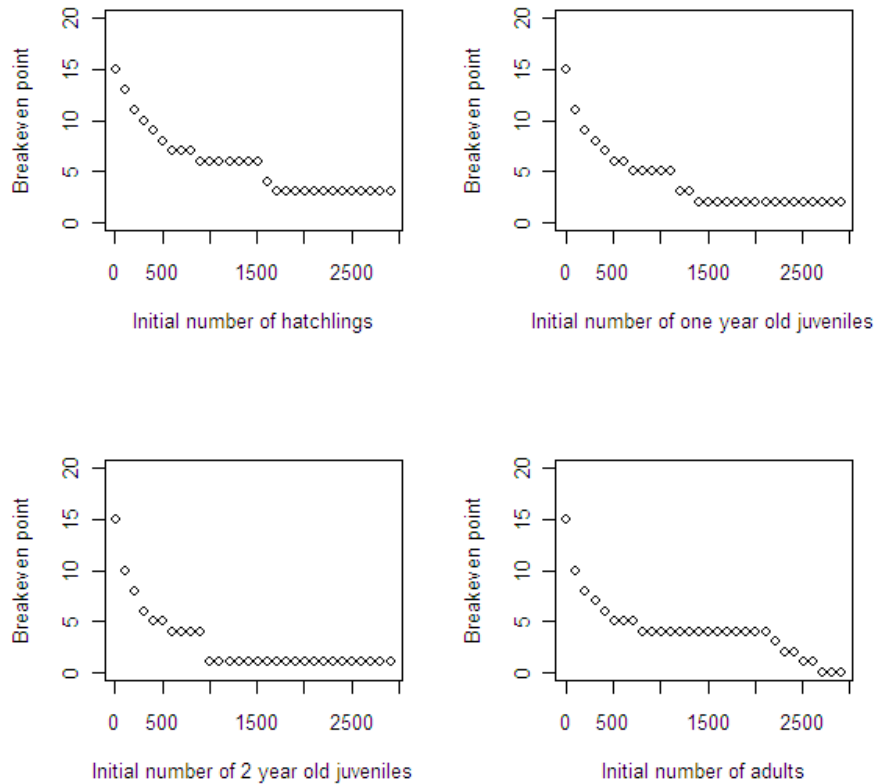


Figure 9. Number of years to reach breakeven point for initial farm investment as a function of the number of individuals in the starting population.

Figure 9 shows that the two year old juvenile population allows reaching a breakeven point to be reached in less time for a lower number of individuals. In the case of the adult population, the breakeven point is only reached after 2500 individuals as a starting population, which is more than the farm can produce, hence it is not a situation a producer would be interested in. Figure 9 also shows that it is not possible to reach a breakeven point in less than one year with a population stage other than adults. This is the case because hatchlings, 1 year old juveniles and 2 year old juveniles require 3, 2 and 1 years to grow to a stage where they can be sold, respectively, and hence make profit to pay the farm's initial investment. On the other hand, adults are ready to be sold in the current time step, and for this reason it is possible to reach a breakeven point in the current time step, if there are enough adults available to be sold.

It is also possible to observe that the greater the starting population, the earlier the breakeven point is reached.

3.4 Different price scenarios

Given the price variability in the market, especially in what concerns reptile products, an analysis was carried out to understand the impact of price variability in profitability. Skin price and meat price have different reference values, therefore different values were tested for each case.

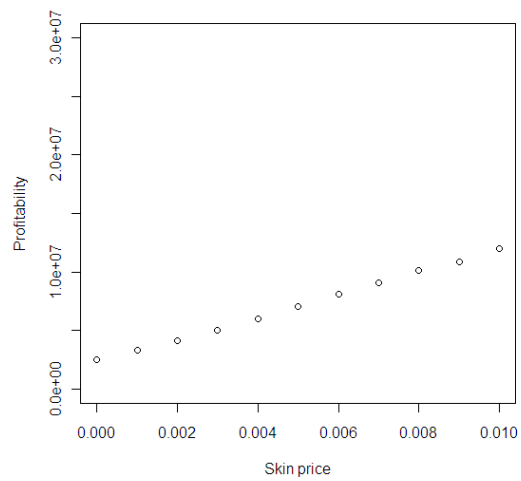


Figure 10. Profitability analysis for different prices of skin.

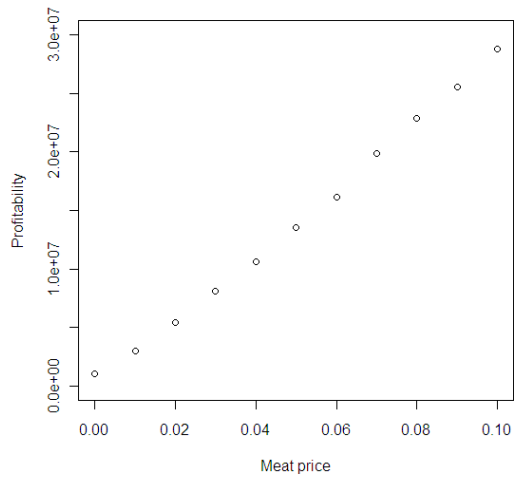


Figure 11. Profitability analysis for different prices of meat.

Slope analysis for different price scenarios of products

Items	Slope value
Meat price (US dollars)	282,311,393
Skin price (US dollars)	965,521,885

Table 5. Slope estimates for changes in profitability under different price scenarios.

Figures 10 and 11 together with Table 5 show that skin price fluctuations have the biggest impact in python farm profitability.

Discussion

The question this study proposed to answer was if python farming is profitable and how can this profit be maximized. To answer these questions, two models were developed, the python growth model and the bio-economic model.

Python growth model

Profitability is dependent on how much an animal can grow in weight and length, since both meat and skin will be the final products to be sold. The python growth analysis showed that both age and feed intake play an important role in growth, which allowed the development of a growth model with these two quantities fitted as explanatory variables. This is in accordance with other studies^{3,94}. The model allowed determining the amount of feed intake for each age class correspondent to the most profitable situation, which is the stage at which the growth rates are still sufficiently high to be adequate to invest in more food.

Pythons suffer from feeding conflict and have to be individually fed. This presents a problem when the python feeding procedure is scaled up to commercial farm operations, both in terms of labour and equipment costs. Hence, a mechanism which would allow for automatic feeding of these animals has to be developed, in order to have an optimum feed intake at minimal costs.

Python growth model- improvements

Temperature is a very important factor in ectothermic animal growth, since most of these animal's metabolic processes depend on it. The python growth model assumes temperature to be constant and optimal, which was a sensible assumption for the data collected, given that the location and habitat in which the pythons were reared, provides these conditions. Nevertheless, there is always a possibility for extreme climate conditions to occur, which might have considerable impacts on an individual's growth. This factor might explain some of the variation not explained by the model. An improvement of the python growth model would be to fit ambient temperature of the python's enclosure as an explanatory variable, assuming that it would be significant, given that these animals are ectotherms. However, this might be an unnecessary

procedure for enclosures that keep the surrounding temperature constant with the proper heating/cooling equipment.

It is also observed in the python growth model that the collected data for skin shows more deviation from predictions than the collected data for weight. This might be caused by measurement error of python length. When pythons are measured in terms of length, they usually show movements of contraction and expansion due to stress. For this reason it is difficult to obtain accurate measurements for length. This can be corrected for if new improved methods are found to measure these individuals. Additionally, measurement error can be fitted as a random effect, if there are repeated measures for the same individual, at the same time step. Also, the fact that the surface area calculated is an approximation to the actual surface area of the python's skin, since it was assumed that the body shape of the python was cylindrical, may also have influenced the python growth model's predictions for skin.

Python growth model- broadness

The python growth model was built on the data collected from 11 pythons reared at MCBT. The pythons used had no special treatment; they were fed once a week, with some variation, since not all individuals accepted food on every occasion (eg when in a shedding cycle). This should not be very different in other cases where pythons are reared. However, the nutritional content of the food given may influence growth. Hence, the model presented should be applied to pythons with similar diets to the ones used in this study.

By taking into account python ID as a random effect, individual variation is reduced to a minimum in the model's predictions. Hence the pythons used in this study are assumed to be representative of the average python. However, to further validate the model, larger samples need to be used to make the model's predictions more representative. The model also needs to be validated for 36 months, since the data collected only covered 21 months, in order to test if the assumptions made are valid.

Bio-economic model

The economic component of this model is based on cost-benefit analysis, to which a discount rate was applied. The way in which the biological component and the economic component are modelled make the bio-economic model proposed an integrated bio-economic model, which is in trend with current bio-economic models proposed⁸. Demand and supply are not modelled directly in this model, since they are assumed to be provided by external analysis. Hence, a future model development would be to incorporate a more detailed economic analysis.

Nevertheless, the model provides a tool to manage captive populations of pythons, and to make management decisions which maximize the profitability of the farm operations. The farm set up was assumed in detriment of a ranch setup given that, currently, there are no policy measures in regards to harvesting python eggs from the wild. Nonetheless, ranching setups are more favourable, since they provide income for rural stakeholders and incentive to conserve natural populations of pythons.

The analysis made on the bio-economic model showed that python farming profitability depends on several factors, which can be optimized to yield maximal profitability. Firstly, the fact that a farm is being set up for the first time or it is already running has a considerable impact on profitability. In the first case the costs of setting up a farm need to be accounted for. These costs depend on the number of individuals the producer wants to be able to sell, hence on farm size, and represent the initial investment required to set up the farm. The amount of time required to pay such costs depends on the amount of individuals available to be sold at each time step. This quantity depends on the number of individuals in the starting population. The analysis carried out in this study showed that the more individuals there are in the starting population the less time it takes to reach a breakeven point for farm costs, especially if these individuals are mainly two year old juveniles. This means that the two year old juvenile population has the greatest impact in profitability; hence it should be the stage where investment is more favourable. The fact that adults are a less profitable investment occurs because they are much more expensive to acquire than any other population stage. These costs are much higher than the costs of raising the animals to an adult stage. Hence, it would be more profitable for a producer to invest a two year old

juvenile population, than to buy an already grown individual, despite the fact that there is a one year time lag. Hatchlings and one year old juveniles are not as profitable as two year old juveniles given their lower survival rates and increased time lags to reach maturity.

The percentage of individuals being allocated for commercial purposes and breeding has also a great impact on profitability. The percentage of individuals being sold at each time step which provided the most profit was shown to vary with population size and corresponded to the maximal individuals available to be sold at a particular time step without compromising to a great extent the number of individuals available to be sold in the following time steps.

Fluctuations in skin and meat price have a significant impact in the profitability of farming operations. This analysis shows that skin price variability has more impact on profitability, than meat price. Fluctuations in skin and meat price are to a great extent correlated to fluctuations in market demand. The model presented aims to provide flexibility in decision making in order to cope with these variations. Assuming that market demand can be predicted with relative accuracy a year before the product is sold, it is possible to make management decisions to have optimal output, both in terms of individuals being sold and in the total population size. The number of individuals being sold may be regulated by the percentage to sell values, whereas total population size may be controlled by both percentage to sell values and also by the number of females being allocated for breeding purposes. With model analysis it is possible to predict what should be the optimal values for both of these parameters, in order to have the desired output in the next time step. The above depends on the predictability of the python's biology, which requires further validation. The predicted value of demand allows us to manage the population in order to have enough individuals to sell to meet demand, but not more than that. These values of individuals available to sell are constrained by the farms maximum capacity of producing them.

The models presented are run for 15 years. This corresponds approximately to the reproductive time span of a python⁷⁶; therefore it will correspond to the lifetime of adult pythons in the starting population. The survival rate assumed in the bio-economic model, for each population stage, is static. However, this lacks in biological realism if

the model is simulated for more than 15 years. Therefore, a necessary improvement of the model is to incorporate a survival rate that decreases with time for the adult population, to be possible to have more accurate predictions for simulations over 15 years.

Answers

The main conclusion from this study is that python farming profitability depends on the producer being able to pay an initial investment if the farm is being set up for the first time, and having enough individuals to sell to pay off these costs in a short period of time, in order to be able to make profit. Pythons are animals that grow and reproduce remarkably well in captivity⁷⁶; therefore it is possible for the population to increase exponentially in a short period of time. For this reason, it seems that, as long as it is possible to cope with market fluctuations with proper management decisions, python farming can establish itself as a competitive industry.

Uncertainty in the model presented has two main sources: the biology of the pythons and estimates in demand. If the python's biology remains constant and predictable, and the estimates in demand are accurate, the model's predictions should be precise.

Investment in python meat should be able to provide a buffer for variability in skin sales, since reptile meat is less subject to variability in price³⁴, which in itself has less impact on profitability of the farm operations.

The models presented may provide a framework which can be adapted to manage other reptile populations, such as crocodiles. It is clear however, that a different formula for surface area needs to be developed, different parameters need to be estimated, and significance of variables might change.

The parameter estimates assumed for the model (Table 1) are conservative, which makes these results incorporate less risk. The costs of setting up a farm were based on a crocodile farm with a capacity for 1800 cull animals. However, it has been reported that pythons show social aggregation⁶⁶ and also make a 3D use of space⁷⁶, given their arboreal habits. Additionally, these animals do not show inter-specific stress, in contrast to crocodiles². For this reason, the space required to rear should be considerably lower

than the space required to rear crocodiles. Furthermore, pythons make use of aggregation as a mechanism of buffering environmental temperature variation⁶³. This phenomenon should provide sustainability to the farm operations, since less investment is required in heating the environment. Nevertheless, further studies need to be carried out to quantify precisely how pythons buffer surrounding temperature variations.

Conclusion

In summary, the findings presented in this study provide a good argument for further research on the remarkable potential of pythons for the sustainable and efficient production of protein to “meat” higher demands.

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Appendix

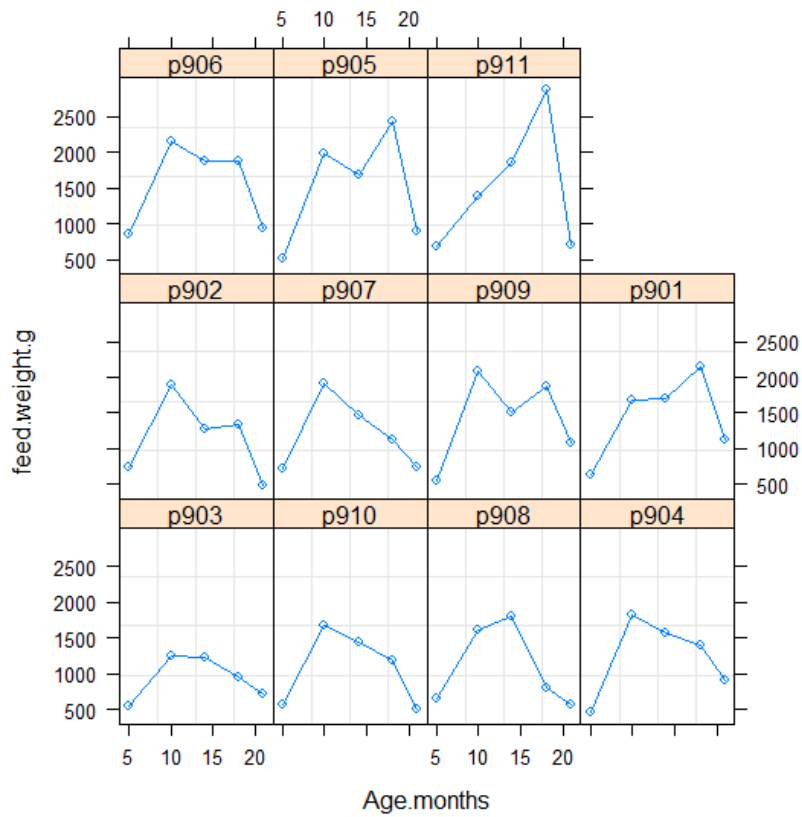


Figure 1. Feed intake as a function of age for each python.

Linear mixed effects model- Assumption testing

Assumption 1: within group error

Assumption 1 was tested through graphical analysis of the within group residuals, as described in Pinheiro, J. C. & Bates, D. M. (2000).

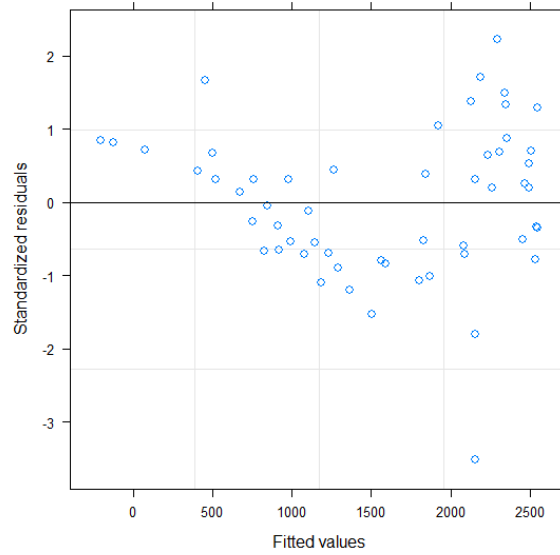
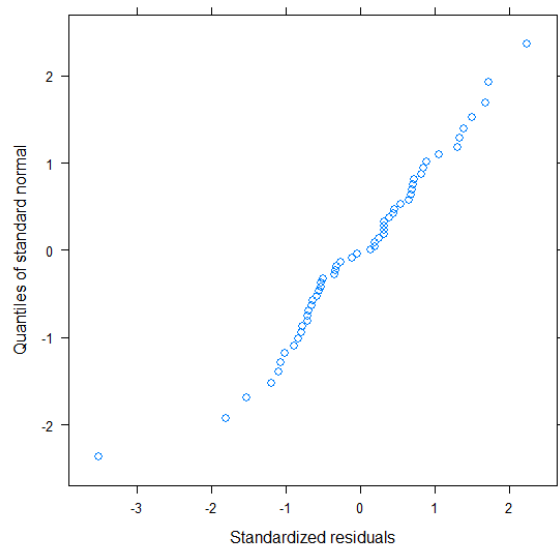


Figure2. Diagnosis of model for growth kernel of skin.

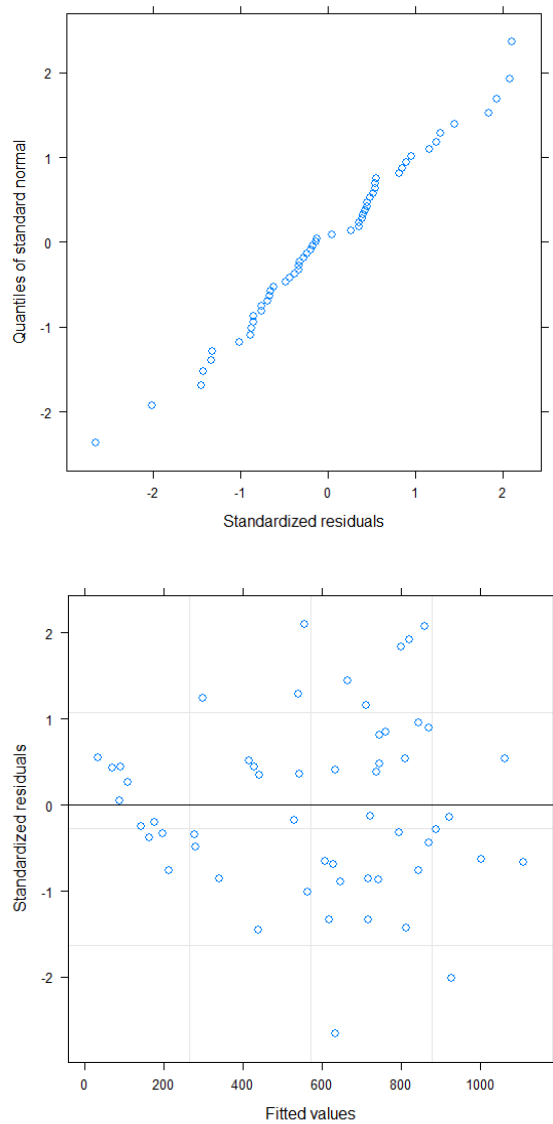


Figure 3. Diagnosis of model for growth kernel of weight.

The above diagnostic plots (Figures 2 and 3) show that errors are approximately normal. The heteroscedasticity observed in variance for the growth kernel of skin can be corrected if a bigger sample is used. Variance in the growth kernel of weight is constant. Therefore, assumption 1 is valid.

Assumption 2: random effects

A normality plot was used to test the assumption of normally distributed random effects, as described in Pinheiro, J. C. & Bates, D. M. (2000).

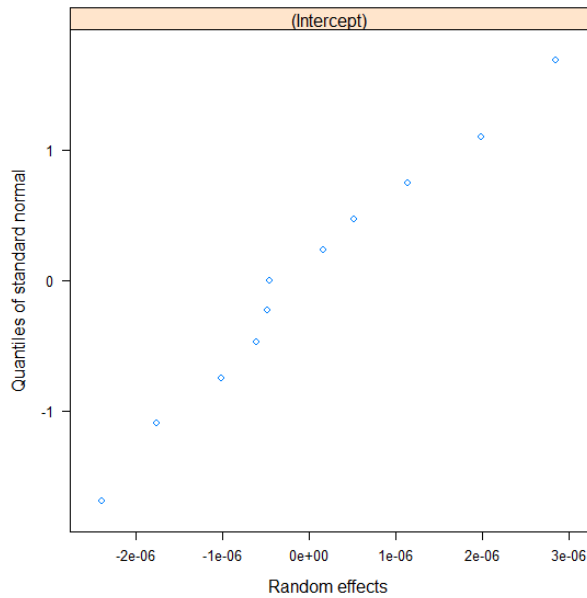


Figure 4. Diagnosis plots for random effect structure on growth kernel of skin

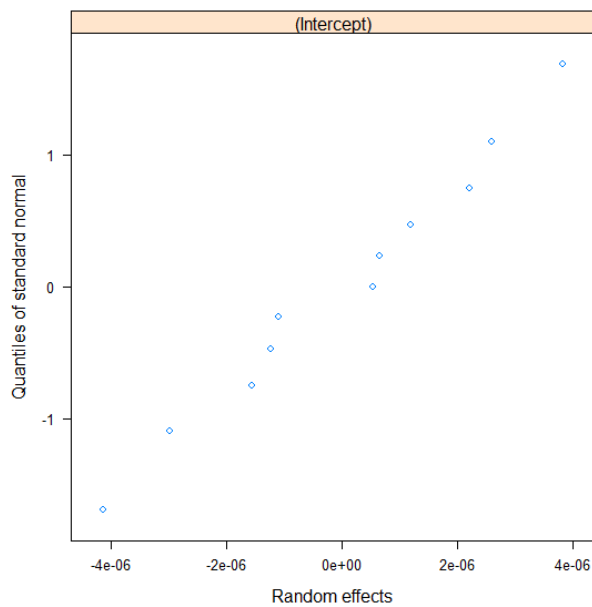


Figure 5. Diagnosis plots for random effect structure on growth kernel of weight

Figures 4 and 5 indicate that there are no significant departures from normality in both the growth kernel model for weight and in the growth kernel model for skin. Therefore, assumption 2 is also valid.

Model fit for growth kernel

Goodness of fit of both the growth kernels models and goodness of fit for the time series analysis model were assessed.

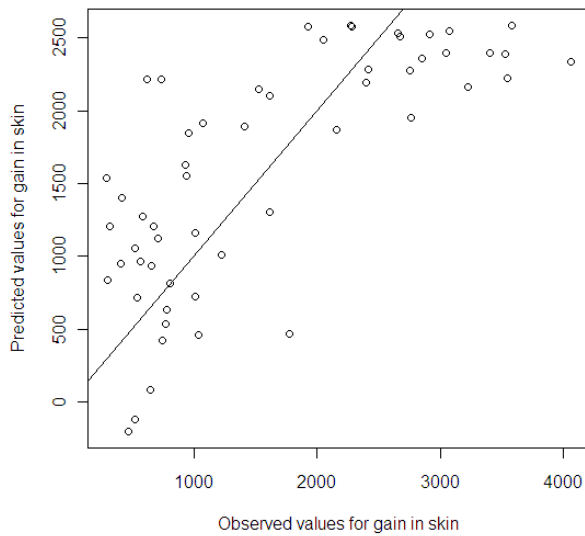


Figure 6. Assessment of model fit for growth kernel of skin

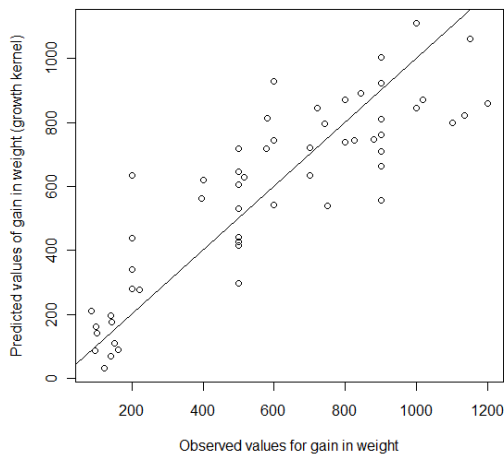


Figure 7. Assessment of model fit for growth kernel of weight

The scatter visible in Figures 6 and 7 shows that some variation remains unexplained. Also, there are two negative values predicted for gain in skin (Figure 6), which were assumed to correspond to zero growth.

The growth kernel shows a better fit for weight than for skin. R^2 values were calculated for each model, and the values obtained (Table 1) confirm the above findings.

<u>R^2 values</u>	
Model	R^2
Growth kernel of skin	0.4930162
Growth kernel of weight	0.7493199

Table 1. R^2 values for growth kernel models

From the R^2 values in Table 1, it is possible to conclude that both models explain a good portion of the variation, with the growth kernel model for weight explaining more than the growth kernel of skin.

When both growth kernel models are incorporated into the time series analysis to estimate total skin and total weight for the average python at each time step, the accuracy is much improved. This is probably the case because the time series analysis is made on the average python.