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Allometric Regression of Snake Body Length from Head Image Measurements

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ABSTRACT As in many fields of wildlife research and management, camera devices and photogrammetry have become an integral part of the toolkit for exploring otherwise-unseen aspects of the biology, behavior, and control of the invasive brown treesnake (*Boiga irregularis*) on Guam. Because brown treesnakes are cryptic and nocturnal, and nearly all aspects of their ecology are influenced by snake size, methods are needed to estimate snake size from images captured by infrared wildlife cameras. Unfortunately, it is difficult to capture images of an entire snake's length at a controlled distance from a simple camera setup. Here, I describe the allometric relationships between brown treesnake body length and potential predictors: head measurements, sex, and body condition. Head length (HL) was the most important predictor of body length, alone accounting for 95.9% of the variation in brown treesnake snout-vent length (SVL). We provide simple regression equations for predicting brown treesnake length from head measurements, an example of how to extract measurements from images, and a convenient lookup table for predicting SVL and 80% prediction intervals from HL alone. Coupled with a simple camera setup that controls subject distance and includes size standards in the image, we can estimate brown treesnake body size from images that include only the head when photographed from above. These methods have been developed to enable ongoing assessments of brown treesnake predation risk following landscape-scale suppression efforts that could enable the reintroduction of extirpated native wildlife. Published 2021. This article is a U.S. Government work and is in the public domain in the USA. *Wildlife Society Bulletin* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

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Allometry, or mathematical relationships among anatomical measurements (Schmidt-Nielsen 1984), can be used to predict physiological states of individuals from isolated measures when direct measurement is difficult or impossible. Allometric equations have been used to predict body measurements in a broad range of taxa (Mollet and Cailliet 1996, Hile et al. 1997, Verdade 2000, McKinney et al. 2004, Morris and Mead 2016). Inference on animal size, as opposed to direct measurements, is often needed for wildlife that cannot be captured or handled due to crypsis, inaccessibility, potential behavioral effects, or safety of the animals or observers. Photogrammetry, or indirect measurements taken from camera images, has been coupled with allometric relationships to predict various morphometrics from animal images without making direct contact (e.g., Breuer et al. 2007, Krause et al. 2017, Ortega-Ortiz et al. 2018, Gray et al. 2019). The proliferation of the use of inexpensive wildlife cameras (i.e., game cameras, trail cameras, or camera traps) has greatly benefitted wildlife research and management by providing an affordable, safe, and non-invasive means of detecting and sampling wildlife. Photogrammetry using wildlife camera images has been employed to collect body measurements from disparate taxa, from large ungulates to reptiles and invertebrates (e.g., Collett and Fisher 2017, Muneza et al. 2019, Moore et al. 2020).

Since the accidental introduction of brown treesnakes (*Boiga irregularis*) to the formerly snake-free island of Guam in the western Pacific, they have invaded all terrestrial habitats and have reached extraordinarily high densities (up to 100 per ha at the height of the irruption; Rodda et al. 1999*a*). Brown treesnakes have caused millions of dollars of damage to the island's power infrastructure, inflicted painful bites to humans, preyed on domestic animals, and caused the extinction or extirpation of nearly the entire forest avifauna, with cascading ecological consequences such as loss of seed dispersal (Savidge 1987, Atkinson 1996,

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Rodda and Savidge 2007, Caves et al. 2013). The brown treesnake has become a textbook example of the potential harm of an invasive predatory species and is considered one of the world's 100 worst invasive species (Lowe et al. 2000, Sodhi and Ehrlich 2010, Lockwood et al. 2013, Simberloff 2013). To mitigate damages, enormous investment has been made in research on the behavior, biology and ecology of the species, development, testing and implementation of control tools, and inspections of outbound cargo to prevent the spread of brown treesnakes to other snake-free islands in the Pacific (Rodda et al. 1999*b*, Rodda and Savidge 2007, Clark et al. 2018, Engeman et al. 2018).

The most notable recent technological innovation in brown treesnake control has been the development of an automated system for aerial distribution of toxic bait cartridges containing a dead neonatal mouse treated with acetaminophen (paracetamol). The cartridges are designed to hang in the forest canopy where the baits can be consumed by arboreally-foraging snakes (Siers et al. 2019). The automated delivery system has been demonstrated to significantly reduce brown treesnake activity in large, experimental treatment plots (Siers et al. 2020*a*,*b*), opening the possibility that some native birds and lizards may be reintroduced to Guam's forests if snake numbers can be sufficiently suppressed.

However, accurate assessment of the suppressive effects of the automated aerial delivery system (ADS) is hampered by difficulties in estimating densities of brown treesnakes. Brown treesnakes have very low detection probability (probability of finding an individual known to be in a sampling area) and violate many of the assumptions of mark-recapture or distance sampling density estimation models, making reliable density estimates impractically expensive and potentially biased and imprecise (Rodda et al. 1999*a*, Rodda and Campbell 2002, Rodda et al. 2007, Tyrrell et al. 2009, Christy et al. 2010). Simpler and more economical indices of brown treesnake activity or abundance, such as nontoxic bait disappearance rates (Siers et al. 2020*a*), are useful but potentially biased and do not provide any demographic data.

Lacking reliable estimators, evaluations of the effectiveness of snake suppression and ability to make management decisions may be limited to assessing the rates at which brown treesnakes come into contact with live lures, as an index of residual predation risk. Yackel Adams et al. (2019) used wildlife cameras framed on brown treesnake traps that contained live bird lures in protective chambers as surrogates for nesting birds to evaluate contact rates. Image captures of snakes at traps were a far more sensitive metric of snake activity and predation threat than trap captures of snakes, as camera-recorded contact rates were almost 15 times higher than trap capture rates.

Live-lure contact rates may be the best practical metric of the frequency of brown treesnake predation attempts. However, not all snake encounters carry the same risk of predation. Through the course of a brown treesnake's lifetime, a 5-g, 350-mm snout-vent length (SVL) hatchling may grow by orders of magnitude to a 700-g, 1,500-mm female or 2,000-g, 2,000-mm male (Savidge 1991, Siers 2015, Siers et al. 2017*a*). Brown treesnakes under 750 mm SVL feed almost exclusively on small lizards, transitioning to primarily bird and rodent prey as they grow larger (Savidge 1988, Lardner et al. 2009, Siers 2015), and nearly all other aspects of brown treesnake biology, behavior, invasion risk, and susceptibility to control tools also vary with size (Siers et al. 2017*a*, Clark et al. 2018, Nafus et al. 2020). In essence, predation threat scales up with snake size. A monitoring method that provides not only an index of abundance but also a size distribution can help managers to optimize tool selection, such as using larger acetaminophen doses or alternative trap designs when very large snakes are present (Siers et al. 2021). Data indicating the absence of snakes of mature size classes could increase confidence that management techniques are effectively interrupting reproduction, informing management decisions.

The camera system employed by Yackel Adams et al. (2019) reliably recorded live-lure contact rates but was not optimized for measuring snake size. Snake length can be measured from photographs when the entire length of the snake is in the same frame along with a size standard (Penning et al. 2013). However, in the field, it is extremely difficult to get reliable images of a snake's entire body on a controlled plane at a fixed or known distance from the camera or with adequate size standards, particularly for an arboreal snake. The U.S. Department of Agriculture Wildlife Services National Wildlife Research Center (WS-NWRC) is currently beginning to employ a simple system of commercial wildlife cameras mounted overhead of live lures in protective chambers on small platforms marked with size standards (Fig. 1) that can be elevated into the forest canopy in order to take measurable images of a snake's head as it investigates and attempts to prey on the lure (e.g., live mouse or bird). My objective was to describe the allometric relationships between snake head measurements and body length and extraction of measurements from head images to estimate snake sizes, enabling better characterization of contact rates and the size distributions of brown treesnakes posing predation threat.

Figure 1. Camera platform comprised of a pattern of circular size standards printed on lightweight sign material, with an inexpensive wide-angle wildlife camera mounted overhead of a live mouse lure chamber, used in a study of brown treesnakes in Guam, USA, 2019–2021.

METHODS

Specimen Collection and Measurement

We obtained measurements from brown treesnakes collected during various research and management activities by WS-NWRC and the U.S. Geological Survey, primarily in northern Guam over the span of approximately 2 years (4 September 2018–14 September 2020). We measured head length (HL) with calipers from the tip of the snout to the rear of the jaw, and head width (HW) at the broadest part of the rigid portion of the skull, approximately halfway between the eyes and the rear of the jaws; measurement further back on the head would be inconsistent due to lateral flaring of the jaws. We recorded head dimensions to the nearest 0.1 mm. We measured snout-vent length (SVL, mm) by gently stretching the body of the snake along a flexible tape as muscle contractions relaxed; this has been the standard method for brown treesnake body length measurements, having been conducted tens of thousands of times including on individuals that are repeatedly measured with no apparent ill effect. Although length measurements from unanesthetized snakes are less precise than those from anesthetized or preserved specimens (Cundall et al. 2016), stretching along a tape without anesthesia is typically the only practical method for field studies using free-ranging snakes. We measured body mass (g) with hanging spring scales (Pesola Präzisionswaagen AG, Schindellegi, Switzerland) or electronic balances, in increments of 1 to 10 g, depending on the range and precision of the scale and mass of the snake. We determined sex (SEX) by probing for inverted hemipenes as per Reed and Tucker (2012); 24 snakes that were too small to be reliably probed were classified as juvenile. Although many of the snakes in the data set were captured and measured multiple times, we used only the first measurement for each individual to preclude concerns of pseudoreplication. All animal use was approved by the USDA National Wildlife Research Center Animal Care and Use Committee under Protocol #QA-2830.

We derived relative head width (RHW) as HL/HW, or head width controlling for head length, for a noncorrelated additional measure of head geometry. We calculated a body condition index (CI), as the ratio of observed to expected snake mass. Therefore, a snake of average body condition would have a CI of 1.0, and higher or lower values indicate snakes in better or poorer body condition, respectively. Expected mass was predicted from a linear regression based on a quadratic transformation of ln(length) as a predictor of ln (mass) for all snakes in the data set, to better fit the curvilinear relationship between these measures. During preliminary data exploration, the CI model containing a quadratic transformation of length outperformed the model containing only the untransformed length data by 391.52 AIC_c units and improved the R^2 of the relationship from 94.2 to 97.2%.

Obtaining Measurements from Images

Lure platforms were 50.8×76.2 cm custom images printed on a lightweight outdoor sign product (poly foam material sandwiched between 2 layers of aluminum laminate) with a commercial infrared trail camera mounted overhead (Apeman H68, Apeman International Co., Ltd, Shenzhen, Guangdong, CN). Because of the barrel distortion in images resulting from use of a wide-angle lens at close distance (Fig. 1), we elected to use circular size standards (as opposed to a right-angle grid) so that standard measurements can be taken on the same angle as the head measurement to correct for this distortion. We arranged 20-mm circular size standards in a concentric ring pattern around the center of the image (where the lure chamber would be situated; Fig. 2), allowing us to consider the distance of the head from the center of the image in judging the quality of the image captured.

Image measurements can be obtained by opening the photograph file in any image editing software that includes

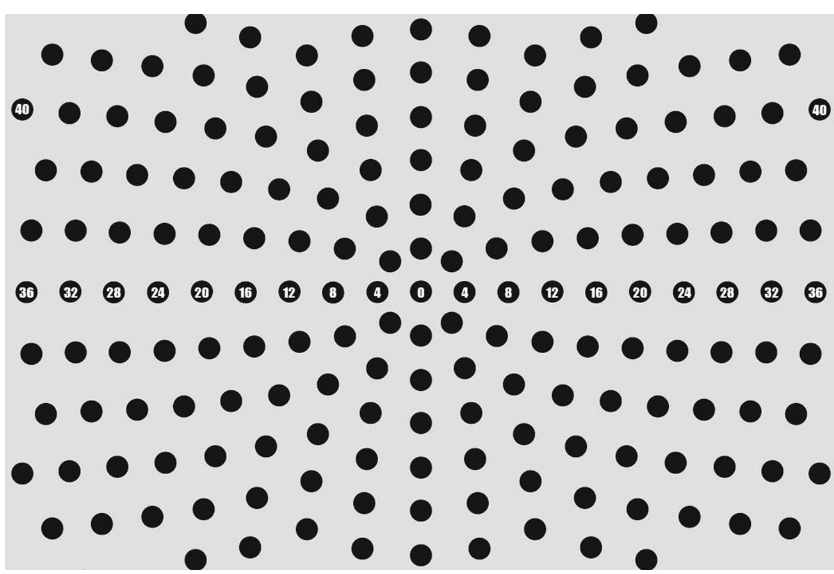

Figure 2. Image from camera platforms printed on lightweight outdoor sign material, used in a study of brown treesnakes in Guam, USA, 2019–2021. Size standards are 20-mm circles arranged in concentric rings around the center of the image where the lure chamber would be positioned. Numbers on the center row of standards depict the distance (cm) from the center of the image for all standards in that ring.

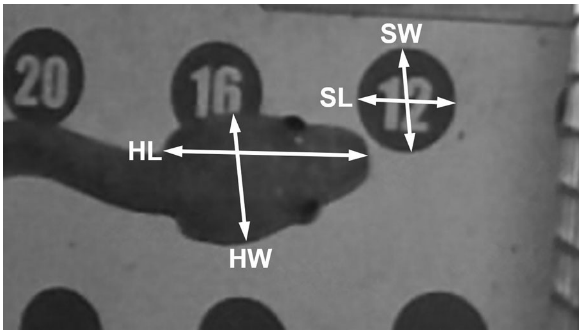

Figure 3. Cropped example of a brown treesnake head image from an overhead infrared camera in Guam, USA, 2020. Head length (HL) or head width (HW) can be calculated from image measurements by scaling standard length (SL) or standard width (SW) with known dimensions size standards (dark circles) in the image. Taking head and size standard measurements from the nearest size standard and along the same axes helps to correct for lens distortion.

a measurement tool (e.g., Adobe® Photoshop®, GIMP, ImageJ). Using the measurement tool, head length, head width, standard length, and standard width are measured, with head and standard measurements taken on the same angles (Fig. 3). Conversion from image dimensions to true dimensions is achieved by the simple equation:

$$\text{Body measurement} = \frac{\text{image body measurement} \times \text{known standard measurement}}{\text{image standard measurement}},$$

where image units (pixels, mm, etc.) are irrelevant as they cancel out leaving the estimated body dimension in the same units as the known standard dimension (see the worked example in Results). Snake size estimation will occur after completion of field trials so results are not reported here; this section of the article is presented to demonstrate how others might apply similar methods.

Statistical Methods

We performed all statistical tests and data visualization in the R environment for statistical computing, Version 3.5.3 (R Core Team 2019). We evaluated the effects of candidate predictor variables on the response variable (SVL) with linear regression models. We compared candidate models based on Akaike's information criterion corrected for small sample size (AIC_c) using the R package MuMIn for multimodel inference (Bartoń 2020). We considered models within $\Delta AIC < 2$ of the top model to be plausible alternative models, and we assessed relative variable importance (RVI) as the sum of weights (ω) of all models that contained the term of interest (Anderson 2008). All models with interaction or polynomial terms also included the primary effects (e.g., the model reported as HL*SEX also included HL + SEX). During exploratory modeling, we confirmed that head length and head width are highly correlated ($R^2 = 84.7\%$). We determined that HL was a more precise predictor of snake length than HW when modeled as sole predictors ($R^2 = 91.5$ vs. 80.3% and ΔAIC_c of 455 between models) so elected to focus on HL as the primary predictor in model comparisons. Head width added value to the model through the derived and uncorrelated RHW term.

We first evaluated a biological model considering effects of all candidate predictor variables. This included a quadratic transformation of head length (HL^2), allowing for a curvilinear relationship between HL and SVL as observed during data exploration, and an interaction between HL and sex (HL*SEX) to allow for sexual dimorphism in allometry. The biological model included only records for which snake sex could be determined, eschewing 24 data points for juvenile snakes, and model selection was only performed on this subset of data. Although sex and body condition cannot be observed from head images, they were included in the biological model as potential additional sources of variation in the allometric relationship between head measurements and body length.

We then evaluated a photographic model using only the predictors that could be measured from camera images (HL, HL^2, and RHW) including the 24 juvenile snakes. Finally, we revised the data set to drop outliers that are likely to represent measurement error (residuals >3 times the standard deviation) and generated predicted SVL values based on HL alone, with 80% prediction intervals. This provided a convenient reference to quickly estimate brown treesnake SVL from HL measured in camera images. Data are available from the USDA WS-NWRC Quality Assurance Unit archives upon request.

RESULTS

Throughout the course of the study, we collected head and body measurements on 543 unique snakes (223 females, 296 males, and 24 juveniles). For the biological model, all candidate terms were significant predictors of SVL. The top model included all terms and carried 100% of the model weights (Table 1). Relative variable importance was 1.00 for HL and HL^2 (i.e., included in models that carried 100% of the model weights), 0.99 for CI, RHW, and SEX, and 0.98 for the HL*SEX interaction. The top model outperformed the next top model ($HL + HL^2 + CI + RHW$) by 9.14 AIC_c units and carried 96.6% of the model weight, clearly indicating a robust top model. The HL-only model outperformed the highest-ranking model without a HL term by 1120 AIC_c units. SEX and HL*SEX effects were significant, though the effect size was minor (Fig. 4), with females exhibiting a slightly steeper slope in the relationship than males. The coefficient for RHW (-64.3 ± 19.0 SE) was negative, indicating that snakes with a narrower head in relation to body length tended to be shorter. The coefficient for CI (-68.23 ± 19.3 SE) was negative in the top models, indicating that head lengths for heavier, more robust snakes were slightly shorter when controlling for other terms in the model; this pattern is consistent with differences in head length for captive juvenile vipers fed a relatively high-intake diet (Bonnet et al. 2001). Although all terms have predictive significance in the model selection process, their inclusion only improved R^2 from 90.9 to 91.8% over the HL-only model. The top biological model outperformed the

Table 1. Subset of 12 of 32 possible models from the Akaike Information Criterion (AIC) model selection table for candidate predictors of brown treesnake snout-vent length in Guam, USA, 2018–2020. Subset includes: 1) models carrying 100% of summed model weights (ω); 2) highest-ranking models without each of the candidate predictors; 3) models containing each predictor alone; 4) the photographic model only containing terms that can be measured from camera images; and 5) the null model (intercept only). Predictors are head length (HL) and its quadratic term (HL^2), relative head width (head length/head width, RHW), body condition index (CI), sex (SEX), and a head length by sex interaction term (HL*SEX).

Model	*df* [a]	logLik[b]	AIC_c [c]	ΔAIC_c [d]	ω[e]	R^2
$HL + HL^2 + RHW + CI + SEX + HL*SEX$	8	−3057.52	6131.32	0.00	0.966	0.918
$HL + HL^2 + RHW + CI$	6	−3064.15	6140.47	9.14	0.010	0.916
$HL + HL^2 + CI + SEX + HL*SEX$	7	−3063.28	6140.77	9.45	0.009	0.917
$HL + HL^2 + RHW + SEX + HL*SEX$	7	−3063.76	6141.73	10.41	0.005	0.916
$HL + HL^2 + RHW$ (photographic model)	5	−3073.26	6156.64	25.31	0.000	0.913
$HL + HL^2$	4	−3077.38	6162.84	31.51	0.000	0.912
HL	3	−3085.52	6177.09	45.77	0.000	0.909
RHW + CI + SEX	5	−3643.61	7297.33	1166.00	0.000	0.219
SEX	3	−3679.34	7364.74	1233.41	0.000	0.104
RHW	3	−3682.16	7370.36	1239.04	0.000	0.094
CI	3	−3698.26	7402.57	1271.24	0.000	0.036
Null model (intercept only)	2	−3707.84	7419.71	1288.38	0.000	0.000

[a] Degrees of freedom;
[b] log-likelihood;
[c] Akaike information criteria corrected for small sample size;
[d] Difference between top model and current model in AIC_c units;
[e] Model weights.

photographic model by 25.31 AIC_c units, but only improved R^2 from 91.3 to 91.8%.

Several outliers were evident, likely due to measurement or data entry errors (Fig. 4). When reducing the data set by removing the outliers (28 observations >3 times the standard deviation), the predictive power of the photographic model improved to $R^2 = 96.0\%$ and $HL + HL^2$ alone accounted for 95.9% of the variation in SVL; in comparison, HW accounted for only 83.8%. Predicted snake lengths based on head length only, with 80% prediction intervals, are tabulated in a convenient reference (Table S1, available online in Supporting Information); prediction intervals are roughly ±85 mm from the predicted SVL, regardless of length.

Regression Equations

The estimated regression equation for the photographic model ($R^2 = 96.0\%$) was:

$$SVL = -39.94 + (41.61 * HL) + (-0.1324 * HL^2) + \left(-55.61 * \frac{HL}{HW}\right).$$

The equation for the simplified $HL + HL^2$ model ($R^2 = 95.9\%$) is:

$$SVL = -158.4 + (43.09 * HL) + (-0.1486 * HL^2).$$

All measurements are in mm.

Using the image with head and size standard measurement landmarks (Fig. 3):

$$\text{Head length} = \frac{472 \text{ pixels} \times 20 \text{ mm}}{229 \text{ pixels}} = 41.2 \text{ mm}.$$

Using the lookup table provided (Table S1), this specific snake would be estimated at 1,368 mm SVL with an 80% prediction interval of 1,284–1,453 mm.

DISCUSSION

Head length alone is a relatively precise predictor of brown treesnake length, explaining 95.9% of the variation in SVL after removing outlier measurements. Given the challenge of measuring a prehensile and uncooperative snake over a flexible tape, and interobserver differences in the force with which snakes are stretched (Penning et al. 2013, Cundall et al. 2016), much of the remaining 4.1% of unexplained variation could be due to error in SVL measurement. It may be that brown treesnake head length is a more precise predictor of body length than direct measurement of SVL with a flexible tape, given the less difficult task of measuring a relatively small, rigid, and easily restrained part of the anatomy with calipers. Estimating snake length from head length may also reduce the amount of animal handling necessary, prevent possible snake injury from overly forceful stretching, and reduce risk of venomous bites during attempts to measure snakes at full stretched length.

Head width was a comparatively poor predictor of SVL. Measurement of HL is limited primarily to one rigid bone assembly (lower mandible) and how it articulates with the premaxillary (snout). In comparison, HW may be more prone to observer error (Cundall et al. 2016), given the less precise landmarks for measurement and the potential for improper inclusion of both lower mandibles in measurements, as they are laterally mobile. Head width has also been reported as a poor predictor of other allometric relationships in snakes such as gape size (Hampton 2014). Inclusion of relative head width (controlling for head length) in models increased predictive power; however, the highest-ranked model without RHW was

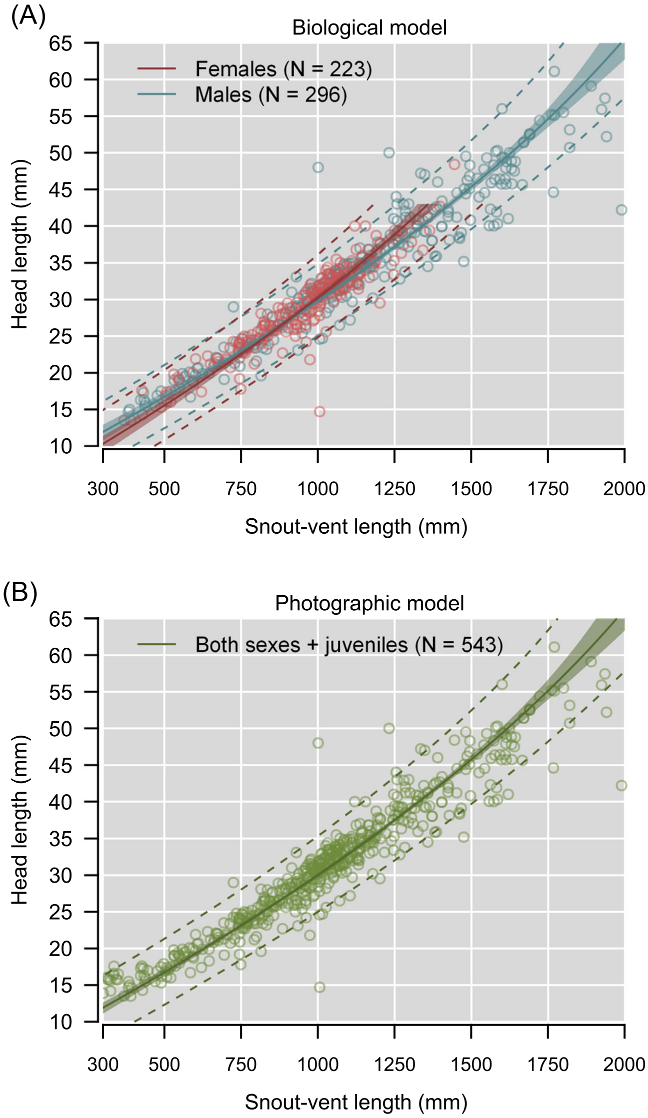

Figure 4. Linear regression predictions of brown treesnake snout-vent length as a function of head length. The biological model (A) includes all recorded predictor terms: head length and head length^2, relative head width (head length/head width), body condition index, sex, and a head length * sex interaction term. The prediction range for females is shorter because males grow much larger. The photographic model (B) includes only predictors that can be measured in camera images: head length, head length^2, and relative head width; data for this model include an additional 24 measurements of snakes too small to be sexed for the biological model. Circles represent individual measurements in the data set. Shaded areas around regression lines are 95% confidence intervals for the estimate (1.96*standard error), and dashed lines are 95% prediction intervals. Data were collected in Guam, USA, 2018–2020.

outperformed by the next higher-ranking model that included RHW by only 0.16 AIC$_c$ units and R^2 was not improved. With an R^2 of 83.8%, cautious estimation of body length from head width could be made if a suitable image of head length is not available. While the contributions of relative head width to predictive models were statistically significant, the improvement in R^2 by including RHW in the photographic model was negligible at 0.1%; if seeking to reduce animal handling, streamline data collection, and simplify predictive equations, head width measurements could be eliminated from field protocols.

Although all other potential predictors of body length were included in the top biological model (CI, SEX, and SEX*HL), their addition to the model reduced variance but did little to explain variation in snake length in meaningful terms. The slope of the regression line is slightly steeper for females than for males, indicating that female body length does not grow as quickly in relation to the head. This relationship could be interpreted as supporting speculation that females make less metabolic investment in increasing body length in favor of accumulating mass and-or energy stores for reproduction (Savidge 1991, Siers et al. 2017*b*). However, addition of SEX and HL*SEX increased R^2 by only 0.19%. Head images cannot be used to determine sex of the snake.

For simplicity, we recommend that brown treesnake body length predictions can be made from head length measurements ($HL + HL^2$) alone (Table S1). Although these values are predicted to 1 mm precision, Cundall et al. (2016) caution that the flexibility of anatomical elements of snakes and inherent imprecision in measurements within and among measurers and under varying specimen conditions (preserved, anesthetized, unanesthetized) indicate that there may be no true length of snakes. Such measurements are not repeatable with high precision, and Cundall et al. (2016) advocate for rounding off values or accepting that accurate length descriptions might require reporting means and standard deviations from multiple repeated measurements of the same individual. For most ecological inquiries, the reduction in precision will have little consequence.

If a size standard is included in the image at the same distance from the lens as the snake, brown treesnake size can be estimated from head images captured with wildlife cameras. Coupled with live lures, our methods can be used to describe size distributions of brown treesnakes and frequency of predation attempts, as estimated by contact rates, to evaluate the remaining predation threat where brown treesnake numbers have been suppressed through management efforts. Such data may be the most practical and direct information upon which to base decisions about whether suppression efforts have been effective enough to reintroduce native vertebrates that were extirpated by this harmful invasive predator. Similar methods may be applied for innumerable other study systems where direct physical measurements of wildlife are impractical or impossible.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1 provides a convenient lookup table for estimating brown treesnake length from head length, including 80% prediction intervals.