Manuscript Details

Manuscript number	ZOOL_2018_144_R2
Title	Extrinsic factors affecting cub development contribute to sexual size dimorphism in the European badger (Meles meles)
Article type	Research Paper

Abstract

Abstract Sexual size dimorphism (SSD) is common among mammals, with males typically being larger than females, as a product of sex-specific differences in growth rate and growth duration. The Musteloidea, however, exhibit a hypo-allometric reduction in SSD with increasing body size (contrary to Rensch's rule). A variety of extrinsic factors can affect juvenile growth rates and end body size, where one sex may demonstrate greater vulnerability than the other towards a specific factor, moderating patterns and degrees of SSD. Here, we analyse how male and female European badgers (Meles meles) differ in their somatic growth patterns. We compare the sex-specific growth curves across a range of somatic parameters and investigate what extrinsic (social and environmental) factors affect cub growth rates during the first 2 years of life leading to their sexual-dimorphic adult sizes. We found that average male final size of all measurements was significantly larger than those of females. Although male and female weanling cubs had similar body sizes, growth curves diverged significantly from ca. 11 months onwards due to continuous rapid growth of males versus slowing female growth. Consequently, females always concluded growth earlier than did males. In both sexes, extremities ceased to grow at an earlier age than did body length and zygomatic arch width. All badger cubs were impacted by their social environment as well as by weather conditions; however, male cubs were more sensitive to social factors, remaining smaller in social groups with more adult males present, whereas female final size was predominantly affected by weather and associated food availability. We discuss how extrinsic parameters can moderate patterns of SSD in the context of the differential equilibrium model.

Keywords	development; differential equilibrium model; skeletal measures; sexual size dimorphism; final size; growth patterns; weather
Manuscript category	Developmental Biology
Corresponding Author	Christina Bueschung
Corresponding Author's Institution	Wildlife Conservation Research Unit - Department of Zoology, University of Oxford
Order of Authors	Nadine Adrianna Sugianto, Chris Newman, David Macdonald, Christina Buesching
Suggested reviewers	Andrew Kitchener, Andrew Derocher, Alexander Badyaev

Submission Files Included in this PDF

File Name [File Type]

Response to the editors and reviewer comments.docx [Response to Reviewers]

Sugianto et al. Badger development and SSD - Highlights_edited.docx [Highlights]

Sugianto et al. Badger development and SSD revised resubmission edited ms.docx [Manuscript File]

Fig1.tif [Figure]

Fig2.tif [Figure]

Fig3.tif [Figure]

Fig4a.tif [Figure]

Fig4b.tif [Figure]

Fig4c.tif [Figure]

Fig4d.tif [Figure]

Fig4e.tif [Figure]

Fig1_blackandwhite.tif [Figure]

Fig2_blackandwhite.tif [Figure]

Fig3_blackandwhite.tif [Figure]

Fig4a_blackandwhite.tif [Figure]

Fig4b_blackandwhite.tif [Figure]

Fig4c_blackandwhite.tif [Figure]

Fig4d_blackandwhite.tif [Figure]

Fig4e_blackandwhite.tif [Figure]

To view all the submission files, including those not included in the PDF, click on the manuscript title on your EVISE Homepage, then click 'Download zip file'.

Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
Data will be made available on request

Zoology Editorial Office

27th April 2019

<u>*Re*: Sugianto *et al*.: Badger development and SSD correction of resubmission</u>

Dear Reviewer and Managing Editor of *Zoology*,
We would like to thank you for your additional comments and input that you have provided on our manuscript " Extrinsic factors affecting cub development contribute to sexual size dimorphism in the European badger (*Meles meles*)" by Nadine A. Sugianto, Chris Newman, David W. Macdonald, and Christina D. Buesching. We have addressed all reviewer suggestions corrections and implemented all comments from the copy editor. Below we list the specific changes we have made in response to the reviewer's suggestions and hope that you will find our manuscript now suitable for publication.

Best regards
Christina D. Buesching

Comments from the editors and reviewers:
-Editor

In the attached file, you will find some corrections and suggestions by the journal's copy-editor. Please finalize your manuscript accordingly.

We have implemented all comments and correction from the copy-editor

-Reviewer 1

- I do believe that the authors did a good job in revising their manuscript. I really like this study because it is based on a large amount of data, tackles an interesting question and is placed in the realms of classic behavioural ecology. There are only some details that I would like to bring to the author's attention.

1) It is stated several times that sexual selection drives the larger size of males. E.g.: «Sexual selection is generally proposed as the ultimate cause of SSD (Hoogland 2003; but see Isaac 2005), where larger males have an advantage when competing for mates, territories, and resources (e.g., Trivers 1972).» This is only true if sexual selection on males is stronger than fecundity selection on females (assuming that viability selection does not vary among sexes). This is one of the arguments of the differential equilibrium model and I think it would be good to follow this line of argumentation throughout.

Indeed, thanks for highlighting that we should explain this a bit better. As the reviewer states, we are focused here predominantly on the developmental and behavioural basis of how SSD arises in this species, rather than the underlying selection pressures that may cause it. Nevertheless, we incorporated this broader explanation of the differential pressures on selection in the Introduction and the Discussion.

We have thus rephrased the start of the Introduction as "SSD is common among mammals, where male size typically exceeds that of females (Badyaev 2002 Hoogland 2003; but see Isaac 2005) in species

where sexual selection on males is stronger than fecundity selection on females, in accord with the differential equilibrium model (assuming that viability selection does not vary among sexes; Blackenhorn 2005). Consequently, larger males have an advantage when competing for mates, territories, and resources (e.g., Trivers 1972)." *We have also added a sentence at the end of the first paragraph stating that fecundity selection is low in musteloids:* "Furthermore, neonates of musteloids are highly altricial and litter sizes tend to be small compared to most other carnivores (e.g., canids: see Ferguson and Lariviere 2005), reducing fecundity selection which might otherwise promote female size." *We also added in the second to last paragraph of the introduction* "and a mean litter size in our study population of 1.4 with a typical neonate birth weight of 110g (Macdonald & Newman 2017) as low fecundity conditions unlikely to drive female size selection."
To carry through this line of reasoning, we added in the fifth paragraph of the Discussion: "This is likely particularly important in species, such as badgers, where low fecundity selection on females will not drive female body-size up in opposition to sexual selection for (somewhat) larger body-size of males (differential equilibrium model of SSD: Blackenhorn 2005)." *and in the second to last paragraph of the Discussion* ", while the opposing force of fecundity selection (and viability selection; Blackenhorn 2005) is not not under suffient positive selection pressure to oppose this SSD in male size dominanted species".

2) Last line of first paragraph of introduction: I disagree with this statement in that it definitely should reduce the effect of PREcopulatory sexual selection but probably increases the intensity of POSTcopulatory sexual selection. This also applies to the second last paragraph of the discussion.

We agree with the reviewer and have made this clear in the revised version. We have thus rephrased as "Under these conditions, the optimal strategy for males of larger species tends not to involve defending access to multiple females, obviating any competitive advantage of relatively greater size, reducing the effect of pre-copulatory sexual selection pressure." in the introduction and in the discussion as "In addition, female mate selection is likely to be cryptic, e.g. through post-copulatory sperm competition …"

3) I like that it is now clear that the weather and social variables that are included have previously been shown to affect badger biology. However, it is still not immediately clear to me how the analyses were set up. Even though this is explicitly stated in the manuscript, as a reader without having seen the data, it is hard to grasp why all the predictors are uncorrelated. Were the number of male cubs and the number of female cubs within a social group really added simultaneously to the same model?

YES

If so, how come they are uncorrelated? Maybe I misunderstood the statistical procedure, but I would expect that the two variables are correlated in a species with a 50/50 sex ratio (at birth). Or is the lack of a correlation caused by the nested structure of setts and social groups and populations?

The 50/50 sex ratio is evident across our long-term dataset the whole population (see Dugdale et al. 2003 Ecology). Nevertheless, trapping, particularly of young cubs, is of course a random process and thus does not always return a 50/50 capture ratio of each cohort (particularly within one year). This is especially true when the number of captures is separated for each social group and sett; indeed there are some social groups/setts which show a strong (male or female) sex-bias, and might have only male (or female) cubs in a given year. Thus, the lack of a correlation is indeed caused to some degree by the nested statistical design, but predominantly also by trapping effects, which is already clarified in the text.

4) Similarly, some people might still argue that given the hierarchical social structure of setts, groups, cohorts and populations, one should somehow accommodate this in the analyses (either using random effects or nesting). It might be worth stating that adding populations as random effect did not change the results.

We are aware of this problem and tried to accommodate this as much as possible in our analyses. However, unfortunately, adding social group and sett as a random effects would require complete data points for each parameter tested (e.g., number of male and female cubs) in each social group and sett *per year, but - as we explained above - trapping is a random process and we may not always obtain badgers that cover all parameters we are interested in for each social group and sett for a given year (this does not mean the badger is not necessarily there, but just not trapped). Moreover, there are quite a lot of social groups/setts in comparison to the data points in the Y axis (e.g., 227 data points for body length derived from cubs belonging to 26 different social groups and 54 setts). Thus, it is unfortunately methodologically impossible to add social group and/ or sett as random effects in combination with year (already added as random effect). Instead we had opted to add, within each model, other parameters unique to (and thus differentiate for) social groups/ setts (such as number of male and female adults, number of male and female cubs). As this is already clarified in the text, we have kept the original description of the methods.*

5) the statement that SSD is defined as sex difference in skeletal size is still technically incorrect, also in mammals.

We have rephrased as "Sexual size dimorphism (SSD) is defined as differences in body size between males and females of the same species (Lammers et al., 2001; Badyaev 2002)…" Noting that we specify sexual SIZE dimorphism, specifically, rather than simple sexual dimorphism.

Highlights

- Mean skeletal measures developed to be larger in males than in females.
- Growth curves of males and females diverged from ca. 11 months onwards.
- Females consistently concluded skeletal growth earlier than males.
- In both sexes, extremities ceased to grow earlier than other somatic parameters, altering body proportions.
- Social factors predominantly affected male end size, whereas weather conditions predominantly affected females.

Extrinsic factors affecting cub development contribute to sexual size dimorphism in the European badger (*Meles meles*)

Sugianto N. A.[a], Newman, C.[a], Macdonald D.W.[a], Buesching C. D.[a*]

[a] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Abingdon Road, Tubney House, Tubney, Oxfordshire OX13 5QL, UK.

[*]Corresponding author: christina.buesching@zoo.ox.ac.uk

Abstract

Sexual size dimorphism (SSD) is common among mammals, with males typically being larger than females, as a product of sex-specific differences in growth rate and growth duration. The Musteloidea, however, exhibit a hypo-allometric reduction in SSD with increasing body size (contrary to Rensch's rule). A variety of extrinsic factors can affect juvenile growth rates and end body size, where one sex may demonstrate greater vulnerability than the other towards a specific factor, moderating patterns and degrees of SSD. Here, we analyse how male and female European badgers (*Meles meles*) differ in their somatic growth patterns. We compare the sex-specific growth curves across a range of somatic parameters and investigate what extrinsic (social and environmental) factors affect cub growth rates during the first 2 years of life leading to their sexual-dimorphic adult sizes. We found that average male final size of all measurements was significantly larger than those of females. Although male and female weanling cubs had similar body sizes, growth curves diverged significantly from ca. 11 months onwards due to continuous rapid growth of males versus slowing female growth. Consequently, females always concluded growth earlier than did males. In both sexes, extremities ceased to grow at an earlier age than did body length and zygomatic arch width. All badger cubs were impacted by their social environment as well as by weather conditions; however, male cubs were more sensitive to social factors, remaining smaller in social groups with more adult males present, whereas female final size was predominantly affected by weather and associated food availability. We discuss how extrinsic parameters can moderate patterns of SSD in the context of the differential equilibrium model.

Keywords: *development, differential equilibrium model, extrinsic factors, sexual size dimorphism, final size, growth patterns,weather.*

1. Introduction

Sexual size dimorphism (SSD) is defined as differences in body size between males and females of the same species (Lammers et al., 2001; Badyaev 2002). SSD is common among mammals, where male size typically exceeds that of females (Badyaev 2002 Hoogland 2003; but see Isaac 2005) in species where sexual selection on males is stronger than fecundity selection on females, in accord with the differential equilibrium model (assuming that viability selection does not vary among sexes; Blackenhorn 2005). Consequently, larger males have an advantage when competing for mates, territories, and resources (e.g., Trivers 1972). Rensch's rule states that, within an evolutionary lineage, SSD increases with mean body size in those taxa with larger males (note: when females are larger, SSD declines with increasing body size: Rensch 1959; Abouheif and Fairbairn, 1997). Nevertheless, not all taxa conform to this rule. For example, the Musteloidea demonstrate a hypo-allometry contrary to Rensch's rule, with less SSD associated with larger body size; although males are larger than females in this super-family (Noonan et al., 2016). Noonan et al. (2016) suggested that feeding ecology was pertinent to this aberrant pattern. Musteloid species with less carnivorous diets tend to form promiscuous social groups when the dispersion of alternative lower-energy food resources dictates (Macdonald and Johnson, 2015). Under these conditions, the optimal strategy for males of larger species tends not to involve defending access to multiple females, obviating any competitive advantage of relatively greater size, reducing the effect of pre-copulatory sexual selection pressure. Furthermore, neonates of musteloids are highly altricial and litter sizes tend to be small compared to most other carnivores (e.g., canids: see Ferguson and Lariviere 2005), reducing fecundity selection which might otherwise promote female size.

Diverging growth patterns (i.e., growth rate and/ or duration: Badyaev 2002) between males and females appear to be the primary physiological mechanism leading to SSD (Isaac 2005), and a variety of extrinsic factors likely affect juvenile growth rates and end body size in both sexes (Badyaev 2002). Typically, one sex will demonstrate a greater vulnerability to key socio-environmental factors than the other, moderating patterns and degrees of SSD (Leberg and Smith 1993; Post et al., 1999; Leblanc et al., 2001). For example, in white-tailed deer (*Odocoileus virginianus*; Leberg and Smith 1993) and bighorn sheep (*Ovis canadensis*; Leblanc et al., 2001) male juvenile development to adult size tends to be more sensitive to adverse social conditions than female development (such as high population density: Leberg and Smith 1993; Leblanc et al., 2001). In contrast, females are often more sensitive to adverse environmental factors, such as weather and food availability (e.g., red deer, *Cervus elaphus*: Post et al., 1999) and appear better able to compensate for poor early growth (Festa-Bianchet et al., 1994).

Due to the Mustelidae's SSD hypo-allometry (Noonan et al., 2016), SSD is lower in the European badger (*Meles meles*, henceforth 'badger') compared to other smaller, more carnivorous mustelids, with a typical badger male:female body mass ratio of 1.1:1 (Noonan et al., 2016), and a mean litter size in our study population of 1.4 with a typical neonate birth weight of 110g (Macdonald & Newman 2017) as low fecundity conditions unlikely to drive female size selection. Consequently, we predict that the development of SSD through juvenile development in badgers may be particularly sensitive to extrinsic factors, if one sex responds more to environmental versus social stressors. For instance, juvenile badger growth patterns and mortality rate are known to correlate negatively with aberrant weather conditions that influence food (mainly earthworm) supply (i.e., wetter or drier than average: Macdonald et al., 2010; Novellet et al., 2013) and density-dependent effects (Macdonald et al., 2002b), causing resource competition for food (Woodroffe and Macdonald 2000) and potentially driving infanticide (Woodroffe and Macdonald 1993).

Here, we investigate: i) how somatic growth patterns differ between males and females, comparing sex-specific growth curves across a range of somatic parameters during the first 2 years of life; ii) what extrinsic (social and environmental) factors affect male and female cub growth rates differentially during the first 2 years of life; and iii) how these parameters affect emergent patterns of adult sexual size dimorphism. We consider our findings in the context of counter-selection and the differential equilibrium model (Arak 1988) in this group-living promiscuous species without any clear mating hierarchy (Dugdale et al., 2011), where Noonan et al. (2016) proposed that natural selection pertaining to feeding ecology may off-set sexual selection for larger males (see Andersson 1994; Blackenhorn et al., 1995).

2. Material and Methods

2.1 Badger Trapping and Sampling

As part of an ongoing long-term research project, data were collected between 1995 and 2016 from a high-density badger population in Wytham Woods, Oxfordshire, UK (51^{o}46'26" N, 1^{o}19'19" W; for details see Macdonald et al., 2015). Following the methodology described in Sun et al. (2015), badgers were trapped three to four times annually: (1) in *spring* (May/June) (at the conclusion of a protective closed season during suckling and maternal care), when cubs were fully weaned, (2) in *summer* (July/August/September) during lowest food abundance, as cubs commence independent foraging, (3) in *autumn* (October/November) when badgers reach maximum body weight, and (4) in *winter* (January) during the main mating season, when ca. 43% of cubs achieve sexual maturity ('early-developers': Sugianto et al., 2019). Captured animals were transported to a central field station, before being sedated by intramuscular injection of 0.2 ml ketamine hydrochloride/ kg body weight (McLaren et al., 2005; Thornton et al., 2005). All badgers received a permanent unique tattoo, allowing individual identification (ID) and aging.

2.2 Body measurements

Following sedation, axial (head-body length [to the nearest 5mm]; zygomatic arch with [mm]), and appendicular measures (pastern length [mm, averaged between left and right foot], radius-ulna [mm, averaged between left and right], humerus [mm, averaged between left and right], tibia-patella [mm, averaged between left and right], patella-femur [mm, averaged between left and right], and tail length [mm]) were made using calipers. These measurements were taken on live animals; however, our choice of body metrics with minimal soft tissue coverage aimed to minimize risks of imprecision. All measurements were standardized and validated between data recorders; also by long-term staff present throughout all data recordings used.

2.3 Population density

Yearly population density was calculated from minimum number alive estimates from 1994 to 2016 (following Macdonald et al., 2009). The total number of badgers as well as the numbers of adult males, adult females, male cubs, and female cubs at each sett, social group, and in the total population were determined annually by assigning residency according to Annavi et al. (2014; see also Macdonald et al., 2008). Cases that were not addressed by either set of rules were accounted for in additional residency rules, given in Supplementary Material.

2.4 Weather data

Weather data (from 1994 to 2016) were obtained from the Environmental Change Network (ECN) data centre. A long-term seasonal trend from 1994 to 2016 (spring: March - May, summer: June - August, autumn: September - November, winter: December - February) for temperature (T, C°) and rainfall (RF, mm) was established. Seasonal mean T and seasonal mean RF were calculated for the six seasons a badger experiences between birth until reaching adult end size at 19 months: 1st spring, 1st summer, 1st autumn, 1st winter, 2nd spring, and 2nd summer. Weather metric deviation from the long-term mean (1995- 2016) for each season (6 seasons) was then applied to the global model, modifying Nouvellet et al. (2013).

2.5 Statistical analyses

2.5.1 Comparison of cub sizes at first capture (3-4 months of age)

To investigate differences in male and female cub morphometrics at first capture in spring (3-4 months of age), we constructed 2 linear models (NB, all datapoints were independent) with sex as predictor and somatic parameter groups (head body length, zygomatic arch width, mean pastern length for the 1st model and radius-ulna length, humerus length, tibia-patella length, patella-femur length, tail length for the 2nd model) as response, including year as covariate to account for inter-annual differences. These 2 groups represented different data sets (1st group 1995 – 2016; 2nd group 2016 only). We applied a principal component analysis (PCA) per group and used first PCA component to summarise growth trends within linear models.

2.5.2 Somatic growth curves

A non-linear mixed model using the nlme and sslogic function in R (producing a logistic growth curve and asymptote value: size = asym/[1+exp{xmid-age}/scal], where asym is the asymptote, xmid is the inflection point and scal is the inverse of the curve slope at xmid, which are all fitted coefficients; Caroli et al., 2010), including ID as a random effect (towards asym, and also xmid if the data permited), was used to analyse somatic parameters against age (in months). To determine at what age different measurements cease to increase (i.e., final growth), the percentage of the predicted value towards the asymptote was calculated. To investigate whether growth curves for a given somatic parameter differed between the sexes, a Maximum Likelihood (ML) test was conducted comparing the non-linear mixed model with and without sex as an independent variable. It is important to note that any averages presented may become more skewed by 'selective removal', where the surviving cub cohort sub-sample is likely to include an increasing proportion of larger, better quality individuals (e.g. Nussey et al., 2011).

2.5.3 Sexual size dimorphism in adults

Simimlar to the analyses conducted in weanlings, to investigate the difference in male and female adult final sizes (18 months above), 2 linear models (NB, all datapoints were independent) were conducted with sex as predictor and somatic parameter groups as response, again using a the 1st component of a PCA to summarise somatic parameters. Year was included as covariate to account for interannual differences.

2.5.4 Environmental effects on cub growth (global and sex-specific models)

The age when growth reached 99% of the asymptote value was assigned as the ‘final point’ of head body length and zygomatic arch width growth (the two measures used as responses in the global model because they were the main indicators of overall growth and development in cubs). Two global linear mixed models with head body length and zygomatic arch width (in badgers aged 19 months when all parameters reached end growth, males and females combined) as respective response variables were run against established predictors of cub health and survival (reviewed in Macdonald et al., 2015) predictors:

- sex,
- the numbers of male and female adults in the cub’s natal social group,
- male and female cubs in the natal group, male and female cubs in the natal sett,
- total adults in the population in the natal year,
- total number of cubs in the respective cohort, deviation of mean T from long term mean in the cubs’ first spring,
- deviation of mean T in first summer,
- deviation of mean T in autumn,
- deviation of mean T in winter,
- deviation of mean T in second spring,
- deviation of mean T in second summer,
- deviation of mean RF from longterm mean in first spring,
- deviation of mean RF in first summer,
- deviation of mean RF in autumn,
- deviation of mean RF in winter,
- deviation of mean RF in second spring, and
- deviation of mean RF in second summer.

Birth year was assigned as a random predictor to account for inter-annual effects. Similar

models were designed for males and females separately thereafter, but including only the significant parameters found in the respective global models above (where male and female data were combined).
Severity of the effects of each factor was judged on the basis of whether they affected both independent growth parameters (i.e., end head body length and zygomatic arch width), or only one parameter. Before any models were run, inter-correlation between continuous parameters was analysed using Pearson correlation tests. All parameters included in the global model were confirmed to be independent.

A drop1 function, giving a comparison of models based on their AIC criteria (i.e., testing whether or not the model excluding a given term was different from the model including that term), was used to determine which factors influenced final body length and final zygomatic arch width significantly for cubs at age 19 months in all models. Catagorization of results (i.e., significant parameters) from all global models elucidated which factors affected adult size in both sexes simultaneously and which factors were sex-specific. For each model, patterns of residuals, normality, and mean variance were checked using diagnostic plots in R. All statistical analyses were carried out using RStudio (0.99.896; RStudio Team 2015) and R (R-3.2.4; R Core Team 2016).

3. Results

3.1 Sexual size dimorphism at weaning

There was no evidence for SSD among weanlings (aged 3-4 months = first capture) for all parameters combined in model 1 and 2 (Table 1).

Table 1. Comparison of somatic parameters in weanling cubs at first capture aged of 3-4 months

Model 1

Combined parameters	PCA1 estimates at 3-4 months of age due to sex			
	% Variance explained by PCA1	n	F value	*p*
Head body length	82.54	501	$F_{1,498} = 0.785$	0.376
Zygomatic arch width				
Mean pastern length				

Model 2

Combined parameters	PCA1 estimates at 3-4 months of age due to sex			
	% Variance explained by PCA1	n	F value	*p*
Radius-ulna length	90.66	48	$F_{1,45} = 2.07$	0.157
Humerus length				
Tibia-patella length				
Patella-femur length				
Tail length				

3.2 Somatic growth curves

The axial skeletal growth curves for male and female head body length differed significantly (Table 2) with females reaching 99% of their end body length at 16 months of age, faster than males, which achieved 99% at 18 months. Although at age 3-4 months both males and females had similar body lengths (Table 1) and similarly rapid growth rates (parallel curves, 45.2 and 44.1 mm/months for males and females respectively; difference in growth rate was non-significant at 1.12 mm/month), female cub growth slowed earlier than male growth (at ca. 6 months; divergence of average line due to larger differences in growth rates of 2.57 mm/month), while males continued to grow rapidly until age ca. 11 months (after which growth rate differences decreased to 1.48 mm/month, and continued to decrease as both sexes slowly reached their final size). By 11 months of age, male and female body lengths diverged sufficiently for the confidence intervals between the two curves to cease to overlap (Fig. 1).

Figure 1

The growth curves for zygomatic arch width also differed significantly between the sexes (Table 2; Fig. 2) although both sexes attained 99% of the asymptote at age 19-20 months. Despite both sexes exhibiting similar widths at 3 months (Table 1), growth rates of males were always higher compared to females (4.14 and 2.25 mm/month respectively at age 3-5 months), resulting in divergent average growth curves at age 5 months. In females, zygomatic arch growth slowed at the age of 7 months, whereas male arches continued to grow rapidly until age 9 months. Zygomatic arch width diverged between the sexes (with confidence intervals no longer overlapping) at the age of 12 month (Fig. 2).

Figure 2

Mean pastern length growth curves also differed significantly between sexes (Table 2; Fig. 3) with males reaching 99% of the asymptote at age 9 months, whereas females reached 99% of the asymptote at age 7 months. Initial growth rates of both sexes (3-5 months) were similar, around 4 mm/month, although initial pastern size at of males at 3 months were slightly longer than that for females; Table 1). Growth in females slowed at 5 months while males continued to grow rapidly until 6 months, leading to a significant divergence in growth curves by 8 months (Fig. 3).

Figure 3

In males, radius-ulna length (Fig. 4a.), humerus length (Fig. 4b.), tibia patella length (Fig. 4c.) and patella-femur length (Fig. 4d.) reached 99% of final length at 13, 15, 18 and 16 months respectively, while in females, growth reached the 99% asymptote significantly earlier at 11,14,15 and 15 months, respectively. In contrast to other parameters, however, tail length (Fig. 4e.) reached 99% of the end length earlier in males (at 8 months) than in females (at 10 months), although end tail length did not differ between the sexes (Table 2).

Figure 4

3.3 Sexual size dimorphism in adult badgers

The asymptotes of the growth curves resulted in males achieving a significantly larger mean size than females in all skeletal measures except for tail length; that is, females have proportionately longer tails relative to their body size than do males (see Table 2 and Fig. 1-4).

Table 2. Comparison of somatic growth curves and asymptote value between adult males and females

Parameters	Asymptote value (mm)		Male and female growth curve difference statistics				
	Male	Female	n_{male}	n_{female}	X^2	Df	*p*
Head body length	**704.06**	**680.81**	**1368**	**1385**	**1076.759**	**10**	**<0.001**
Zygomatic arch width	**88.57**	**84.32**	**1223**	**1298**	**725.597**	**8**	**<0.001**
Mean pastern length	**100.95**	**97.73**	**1006**	**1120**	**95.620**	**8**	**<0.001**
Radius ulna	**113.89**	**109.64**	**101**	**75**	**42.688**	**8**	**<0.001**
Humerus	**119**	**115.01**	**101**	**75**	**37.551**	**8**	**<0.001**
Tibia-patella length	**107.92**	**102.55**	**101**	**74**	**12.751**	**8**	**0.005**

Patella-femur length	**117.19**	**114.44**	**101**	**74**	**7.481**	**8**	**0.006**
Tail length	145.97	146.01	95	62	1.854	8	0.603

Differences in adult end size due to sex

Model 1

Combined parameters	PCA1 estimates at adulthood due to sex			
	% Variance explained by PCA1	n	F value	*p*
Head body length	75.40	364	$F_{1,361} = 114.36$	<0.001
Zygomatic arch width				
Mean pastern length				

Model 2

Combined parameters	PCA1 estimates at adulthood due to sex			
	% Variance explained by PCA1	n	F value	*p*
Radius-ulna length	61.31	40	$F_{1,37} = 6.29$	0.017
Humerus length				
Tibia-patella length				
Patella-femur length				
Tail length				

3.4 Environmental factors affecting adult SSD

In addition to the sex effects described, final head body length (n=226; see Table 3) was also influenced significantly by population density and weather parameters, including number of cubs in the cohort, deviation of mean T in first spring, deviation of mean RF in first spring, deviation of mean RF in first summer, deviation of mean RF in autumn, deviation of mean RF in winter and deviation of mean RF in second summer.

Table 3. Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X^2, and *p*-value) of the global model with body length as response

Parameters	**Body length global model coefficients**			**Body length global model parameter significance**			
	Estimate	SE	t	DF	AIC	X^2	*p*
Global model					2162.2		
(Intercept)	685.974	20.156	34.03				
Sex	**14.158**	**4.056**	**3.49**	**1**	**2173**	**12.844**	**<0.001**

Male adults in natal social group	0.581	0.764	0.76	1	2161.1	0.893	0.345
Female adults in natal social group	-0.794	0.812	-0.98	1	2161.4	1.211	0.271
Male cubs in natal social group	1.838	2.358	0.78	1	2160.9	0.744	0.388
Female cubs in natal social group	-1.763	1.716	-1.03	1	2161.6	1.425	0.233
Male cubs in natal sett	-0.872	3.028	-0.29	1	2160.3	0.106	0.745
Female cubs in natal sett	0.023	2.347	0.01	1	2160.2	0.005	0.944
Total adults in natal population	0.128	0.105	1.22	1	2162.5	2.321	0.128
Total cubs in natal cohort	**-0.583**	**0.327**	**-1.78**	**1**	**2164.5**	**4.359**	**0.037**
Dev. of meanT in 1st spring	**8.764**	**4.975**	**1.76**	**1**	**2165.0**	**4.792**	**0.029**
Dev. of mean T in 1st summer	2.965	6.533	0.45	1	2160.5	0.282	0.596
Dev. of mean T in autumn	6.306	5.826	1.08	1	2161.7	1.525	0.217
Dev. of mean T in winter	2.082	6.348	0.33	1	2160.4	0.197	0.657
Dev. of mean T 2nd spring	1.918	4.122	0.47	1	2160.5	0.287	0.592
Dev. of mean T 2nd summer	-7.213	6.161	-1.17	1	2162.2	2.048	0.152
Dev. of mean RF in 1st spring	**21.047**	**11.255**	**1.87**	**1**	**2165.2**	**4.976**	**0.026**
Dev. of mean RF in 1st summer	**-30.241**	**9.395**	**-3.22**	**1**	**2175.3**	**15.1490**	**<0.001**
Dev. of mean RF in autumn	**-22.503**	**10.555**	**-2.13**	**1**	**2166.8**	**6.622**	**0.010**
Dev. of mean RF in winter	**-30.105**	**10.933**	**-2.75**	**1**	**2171.5**	**11.293**	**<0.001**
Dev. of mean RF in 2nd spring	-2.971	8.239	-0.36	1	2160.4	0.239	0.625
Dev. of mean RF in 2nd summer	**-16.950**	**8.692**	**-1.95**	**1**	**2166.0**	**5.860**	**0.015**

Note: Dev. = Deviation, T= Temperature, RF= Rain Fall. Threshold of significance is *p*<0.05. Significance based on drop 1 function

Final zygomatic arch width (n= 218; Table 4) was highly sexually-dimorphic, and was strongly affected by the number of adult males in the natal social group, total number of adults in the population, number of cubs in cohort, deviation of mean T in first spring, deviation of mean T in autumn, deviation of mean RF in first spring, deviation of mean RF in first summer, deviation of mean RF in autumn, deviation of mean RF in winter, and deviation of mean RF in second summer.

Table 4. Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X^2, and *p*-value) of the global model with zygomatic arch width as response

Parameters	**Zygomatic arch width global model coefficients**			**Zygomatic arch width global model parameter significance**			
	Estimate	SE	T	DF	AIC	X^2	*p*
Global model					1177.4		
(Intercept)	84.084	3.399	24.733				
Sex	**2.957**	**0.523**	**5.650**	**1**	**1206.6**	**31.202**	**<0.001**
Male adults in natal social group	**-0.206**	**0.095**	**-2.176**	**1**	**1179.7**	**4.354**	**0.037**
Female adults in natal social group	0.066	0.101	0.651	1	1175.6	0.189	0.664

Male cubs in natal social group	0.427	0.293	1.460	1	1178.0	2.615	0.106
Female cubs in natal social group	-0.144	0.215	-0.673	1	1176.4	1.007	0.316
Male cubs in natal sett	-0.522	0.383	-1.362	1	1177.4	2.055	0.152
Female cubs in natal sett	-0.187	0.303	-0.615	1	1175.6	0.251	0.616
Total adults in natal population	**0.026**	**0.018**	**1.430**	**1**	**1182.0**	**6.627**	**0.010**
Total cubs in natal cohort	**-0.101**	**0.056**	**-1.806**	**1**	**1184.5**	**9.074**	**0.003**
Dev. of mean T. in 1st spring	**1.236**	**0.871**	**1.418**	**1**	**1183.1**	**7.727**	**0.005**
Dev. of mean T in 1st summer	0.966	1.056	0.915	1	1177.1	1.726	0.189
Dev. of mean T in autumn	**1.604**	**0.989**	**1.622**	**1**	**1181.1**	**5.726**	**0.017**
Dev. of mean T in winter	-0.143	1.097	-0.130	1	1175.4	0.035	0.852
Dev. of mean T 2nd spring	0.068	0.717	0.095	1	1175.4	0.007	0.934
Dev. of mean T 2nd summer	0.059	1.053	0.057	1	1175.4	0.025	0.874
Dev. of mean RF in 1st spring	**2.881**	**1.895**	**1.520**	**1**	**1182.5**	**7.084**	**0.008**
Dev. of mean RF in 1st summer	**-4.604**	**1.588**	**-2.899**	**1**	**1195.9**	**20.552**	**<0.001**
Dev. of mean RF in autumn	**-2.101**	**1.779**	**-1.181**	**1**	**1179.5**	**4.167**	**0.041**
Dev. of mean RF in winter	**-3.643**	**1.858**	**-1.961**	**1**	**1187.6**	**12.193**	**<0.001**
Dev. of mean RF in 2nd spring	-0.093	1.469	-0.063	1	1175.4	0.017	0.896
Dev. of mean RF in 2nd summer	**-2.063**	**1.551**	**-1.330**	**1**	**1182.4**	**7.053**	**0.008**

Note: Dev. = Deviation, T= Temperature, RF= Rain Fall. Threshold of significance is $p<0.05$. Significance based on drop 1 function

In sex-specific models including all parameters that were significant in the global models above (Table 3 and 4), male body length (n = 108; Table 5) was affected significantly only by the numbers of male adults in the cub's natal social group, deviation of mean RF in first summer, and deviation of mean RF in winter; all of which had a negative effect on final body length. Male zygomatic arch width (n= 103; Table 5) was negatively affected by the number of male adults in the cub's natal social group, total number of cubs in the respective cohort, deviation of mean RF in first summer, deviation of mean RF in winter and deviation of mean RF in second summer, while there was a significant positive effect of deviation of mean temp in autumn. Total number of adults in the population in the birth year only approached significance, but was positively correlated with final zygomatic arch width.

Table 5. Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X^2, and *p*-value) of the male models with head body length and zygomatic arch width as response

Parameters	**Male body length model coefficients**			**Male body length model parameter significance**			
	Estimate	SE	t	DF	AIC	X^2	*p*
Male global model					1034.1		
(Intercept)	701.874	25.185	27.868				
Male adults in natal social group	**-2.167**	**0.967**	**-2.242**	**1**	**1037**	**4.960**	**0.026**

Total adults in natal population	0.104	0.145	0.721	1	1032.9	0.857	0.355
Total cubs in natal cohort	-0.407	0.369	-1.105	1	1034.1	2.046	0.153
Dev. of mean T. in 1st spring	-1.732	6.408	-0.27	1	1032.2	0.111	0.740
Dev. of mean T. in autumn	5.437	7.125	0.763	1	1033.1	0.988	0.320
Dev. of mean RF in 1st spring	2.543	11.239	0.226	1	1032.1	0.066	0.797
Dev. of mean RF in 1st summer	**-26.338**	**11.199**	**-2.352**	**1**	**1041**	**8.896**	**0.003**
Dev. of mean RF in autumn	-4.888	13.011	-0.376	1	1032.3	0.269	0.604
Dev. of mean RF in winter	**-25.257**	**12.533**	**-2.015**	**1**	**1038.5**	**6.452**	**0.011**
Dev. of mean RF in 2nd summer	-13.140	10.613	-1.238	1	1034.8	2.706	0.100

Parameters	**Male zygomatic arch model coefficients**			**Male zygomatic arch model parameter significance**			
	Estimate	SE	t	DF	AIC	X^2	*p*
Male global model					577.03		
(Intercept)	87.434	3.786	23.095				
Male adults in natal social group	**-0.309**	**0.130**	**-2.365**	**1**	**580.96**	**5.929**	**0.015**
Total adults in natal population	**0.024**	**0.022**	**1.063**	**1**	**578.06**	**3.032**	**0.082**
Total cubs in natal cohort	**-0.093**	**0.056**	**-1.667**	**1**	**580.14**	**5.112**	**0.024**
Dev. of mean T. in 1st spring	0.203	0.988	0.205	1	575.22	0.194	0.659
Dev. of mean T. in autumn	**1.935**	**1.078**	**1.796**	**1**	**580.41**	**5.384**	**0.020**
Dev. of mean RF in 1st spring	1.605	1.759	0.913	1	576.93	1.904	0.168
Dev. of mean RF in 1st summer	**-5.269**	**1.763**	**-2.989**	**1**	**588.81**	**13.786**	**<0.001**
Dev. of mean RF in autumn	-1.760	2.006	-0.877	1	576.7	1.672	0.196
Dev. of mean RF in winter	**-3.953**	**1.954**	**-2.023**	**1**	**582.73**	**7.699**	**0.006**
Dev. of mean RF in 2nd summer	**-3.237**	**1.697**	**-1.907**	**1**	**582.34**	**7.314**	**0.007**

Note: Dev. = Deviation, T= Temperature, RF= Rain Fall. Threshold of significance is $p<0.05$. Significance based on drop 1 function

Female body length (n = 118; Table 6), in contrast, was affected positively by numbers of male adults (i.e., negatively by the number of competing females) in the cub's natal social group, deviation of mean T in first spring and deviation of mean RF in first spring, while there were significant negative effects of deviation of mean RF in first summer, deviation of mean RF in autumn and deviation of mean RF in winter. Female zygomatic arch width (n = 115; Table 6) was affected positively by the total number of adults in the population in the birth year, deviation of mean T in first spring and deviation of mean RF in first spring, whereas significant negative effects related to the total number of cubs in the respective cohort, deviation of mean RF in first summer, deviation of mean RF in winter and deviation of mean RF in second summer.

Table 6. Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X^2, and *p*-value) of the female models with head body length and zygomatic arch width as response

Parameters	**Female body length model coefficients**			**Female body length model parameter significance**			
	Estimate	SE	T	DF	AIC	X^2	*p*
Female global model					1115.6		
(Intercept)	665.558	20.284	32.81				
Male adults in natal social group	**2.183**	**0.779**	**2.8**	**1**	**1122**	**8.355**	**0.004**
Total adults in natal population	0.087	0.105	0.83	1	1114.4	0.754	0.385
Total cubs in natal cohort	-0.248	0.314	-0.79	1	1114.3	0.686	0.407
Dev. of mean T. in 1st spring	**12.089**	**4.427**	**2.73**	**1**	**1121.6**	**7.950**	**0.005**
Dev. of mean T. in autumn	1.074	5.390	0.2	1	1113.7	0.044	0.834
Dev. of mean RF in 1st spring	**26.724**	**8.935**	**2.99**	**1**	**1123.1**	**9.474**	**0.002**
Dev. of mean RF in 1st summer	**-25.424**	**8.036**	**-3.16**	**1**	**1124.2**	**10.551**	**0.001**
Dev. of mean RF in autumn	**-31.128**	**8.907**	**-3.49**	**1**	**1126**	**12.371**	**<0.001**
Dev. of mean RF in winter	**-24.227**	**9.636**	**-2.51**	**1**	**1120.4**	**6.773**	**0.009**
Dev. of mean RF in 2nd summer	-8.300	7.766	-1.07	1	1114.9	1.253	0.263

Parameters	**Female zygomatic arch model coefficients**			**Female zygomatic arch model parameter significance**			
	Estimate	SE	t	DF	AIC	X^2	*p*
Female global model					584.24		
(Intercept)	83.033	2.478	33.51				
Male adults in natal social group	-0.001	0.089	-0.01	1	582.24	0.003	0.953
Total adults in natal population	**0.025**	**0.013**	**1.95**	**1**	**587.01**	**4.778**	**0.029**
Total cubs in natal cohort	**-0.088**	**0.038**	**-2.3**	**1**	**589.69**	**7.453**	**0.006**
Dev. of mean T. in 1st spring	**1.542**	**0.572**	**2.69**	**1**	**592.01**	**9.775**	**0.002**
Dev. of mean T. in autumn	0.716	0.662	1.08	1	583.88	1.642	0.200
Dev. of mean RF in 1st spring	**2.611**	**1.134**	**2.3**	**1**	**589.25**	**7.016**	**0.008**
Dev. of mean RF in 1st summer	**-3.784**	**1.049**	**-3.61**	**1**	**597.38**	**15.143**	**<0.001**
Dev. of mean RF in autumn	-1.485	1.138	-1.31	1	584.56	2.330	0.127
Dev. of mean RF in winter	**-3.631**	**1.220**	**-2.98**	**1**	**593.66**	**11.423**	**0.001**
Dev. of mean RF in 2nd summer	**-1.534**	**1.003**	**-1.53**	**1**	**585.84**	**3.609**	**0.057**

Note: Dev. = Deviation, T= Temperature, RF= Rain Fall. Threshold of significance is $p<0.05$. Significance based on drop 1 function

Consequently, in both sexes, deviation of mean RF in the first summer and winter had a significant negative effect on both end body length and zygomatic arch width (axial morphometrics). Zygomatic width arch was additionally affected negatively by the total number of cubs in the respective natal cohort and deviation of mean RF in their 2nd summer; while surprisingly, the total number of adults in the population had a positive effect (Table 7).

Some effects, however, were sex-specific: male body length and zygomatic arch width was affected negatively by the number of male adults in the social group, whereas in females body length was affected positively by the number of adult males in social group. Similarly, deviation of mean T in autumn correlated positively with zygomatic arch width in males, whereas in females, deviation in RF and T in first spring had a positive effect on both body length and zygomatic arch width.

Table 7. Combined results of significant parameters in body length and zygomatic arch global and sex specific models.

Factors	**BL (Global)**	**BL (Male)**	**BL (Female)**	**ZA (Global)**	**ZA (Male)**	**ZA (Female)**
Sex	✓			✓		
Male adults in natal social group		-	+	-	-	
Total adults in natal population				+	+	+
Total cubs in natal cohort	-			-	-	-
Dev. of mean T. in 1st spring	+		+	+		+
Dev. of mean T. in autumn				+	+	
Dev. of mean RF in 1st spring	+		+	+		+
Dev. of mean RF in 1st summer	-	-	-	-	-	-
Dev. of mean RF in autumn	-		-	-		
Dev. of mean RF in winter	-	-	-	-	-	-
Dev. of mean RF in 2nd summer	-			-	-	-

General factors affecting body size for both male and female (both global and sex specific models)		
Both BL and ZA	**BL only**	**ZA only**
Dev. of mean RF in 1st summer (-)	None	Total adults in natal population (+)
Dev. of mean RF in winter (-)		Total cubs in natal cohort (-)
		Dev. of mean RF in 2nd summer (-)

Sex specific factors affecting body size (for both BL and ZA)	
Male only	**Female only**
Male adults in natal social group (-)	Dev. of mean T. in 1st spring (+)
	Dev. of mean RF in 1st spring (+)

Other sex specific factors affecting body size (BL only or ZA only)	
Male only	**Female only**
Dev. of mean T. in autumn (ZA, +)	Male adults in natal social group (BL, +)
	Dev. of mean RF in autumn (BL, -)

Note: BL = Head body length, ZA = Zygomatic arch

4. Discussion

Although musteloids exhibit a hypo-allometric SSD contrary to Rensch's rule (Rensch 1959), and SSD is relatively small in adult badgers (Noonan et al., 2016), we quantified that average male measurements were significantly larger than those of females, with inter-sexual differences greatest in head-body length (3.4%) and zygomatic arch width (5%). Only tail length was an exception, which showed high inter-individual variation (which, combined with pelage variation, can enable observers to recognise individual badgers: Dixon 2003). This mirrors results from previous studies on canine teeth measurements in badgers (male canines are approx. 10% bigger than those of females: Johnson and Macdonald 2001), and cranial characteristics, where males had larger skulls than did females (Harmsen and Van Bree 1998; Abramov and Puzachenko 2005).

We established that this adult SSD arose in badgers through divergent growth patterns, congruent with reports for other species (Badyaev 2002; Isaac 2005). Although weanling cub (3-4 months of age) size did not differ between the sexes, skeletal growth curves diverged significantly beyond age 11 months (i.e., the onset of puberty: Sugianto et al., 2019). This was due to the continuing rapid growth of males versus slowing female growth rate. Divergent growth patterns between the sexes are triggered in mammals by the rapid onset of sex-steroid effects during puberty that induce the release of sex-specific growth hormones (GH: Badyaev 2002). Oestrogens trigger elevated basal GH levels in females and testosterone stimulates high level GH pulses causing rapid growth rates typical for males (e.g., rats: Painson et al 2000). As a result, the average age when mammals exhibit diverging sexually dimorphic somatic growth rates is an indicator for the onset of puberty and can be used to estimate sexual maturity (Gatford et al., 1998; Potau et al., 1999; Painson et al., 2000).

For the majority of measurements, female cubs reached the end of their growth phase (i.e., the asymptote of the respective growth curve) between ages 7 (mean pastern length) to 16 months (head body length), whereas males continued to grow for 1-2 months more until age 8 (mean pastern length) – 18 months (head body length). Among carnivores, similar prolonged growth patterns in males have also been documented in sea otters (*Enhydra lutris*: Bodkin et al., 1993) and in polar bears (*Ursus maritimus*: Derocher et al., 2002) where males reach 97% of their asymptotic body length at 6.2 years, whereas females cease to grow significantly earlier at 4.4 years-of-age. Even in the most sexually dimorphic mammals, however, SSD at birth is low (although often measurable: Derocher et al., 2002), and in many species dimorphism only becomes apparent during juvenile development (e.g., giant panda, *Ailuropoda melanoleuca*, at 4 months: Peng et al., 2001; polar bear, at the end of their first year of life: Derocher et al., 2005), with maternal investment in male offspring being typically higher than that in female offspring (Clutton-Brock et al., 1985; badgers: Dugdale et al., 2003).

In both sexes, limbs (appendicular skeleton) ceased to grow at an earlier age than body length and zygomatic arch width (axial skeleton). As badger cubs reach independence from lactation at around 15 weeks (usually in July: Fell et al., 2006), they must forage for their own food where relatively longer limbs may enable more energetically efficient movement (Pontzer 2012). In addition, (perceived) body size is important in intra-specific (e.g., badgers: Stewart et al., 1999, but see Macdonald et al., 2002b) as well as inter-specific aggressive encounters (Marti et al., 1993; Memmott et al., 2000; Carbone et al., 1999), where badger cubs stand on tip-toe and raise their hackles when encountering potential predators (Roper 2010). As badger cubs are vulnerable to infanticide by conspecifics (Woodroffe and Macdonald 1993) as well as being killed by foxes in the UK (Macdonald et al., 2004; Roper 2010) and other large carnivores in continental Europe (Shaparev 1977; Olsson et al., 1997; Jedrzejewska and Jedrzejewski 1998), longer extremities likely help to project a larger, more fearsome opponent (Blanckenhorn 2000).

Larger body size and the necessary prolonged and/ or rapid growth to achieve it are associated with higher energy requirements (Blanckenhorn 2000). The availability of nutrients that fluctuate with weather conditions as well as population (group, or cohort) density can therefore significantly affect mammalian growth patterns (Mahoney et al., 2001, Eifler et al., 2003). Young badger cubs experience a wide variety of developmental stressors, but especially inclement weather, which exacerbates the impact of endoparasistic gut parasites (*Eimeria melis*, causing coccidiosis) and typically impair their growth, or lower their probability of survival (Newman et al., 2001; Macdonald and Newman 2002; Echols et al., 2004; Macdonald et al., 2010; Nouvellet et al., 2013; Macdonald et al., 2015). Because the metabolic rate of cubs is higher than that of adults due to rapid growth and scale allometries (McClune et al., 2015), any exposure to adverse environmental conditions during this developmental period may impact growth rate causing smaller final body size (Ferguson and McLoughlin 2000; Derocher and Wiig 2002; Mowart and Heard 2006). We found that both prevailing weather and social factors affected end head body length and zygomatic arch width. In terms of weather, high rainfall during their first summer and winter had the most severe effects on both sexes, while effects of high rainfall during their second summer were less severe, due to cubs being closer to reaching their final somatic size. Persistently wet conditions expose cubs to greater hypothermic stress (Kaneko et al., 2010; Nouvellet et al., 2013; Tsunoda et al., 2018), where survival probability and recruitment are lower in years that are wetter than normal (Newman et al., 2001; Nouvellet et al., 2013; Macdonald et al., 2015), particularly when summer flooding occurs (Macdonald and Newman 2002; Macdonald et al., 2010). Weather conditions, especially during the first spring, do not only affect cubs directly, however, but also lactating mothers. Badger milk is very high in fat (Roper et al., 2010), lactation is very energetically demanding (Woodroffe and Macdonald 1995; McClune et al., 2015), and suckling continues until weaning in early to mid-May (approx. 3 months of age; i.e. time of first capture in our study; Fell et al., 2006). Consequently, poor early life conditions can influence the weanling size of both sexes. This is likely particularly important in species, such as badgers, where low fecundity selection on females will not drive female body-size up in opposition to sexual selection for (somewhat) larger body-size of males (differential equilibrium model of SSD:Blackenhorn 2005). In comparison, more rapid growth in brown bear (*Ursus arctos*) and polar bear (*Ursus maritimus*) cubs is associated with higher quality and quantity of milk produced by mothers in better body condition (Robbins et al., 2012).

In addition, social factors also affected male and female growth patterns: Head body length and zygomatic arch width were affected negatively by the number of cubs in the cohort, mirroring the results of Macdonald et al. (2002b) and Delahay et al. (2006) that showed an increase in group size could have negative effects on badger growth. Similarly, in the Ursidae, body-size is often linked to population density, where a higher population density typically results in smaller adult size (Hilderbrand et al., 1999; Ferguson and McLoughlin 2000; Derocher et al., 2002); and, in brown bears, cub-cub resource competition, rather than cub-adult competition, has been suggested as the causal mechanism to explain why average cub size is smaller among bigger cohorts (Dahle et al., 2006).

Importantly, we also discovered a differential impact of environmental factors on growth rates between the sexes (Leberg and Smith 1993; Post et al., 1999; Leblanc et al., 2001):

Although all badger cubs were influenced by their social environment as well as by weather factors, based on the severity of these effects, we found that male cubs were more sensitive to social factors, remaining smaller in social groups with more adult males. In contrast, female end size was affected predominantly by prevailing weather and associated food availability.

Similar patterns have been reported for other mammal species, where male adult size has been shown to be more sensitive to social factors, such as population density (e.g., Leberg and Smith 1993; Leblanc et al., 2001), whereas females are more sensitive to environmental factors, such as weather and food availability (e.g., Post et al., 1999; Atkinson et al., 1996), rather than social factors (Leberg and Smith 1993; Leblanc et al., 2001). For comparison , in big horn sheep *Ovis canadensis* (Leblanc et al., 2001) and white tail deer *Odocoileus virginianus* (Leberg and Smith 1993), population density correlates negatively with body mass in both sexes, but the effect is significantly larger in males than in females, resulting in less SSD at higher population density. This sensitivity of male offspring towards social factors is likely due to their prolonged growth period, that facilitates compensation for shorter-term factors such as adverse weather, but not for long-term adverse social conditions (Leblanc et al., 2001; Festa-bianchet et al., 1994), whereas females lack the ability to compensate for short-term adverse weather effects, due to their shorter growth periods, but are less affected by long-term effects. This prolonged growth in males often results in considerable inter-individual differences in attaining key developmental life stages (Metcalfe and Monaghan 2001), such as puberty/ sexual maturity (Morgan and Metcalfe 2001; Plaistow et al., 2004; Freetly et al., 2011; Alberts 2012; Pusey 2012; Sugianto et al., 2019) and growth cessation (Morgan and Metcalfe 2001).

Previously, sexual selection has provided the dominant explanation for male-biased sexual size dimorphism in mammals (Mueller, 1990; Karubian and Swaddle 2001; but see Lammers et al., 2001). This is mainly because larger males are assumed to have a competitive advantage in mate competition (Hirotani 1994; Howard et al., 1998; Wong and Candolin 2005) and mate attraction (Hirotani 1994), while the opposing force of fecundity selection (and viability selection; Blackenhorn 2005) is not not under suffient positive selection pressure to oppose this SSD in male size dominanted species. Badgers, however, are highly promiscuous (Dugdale et al., 2007) without a clear dominance hierarchy governing mating patterns (Macdonald et al., 2002a; Yamaguchi et al., 2006; Dugdale et al., 2011), and reproductive suppression / failure among females is likely because while all mature females are observed mating only ca. 45.2% of adult females are assigned young each year (Annavi et al., 2014) and infanticide occurs (Woodroffe and Macdonald 1993). In addition, female mate selection is likely to be cryptic, e.g. through post-copulatory sperm competition (Chapman et al., 2003; Wolff and Macdonald 2004; Yamaguchi et al., 2006) and/ or induced ovulation (Yamaguchi et al., 2006). Under these circumstances of low male-male competition and heightened female-female competition, female body size would be expected to be important. This is consistent with the 'Ghiselin—Reiss small-male hypothesis' for the evolution of SSD (Blanckenhorn et al., 1995), where mating systems dominated by scramble competition result in male breeding success being predominantly a function of opportunity, where Annavi et al. (2014) concluded that encounter rate among badgers accounted for mate choice more parsimoniously than any directed selection for genetic traits. Similarly, according to Noonan et al.'s (2016) interpretation of the mustelid Rensch anomally being the product of resource dispersion and feeding ecology, the Ghiselin—Reiss small-male hypothesis proposes that small males may be favoured when food is limiting because they require lower absolute amounts of food.

Ultimately, male-biased sexual size dimorphism in badgers will be subject to phylogenetic inertia, where smaller mustelids benefit from substantial male-biased SSD (Noonan et al., 2016). We expose here, however, that the differential effects of social factors and weather influence juvenile growth patterns in badgers, and plausibly therefore in other carnivore species, and can modify end body sizes and the extent of SSD. As a consequence, SSD may be influenced by population changes / exploitation and/or climate change (Post et al., 1999; Høye et al., 2009).

Acknowledgements

NAS was supported by a DPhil scholarship from LPDP-Indonesia (Indonesia Endowment Fund for Education) 2014-2018, and CDB was supported by a Research Fellowship from the Poleberry Foundation. All animal handling protocols and procedures were approved by the Animal Welfare and Ethical Review board of Oxford University's Zoology Department and conducted under the Animals (Scientific Procedures) Act, 1986 (current PPL: 30/3379) and Natural England licenses (currently 2018-34017-Sci-Sci).

Declarations of interest: none

References

Abouheif, E., Fairbairn, D. J., 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. Am. Nat. 149(3), 540-562.

Abramov, A. V., Puzachenko, A. Y., 2005. Sexual dimorphism of craniological characters in Eurasian badgers, *Meles spp*.(*Carnivora, Mustelidae*). Zool. Anz.-A Journal of Comparative Zoology 244(1), 11-29.

Alberts SC, 2012. Magnitude and sources of variation in male reproductive performance, In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds.), The Evolution of Primate Societies. University of Chicago Press, pp 412-431.

Andersson, M. B. 1994. Sexual Selection. Princeton University Press.

Annavi, G., Newman, C., Dugdale, H. L., Buesching, C. D., Sin, Y. W., Burke, T., Macdonald, D. W., 2014. Neighbouring-group composition and within-group relatedness drive extra-group paternity rate in the European badger (*Meles meles*). J. Evol. Biol. 27(10), 2191-2203.

Anwar, M. A., Newman, C., MacDonald, D. W., Woolhouse, M. E. J., Kelly, D. W., 2000. Coccidiosis in the European badger (*Meles meles*) from England, an epidemiological study. Parasitology, 120(3), 255-260.

Arak, A. 1988: Sexual dimorphism in body size: a model and a test. Evolution 42, 820—825.

Atkinson, S. N., Stirling, I., Ramsay, M. A., 1996. Growth in early life and relative body size among adult polar bears (*Ursus maritimus*). J. Zool., 239(2), 225-234.

Badyaev, A. V., 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends Ecol. Evol., 17(8), 369-378.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology, 111(11), 977-1016.

Blanckenhorn, W. U., Preziosi, R. F., & Fairbairn, D. J. 1995. Time and energy constraints and the evolution of sexual size dimorphism—to eat or to mate?. Evol. Ecol., 9(4), 369-381.

Blanckenhorn, W. U., Mühlhäuser, C., Morf, C., Reusch, T., & Reuter, M. 2000. Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. Ethology, 106(7), 577-593.

Bodkin, J. L., Mulcahy, D., Lensink, C. J., 1993. Age-specific reproduction in female sea otters (*Enhydra lutris*) from south-central Alaska: analysis of reproductive tracts. Can. J. Zool., 71(9), 1811-1815.

Carbone, C., Mace, G. M., Roberts, S. C., Macdonald, D. W., 1999. Energetic constraints on the diet of terrestrial carnivores. Nature, 402(6759), 286.

Caroli, A., Frisoni, G. B., & Alzheimer's Disease Neuroimaging Initiative. 2010. The dynamics of Alzheimer's disease biomarkers in the Alzheimer's Disease Neuroimaging Initiative cohort. Neurobiol. Aging, 31(8), 1263-1274.

Chapman, T., Arnqvist, G., Bangham, J., Rowe, L., 2003. Sexual conflict. Trends Ecol. Evol., 18(1), 41-47.

Clutton-Brock, T. H., Albon, S. D., Guinness, F. E., 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature, 313(5998), 131.

Dahle, B., Zedrosser, A., Swenson, J. E., 2006. Correlates with body size and mass in yearling brown bears (*Ursus arctos*). J. Zool., 269(3), 273-283.

Delahay, R. J., Carter, S. P., Forrester, G. J., Mitchell, A., Cheeseman, C. L., 2006. Habitat correlates of group size, bodyweight and reproductive performance in a high-density Eurasian badger (*Meles meles*) population. J. Zool., 270(3), 437-447.

Derocher, A. E., Wiig, Ø., 2002. Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. J. Zool., 256(3), 343-349.

Derocher, A. E., Andersen, M., Wiig, Ø., 2005. Sexual dimorphism of polar bears. J. Mammal., 86(5), 895-901.

Derocher, A. E., Wiig, Ø., Andersen, M., 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. Polar Biol., 25(6), 448-452.

Dixon, D. R., 2003. A non-invasive technique for identifying individual badgers *Meles meles*. Mammal Rev., 33(1), 92-94.

Dugdale, H. L., Macdonald, D. W., Newman, C., 2003. Offspring sex ratio variation in the European badger, *Meles meles*. Ecology, 84(1), 40-45.

Dugdale, H. L., Macdonald, D. W., Pope, L. C., Burke, T., 2007. Polygynandry, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. Mol. Ecol., 16(24), 5294-5306.

Dugdale, H.L., Griffiths, A., Macdonald, D.W., 2011. Polygynandrous and repeated mounting behaviour in European badgers, Meles meles. Anim. Behav., 82(6), pp.1287-1297.

Echols, K. N., Vaughan, M. R., Moll, H. D., 2004. Evaluation of subcutaneous implants for monitoring American black bear cub survival. Ursus, 15(2), 172-181.

Eifler, M. A., Slade, N. A., Doonan, T. J., 2003. The effect of supplemental food on the growth rates of neonatal, young, and adult cotton rats (*Sigmodon hispidus*) in northeastern Kansas, USA. Acta. Oecol., 24(4), 187-193.

Fell, R. J., Buesching, C. D., Macdonald, D. W., 2006. The social integration of European badger (*Meles meles*) cubs into their natal group. Behaviour, 143(6), 683-700.

Ferguson, S., & Larivière, S. 2005. Is mustelid life history different?. In Martens and Fishers (Martes) in Human-Altered Environments. Springer, Boston, MA, pp. 3-20.Ferguson, S. H., McLoughlin, P. D., 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography, 23(2), 193-200.

Festa-Bianchet, M., Jorgenson, J. T., WUhart, W. D., 1994. Early weaning in bighorn sheep, *Ovis canadensis* affects growth of males but not of females. Behav. Ecol., 5(1), 21-27.

Freetly, H. C., Kuehn, L. A., Cundiff, L. V., 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. J. Anim. Sci., 89(8), 2373-2379.

Harmsen, B. J., Van Bree, P. J. H., 1998. On the presence of first premolars in skulls of badgers, *Meles meles* (Linnaeus, 1758), mainly from the Netherlands. Beaufortia, 48(8), 163-171.

Hilderbrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M., Servheen, C. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can. J. Zool., 77(1), 132-138.

Hirotani, A., 1994. Dominance rank, copulatory behaviour and estimated reproductive success in male reindeer. Anim. Behav., 48(4), 929-936.

Hoogland, J. L., 2003. Sexual dimorphism of prairie dogs. J. Mammal., 84(4), 1254-1266.

Howard, R. D., Martens, R. S., Innis, S. A., Drnevich, J. M., Hale, J., 1998. Mate choice and mate competition influence male body size in Japanese medaka. Anim. Behav., 55(5), 1151-1163.

Høye, T. T., Hammel, J. U., Fuchs, T., & Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. Biol. Letters, *5*(4), 542-544.

Isaac, J. L., 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mamm. Rev., 35(1), 101-115.

Jedrzejewska, B., Jedrzejewski, W., 1998. Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study. Ecol. Stud. 135. Springer-Verlag, Berlin, Heidelberg, and New York

Johnson, D. D., Macdonald, D. W., 2001. Why are group-living badgers (*Meles meles*) sexually dimorphic?. J. Zool., 255(2), 199-204.

Kaneko, Y., Newman, C., Buesching, C. D., Macdonald, D. W., 2010. Variations in badger (*Meles meles*) sett microclimate: differential cub survival between main and subsidiary setts, with implications for artificial sett construction. Int. J. Ecol., 2010.

Karubian, J., Swaddle, J. P., 2001. Selection on females can create 'larger males'. Proc. R. Soc. Lond. [Biol], 268(1468), 725-728.

Lammers, A. R., Dziech, H. A., German, R. Z., 2001. Ontogeny of sexual dimorphism in *Chinchilla lanigera* (*Rodentia: Chinchillidae*). J. Mammal., 82(1), 179-189.

Leberg, P. L., Smith, M. H., 1993. Influence of density on growth of white-tailed deer. J. Mammal., 74(3), 723-731.

LeBlanc, M., Festa-Bianchet, M., Jorgenson, J. T., 2001. Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. Can. J. Zool., 79(9), 1661-1670.

Macdonald, D. W., Newman, C., 2002. Population dynamics of badgers (*Meles meles*) in Oxfordshire, UK: numbers, density and cohort life histories, and a possible role of climate change in population growth. J. Zool., 256(1), 121-138.

Macdonald, D. W., Newman, C., 2017. Musteloid sociality: the grass-roots of society. In: Biology and Conservation of Musteloids. Macdonald, D.W., Newman, C. Harrington, L.A. Eds. Oxford University Press, pp. 167-188.

Macdonald, D. W., Buesching, C. D., Stopka, P., Henderson, J., Ellwood, S. A., Baker, S. E., 2004. Encounters between two sympatric carnivores: red foxes (*Vulpes vulpes*) and European badgers (*Meles meles*). J. Zool., 263(4), 385-392.

Macdonald, D.W., Johnson, D.D.P., 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. J. Zool., 295(2), pp.75-107.

Macdonald, D. W., Newman C., Buesching, C. D., 2015. Badgers in the rural landscape–conservation paragon or farmland pariah: Lessons from the Wytham badger project. In: Wildlife Conservation on Farmland Volume 2: Conflict in the Countryside. Macdonald, D.W., Feber, R. E. Eds. Oxford University Press, pp. 65-95.

Macdonald, D. W., Newman, C., Buesching, C. D., Johnson, P. J., 2008. Male-biased movement in a high-density population of the Eurasian badger (*Meles meles*). J. Mammal., 89(5), 1077-1086.

Macdonald, D. W., Newman, C., Buesching, C. D., Nouvellet, P., 2010. Are badgers 'Under the Weather'? Direct and indirect impacts of climate variation on European badger (*Meles meles*) population dynamics. Glob. Change Biol., 16(11), 2913-2922.

Macdonald, D. W., Newman, C., Nouvellet, P. M., Buesching, C. D., 2009. An analysis of Eurasian badger (*Meles meles*) population dynamics: implications for regulatory mechanisms. J. Mammal., 90(6), 1392-1403.

Macdonald, D. W., Newman, C., Stewart, P. D., Domingo-Roura, X., Johnson, P. J., 2002b. Density - dependent regulation of body mass and condition in badgers (*Meles meles*) from Wytham Woods. Ecology, 83(7), 2056-2061.

Macdonald, D. W., Stewart, P. D., Johnson, P. J., Porkert, J., Buesching, C., 2002a. No evidence of social hierarchy amongst feeding badgers, *Meles meles*. Ethology, 108(7), 613-628.

Mahoney, S. P., Virgl, J. A., Mawhinney, K., 2001. Potential mechanisms of phenotypic divergence in body size between Newfoundland and mainland black bear populations. Can. J. Zool., 79(9), 1650-1660.

Marti, C. D., Steenhof, K., Kochert, M. N., Marks, J. S., 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. Oikos, 6-18.

McClune, D. W., Kostka, B., Delahay, R. J., Montgomery, W. I., Marks, N. J., Scantlebury, D. M., 2015. Winter is coming: seasonal variation in resting metabolic rate of the European badger (*Meles meles*). PloS one, 10(9), e0135920.

McLaren, G. W., Thornton, P. D., Newman, C., Buesching, C. D., Baker, S. E., Mathews, F., Macdonald, D. W., 2005. The use and assessment of ketamine–medetomidine–butorphanol combinations for field anaesthesia in wild European badgers (*Meles meles*). Vet. Anaesth. Analg., 32(6), 367-372

Memmott, J., Martinez, N. D., Cohen, J. E., 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. J. Animal Ecol., 69(1), 1-15.

Metcalfe, N. B., Monaghan, P., 2001. Compensation for a bad start: grow now, pay later?. Trends Ecol. Evol., 16(5), 254-260.

Morgan, I. J., Metcalfe, N. B., 2001. Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. Proc. R. Soc. Lond. [Biol], 268(1464), 295-301.

Mowat, G., Heard, D. C., 2006. Major components of grizzly bear diet across North America. Can. J. Zool., 84(3), 473-489.

Mueller, H. C., 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. Biol. Rev., 65(4), 553-585.

Newman, C., Macdonald, D. W., Anwar, M. A., 2001. Coccidiosis in the European badger, *Meles meles* in Wytham Woods: infection and consequences for growth and survival. Parasitology, 123(2), 133-142.

Noonan, M. J., Johnson, P. J., Kitchener, A. C., Harrington, L. A., Newman, C., Macdonald, D. W., 2016. Sexual size dimorphism in musteloids: An anomalous allometric pattern is explained by feeding ecology. Ecol. Evol., 6(23), 8495-8501

Nouvellet, P., Newman, C., Buesching,C. D., Macdonald, D. W., 2013. A multi-metric approach to investigate the effects of weather conditions on the demographic of a terrestrial mammal, the European badger (*Meles meles*). PloS one, 8(7), e68116.

Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T. H., Pemberton, J. M., Festa-Bianchet, M., Gaillard, J. M., 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. Ecology, 92(10), 1936-1947.

Olsson, O., Wirtberg, J., Andersson, M., Wirtberg, I., 1997. Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. Wildlife Biol., 3(1), 13-25.

Painson, J. C., Veldhuis, J. D., Tannenbaum, G. S., 2000. Single exposure to testosterone in adulthood rapidly induces regularity in the growth hormone release process. Am. J. Physiol. Endocrinol. Metab., 278(5), E933-E940.

Peng, J., Jiang, Z., Liu, W., Huang, S., Zhang, J., Wang, W., 2001. Growth and development of giant panda (*Ailuropoda melanoleuca*) cubs at Beijing Zoo. J. Zool., 254(2), 261-266.

Plaistow, S.J., Lapsley, C.T., Beckerman, A.P., Benton, T.G., 2004. Age and size at maturity: sex, environmental variability and developmental thresholds. Proc. R. Soc. Lond. [Biol] 271(1542), 919.

Pontzer, H., 2012. Relating ranging ecology, limb length, and locomotor economy in terrestrial animals. J. Theor. Biol., 296, 6-12.

Post, E., Langvatn, R., Forchhammer, M. C., Stenseth, N. C., 1999. Environmental variation shapes sexual dimorphism in red deer. Proc. R. Soc. Lond. [Biol], 96(8), 4467-4471.

Potau, N., Ibánez, L., Sentis, M., Carrascosa, A., 1999. Sexual dimorphism in the maturation of the pituitary-gonadal axis, assessed by GnRH agonist challenge. Eur. J. Endocrinol., 141(1), 27-34.

Pusey, A., 2012. Magnitude and sources of variation in female reproductive performance, In: Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B., (Eds.), The Evolution of Primate Societies. University of Chicago Press. 343-366.

R Core Team, 2016. R: A Language Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. URL http://www.R-project.org/.

Rensch, B. (1959). Evolution above the species level (No. 575 R4).

Robbins, C.T., Ben-David, M., Fortin, J.K., Nelson, O.L., 2012. Maternal condition determines birth date and growth of newborn bear cubs. J. Mammal., 93(2), 540-546.

Roper, T. J., 2010. Badger. Volume 114. Harper Collins, United Kingdom. 416 pages

RStudio Team, 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA
URL http://www.rstudio.com/.

Shaparev, Y.P., 1977. Razmeshchenie i chislennost barsuka v lesakh nizhnego Priangarya.[Distribution and numbers of badgers in forests in the lower part of Angara river.]. Ekologiya i ispolzovanie okhotnichikh zhivotnykh Krasnoyarskogo kraya.[Ecology and harvesting of game animals of the Krasnoyarsk country.] Akademiya Nauk SSSR, Sibirskoe Otdelenie, Krasnoyarsk, 60-62.

Stewart, P.D., Bonesi, L., Macdonald, D.W., 1999. Individual differences in den maintenance effort in a communally dwelling mammal: the Eurasian badger. Anim. Behav., 57(1), 153-161.

Sugianto, N. A., Newman, C., Macdonald, D. W., & Buesching, C. D. 2019. Heterochrony of puberty in the European Badger (*Meles meles*) can be explained by growth rate and group-size: Evidence for two endocrinological phenotypes. In press. Plos One 14.3: e0203910.

Sun, Q., Stevens, C., Newman, C., Buesching, C.D., Macdonald, D.W., 2015. Cumulative experience, age-class, sex and season affect the behavioural responses of European badgers (*Meles meles*) to handling and sedation. Animal Welf., 24(4), 373-385.

Thornton, P.D., Newman, C., Johnson, P.J., Buesching, C.D., Baker, S.E., Slater, D., Johnson, D.D., Macdonald, D.W., 2005. Preliminary comparison of four anaesthetic techniques in badgers *(Meles meles*). Vet. Anaesth. Analg., 32(1), pp.40-47.

Trivers, R. L., 1972. Parental Investment and Sexual Selection, In B. Campbell (Eds.), Sexual Selection and the Descent of Man, 1871-1971, pp. 136-179.

Tsunoda, M., Newman, C., Buesching, C. D., Macdonald, D. W., Kaneko, Y., 2018. Badger setts provide thermal refugia, buffering changeable surface weather conditions. J. Therm. Biol., 74, 226-233.

Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. J. Mammal., 79(1), 33-52.

Wolff, J.O., Macdonald, D.W., 2004. Promiscuous females protect their offspring. Trends Ecol. Evol., 19(3), 127-134.

Wong, B.B., Candolin, U., 2005. How is female mate choice affected by male competition?. Biol. Rev., 80(4), 559-571.

Woodroffe, R., Macdonald, D.W., 1993. Badger socility-models of spatial grouping. Symp. Zool. Soc. Lond., 65, 145-169.

Woodroffe, R., Macdonald, D.W., 2000. Helpers provide no detectable benefits in the European badger (*Meles meles*). J. Zool., 250(1), 113-119.

Woodroffe, R., Macdonald, D.W., 1995. Costs of breeding status in the European badger, *Meles meles*. J. Zool., 235(2), 237-245.

Yamaguchi, N., Dugdale, H. L., Macdonald, D. W., 2006. Female receptivity, embryonic diapause, and superfetation in the European badger (*Meles Meles*): implications for the reproductive tactics of males and females. Q. Rev. Biol., 81(1), 33-48.

Figure Captions

Figure 1. Head body length growth curves in males and females aged 3-28 months.

Figure 2. Zygomatic arch growth curve in males and females aged 3-28 months.

Figure 3. Mean pastern length growth curve in males and females aged 3-28 months.

Figure 4. Growth curves of male and female radius-ulna (A), humerus (B), tibia-patella length (C), patella-femur length (D), and tail length (E) in badgers aged 3-28 months.

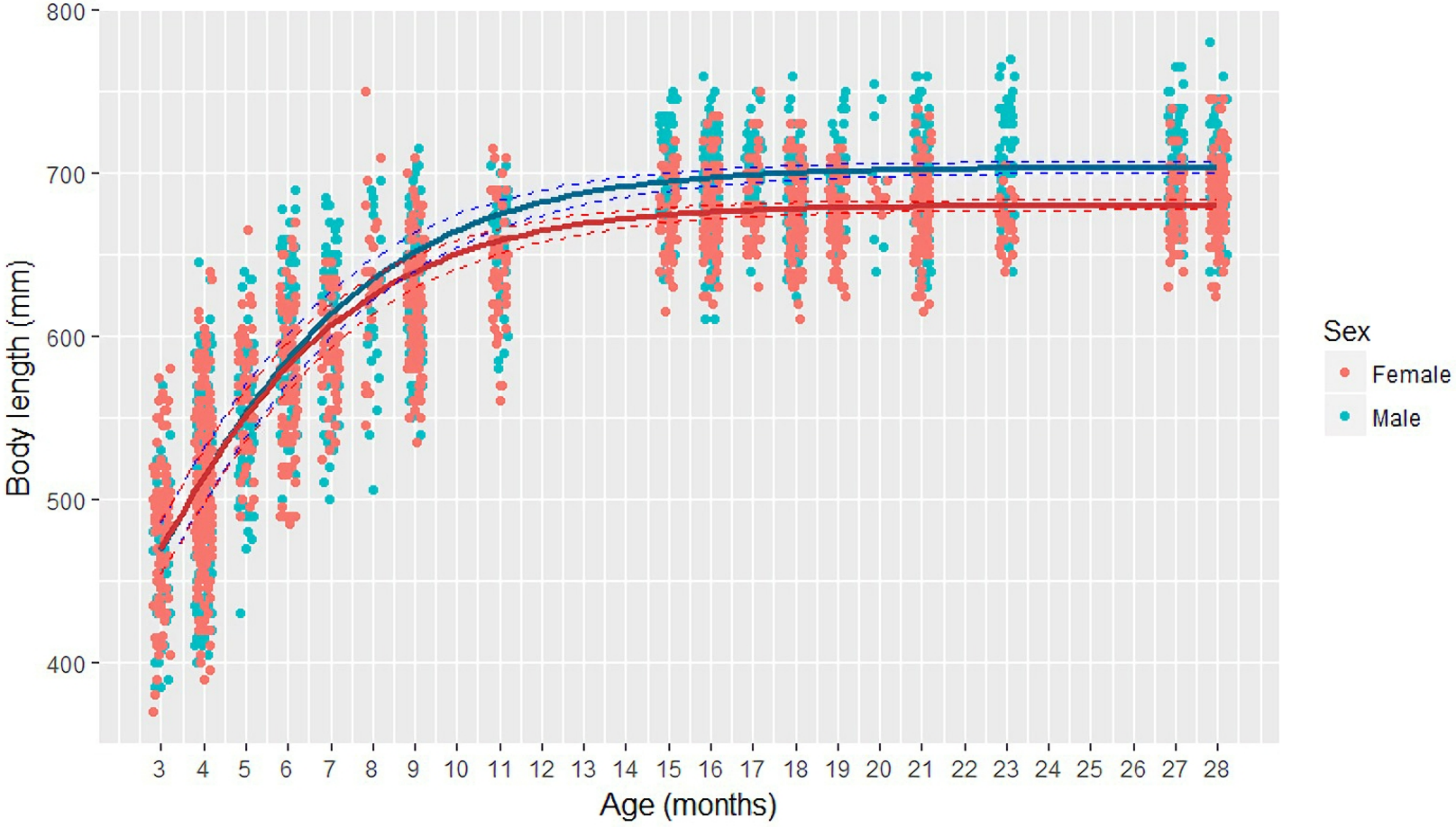
Supplementary Material

New residency rules for yearly population density calculated from minimum number alive estimates:

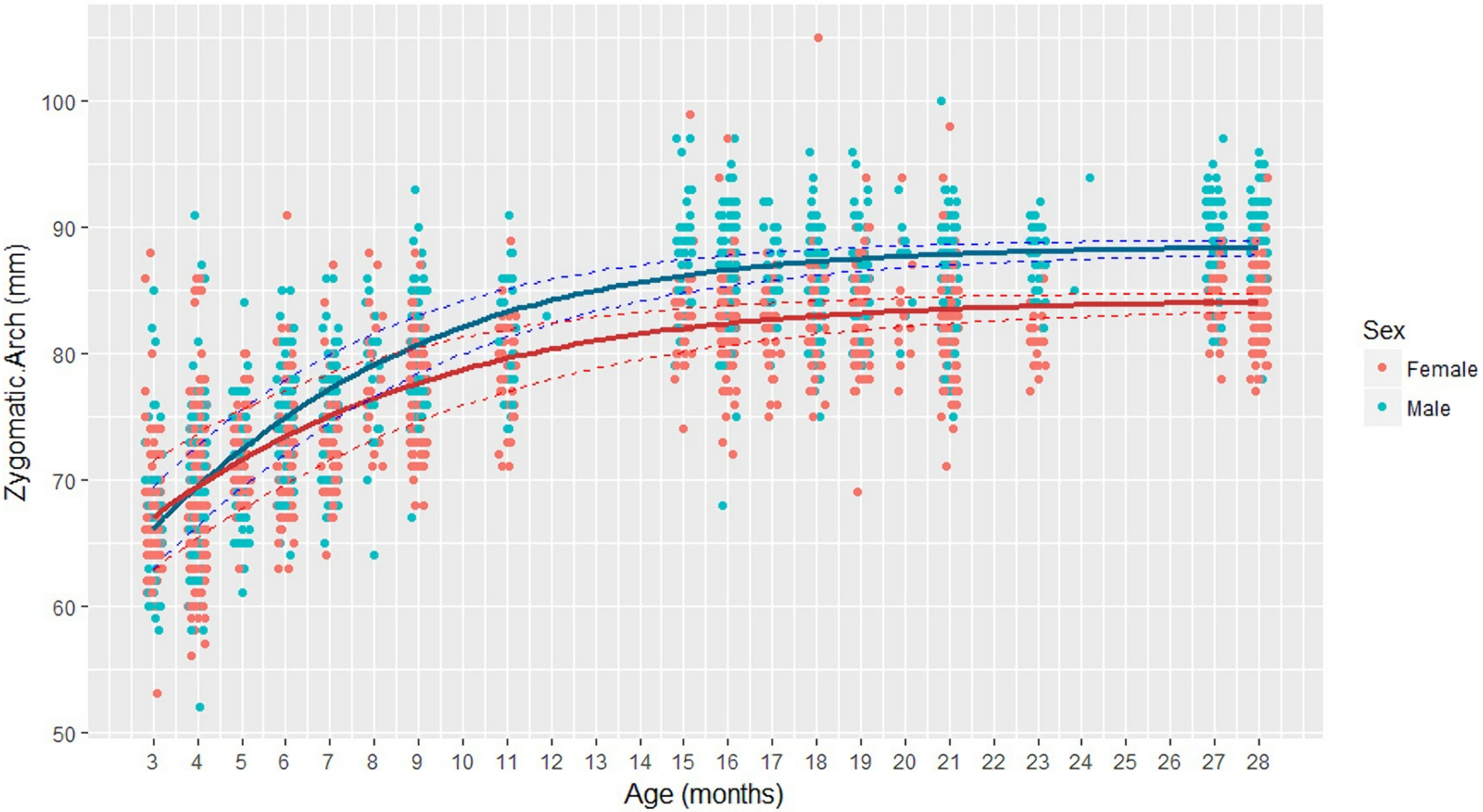
1. When there was a 1-year gap in an individual's capture history and the sett/social group before and after that gap remained the same, the individual was assigned to that same sett/ social group for that year.
2. When there was a 1-year gap in an individual's capture history but the sett/ social group before and after that gap differed, the individual was assigned to the sett/ social group that it was captured at immediately after that gap if it proceeded to have a resident affiliation to that new sett/social group (see Macdonald et al., 2008 for

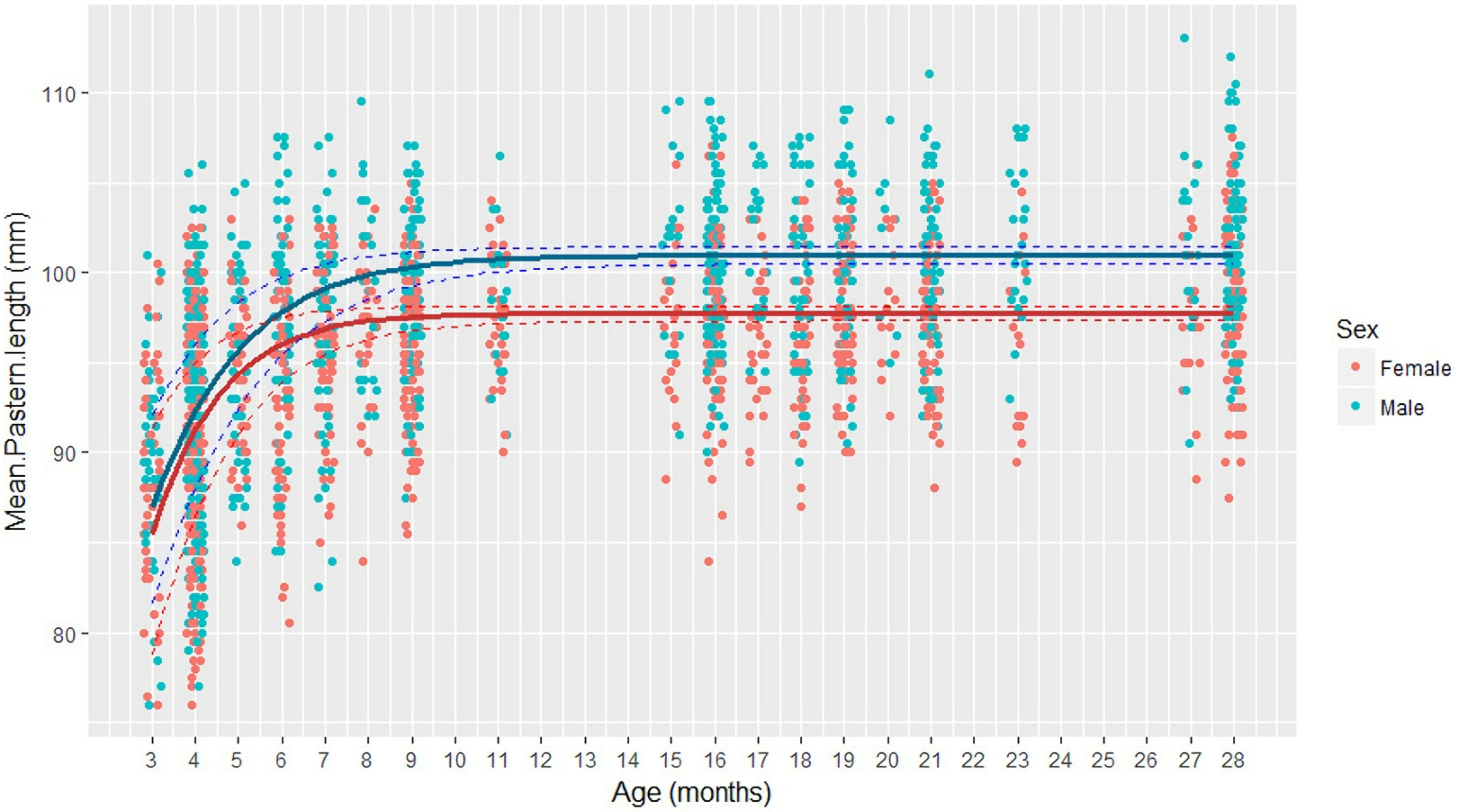
definition). Otherwise, the individual was assigned to the sett/ social group that it was captured at prior to that gap.

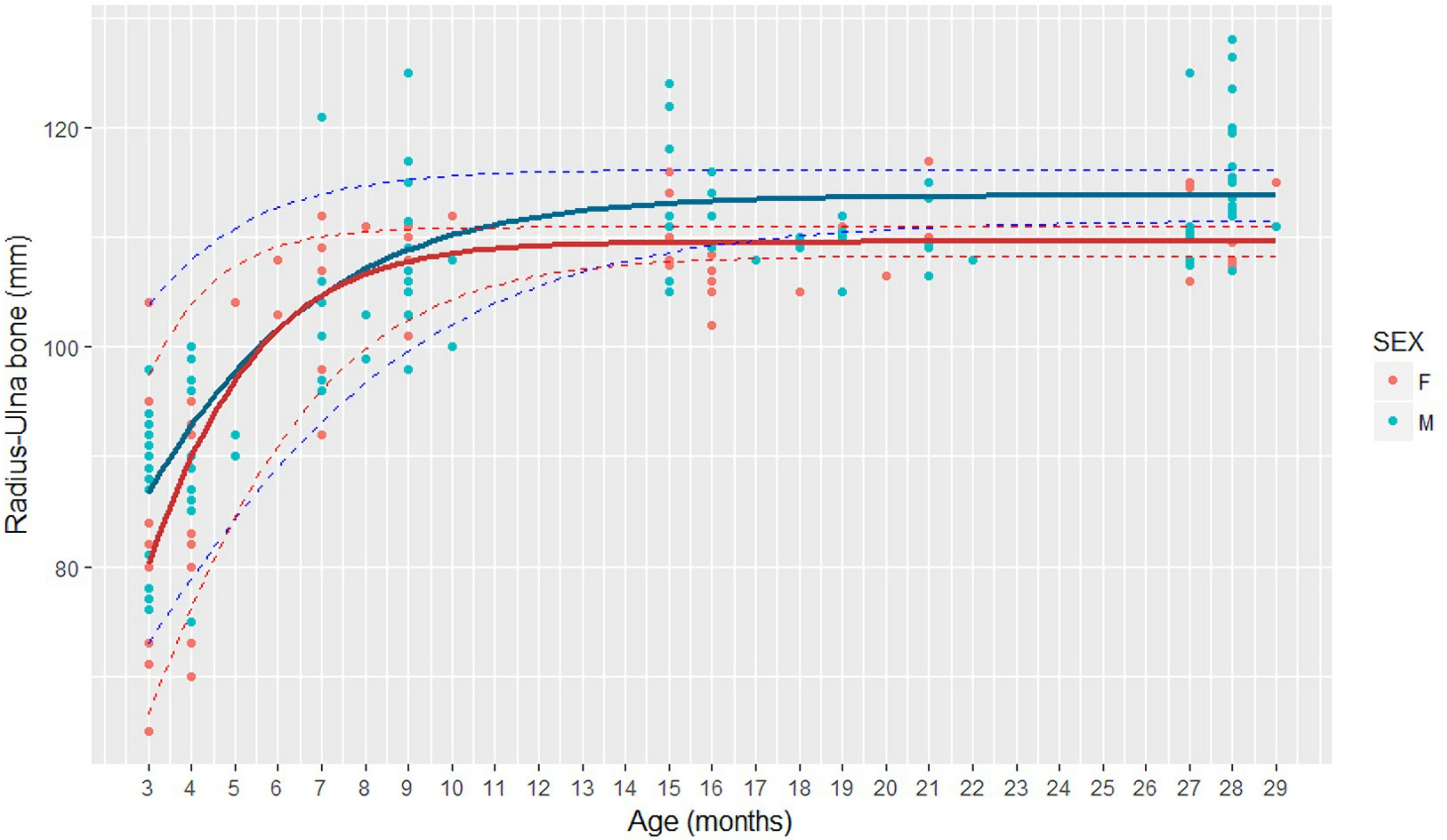
3. When there was an even-numbered gap in an individual's capture history (e.g. 2 years, 4 years, etc.), a proportional assignment was made between the sett/ social group that the individual was captured at immediately prior to and immediately after the gap.
4. When there was an odd-numbered gap in an individual's capture history (e.g. 3 years, 5 years, etc.), a proportional assignment was made between the sett/social group that the individual was captured at prior to and after that gap (e.g. for a 3-year gap, an individual would be assigned to the first sett/ social group for 1 year and assigned to the second sett/ social group for 2 years).
5. When the individual was captured in the same social group but in different setts within that social group during a particular year, it was assigned to the sett that it was captured at most often throughout its entire capture history. Nevertheless, if it showed an equal preference for multiple setts, it was assigned to the sett that it was captured at initially.

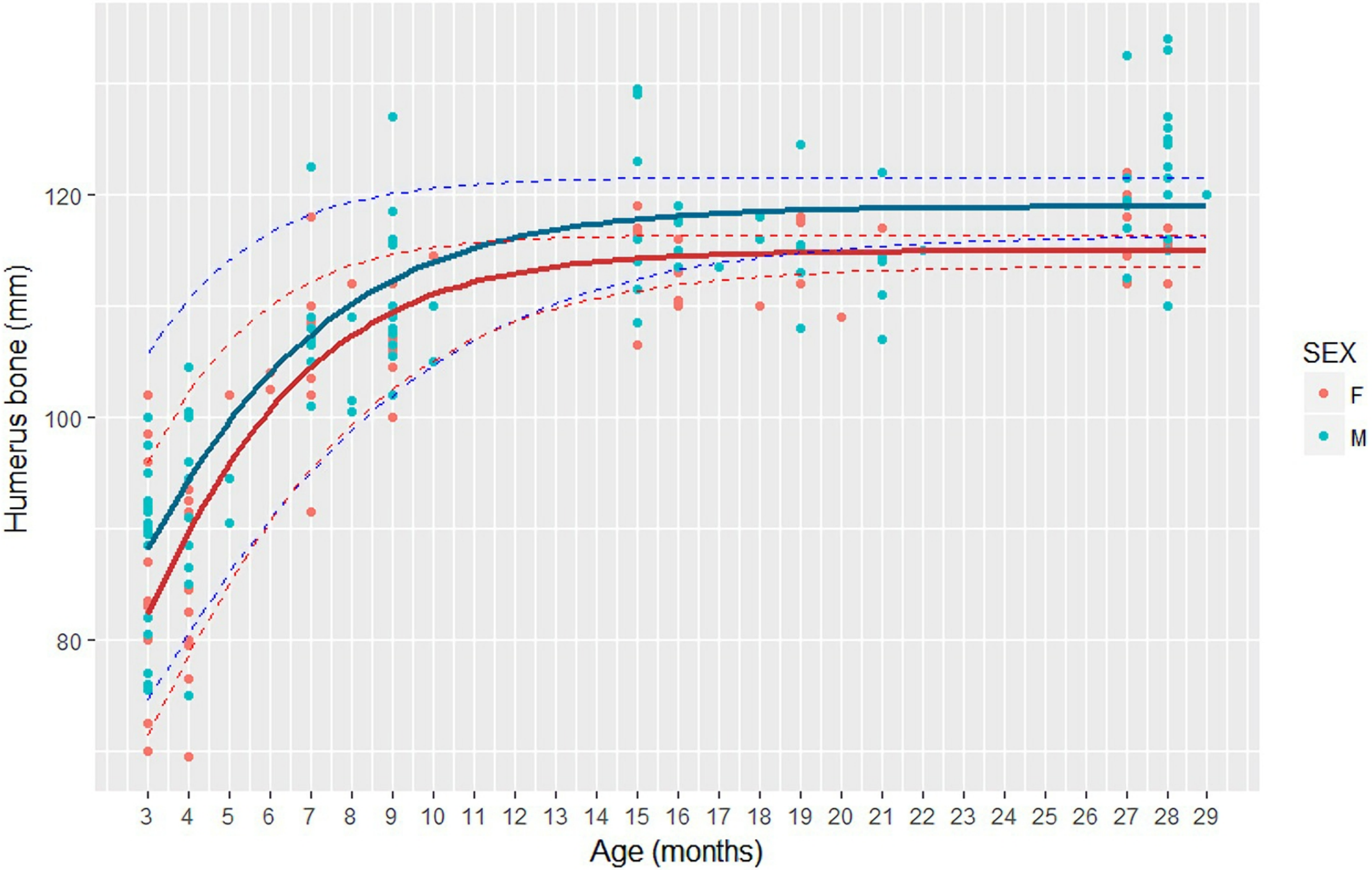


800
700
600
500
400
Body length (mm)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Age (months)
Sex
Female
Male

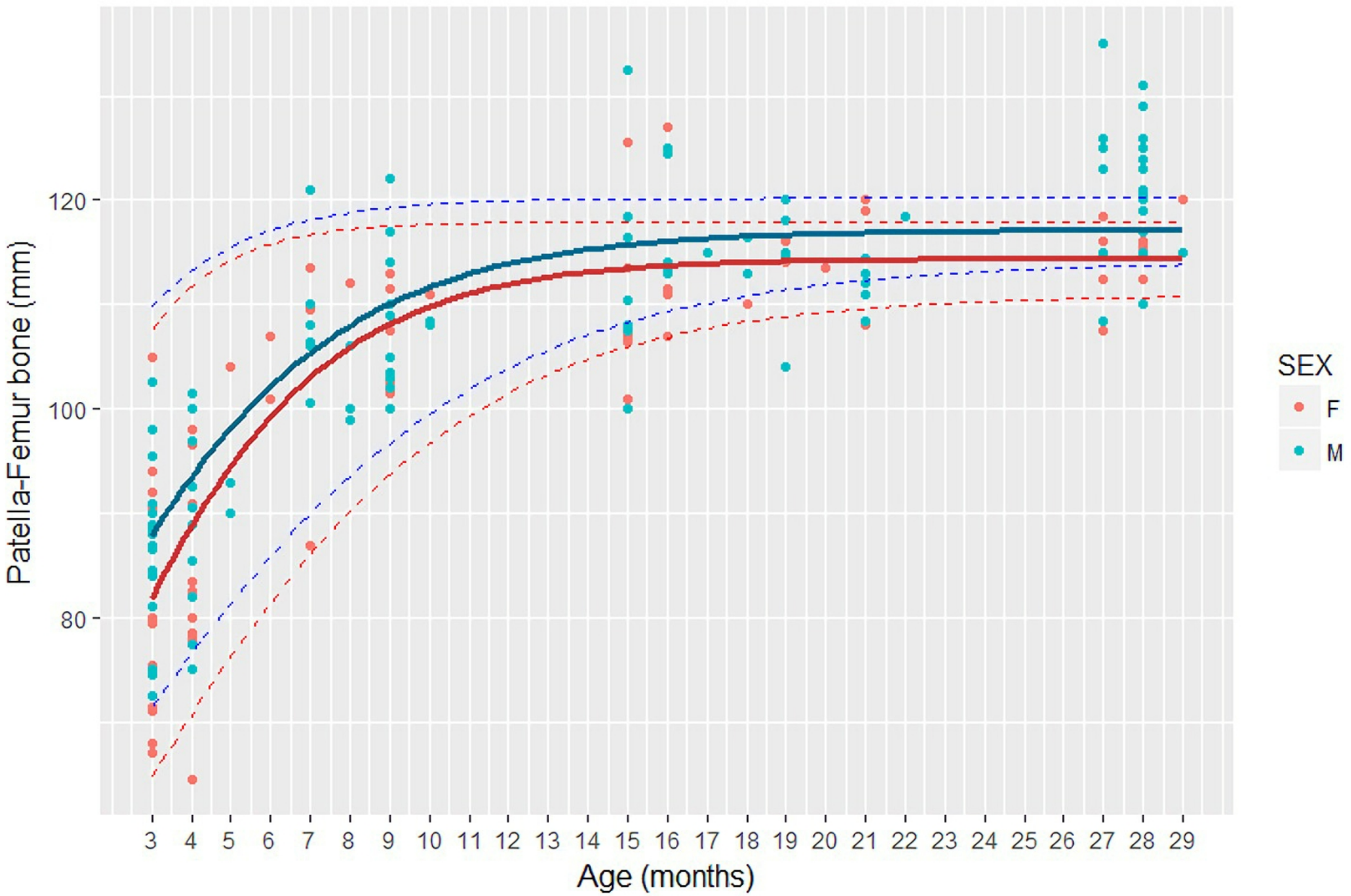

Zygomatic.Arch (mm)
100
90
80
70
60
50
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Sex
Female
Male

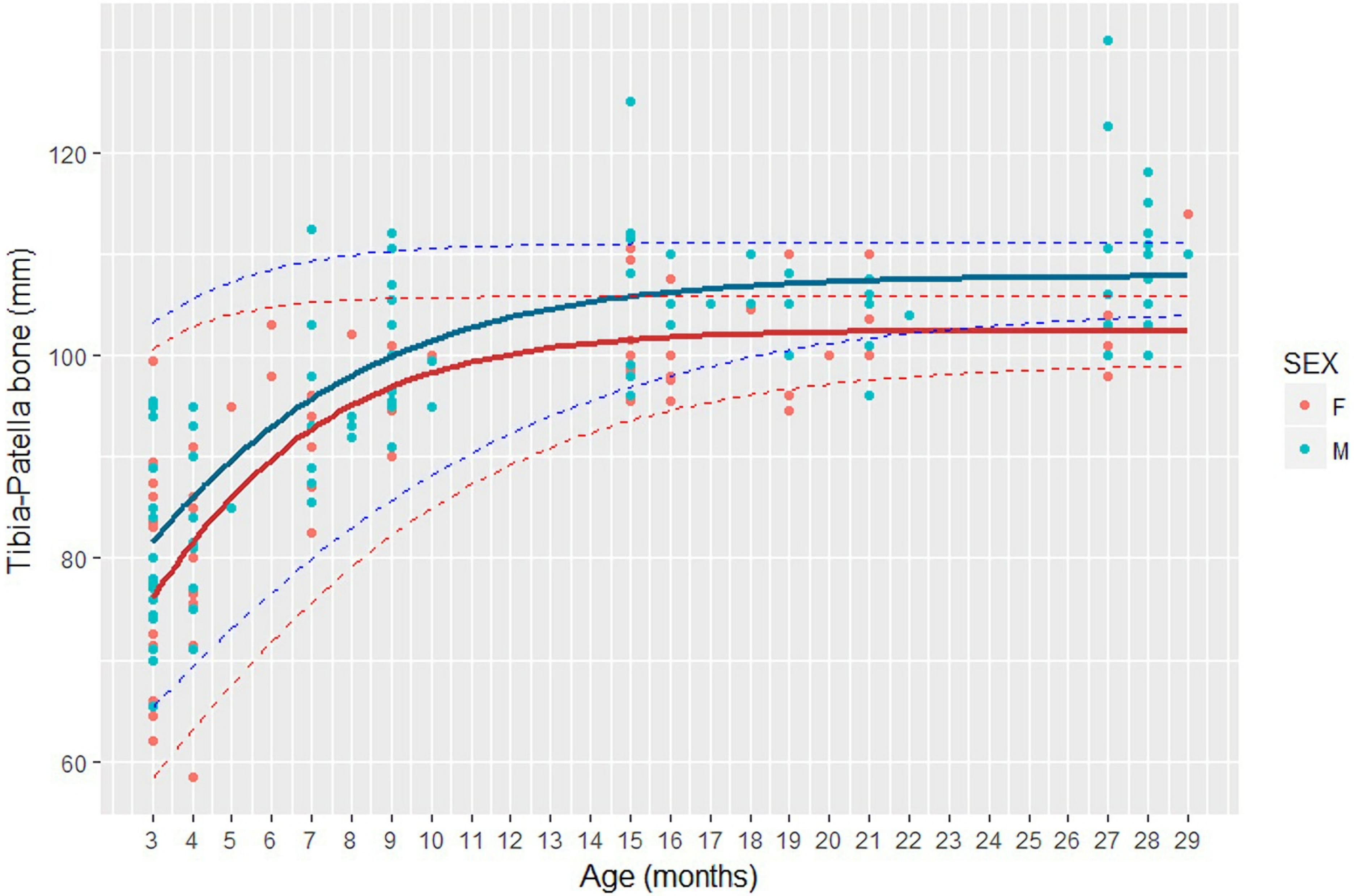

Mean.Pastern.length (mm)
110
100
90
80
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Age (months)
Sex
Female
Male

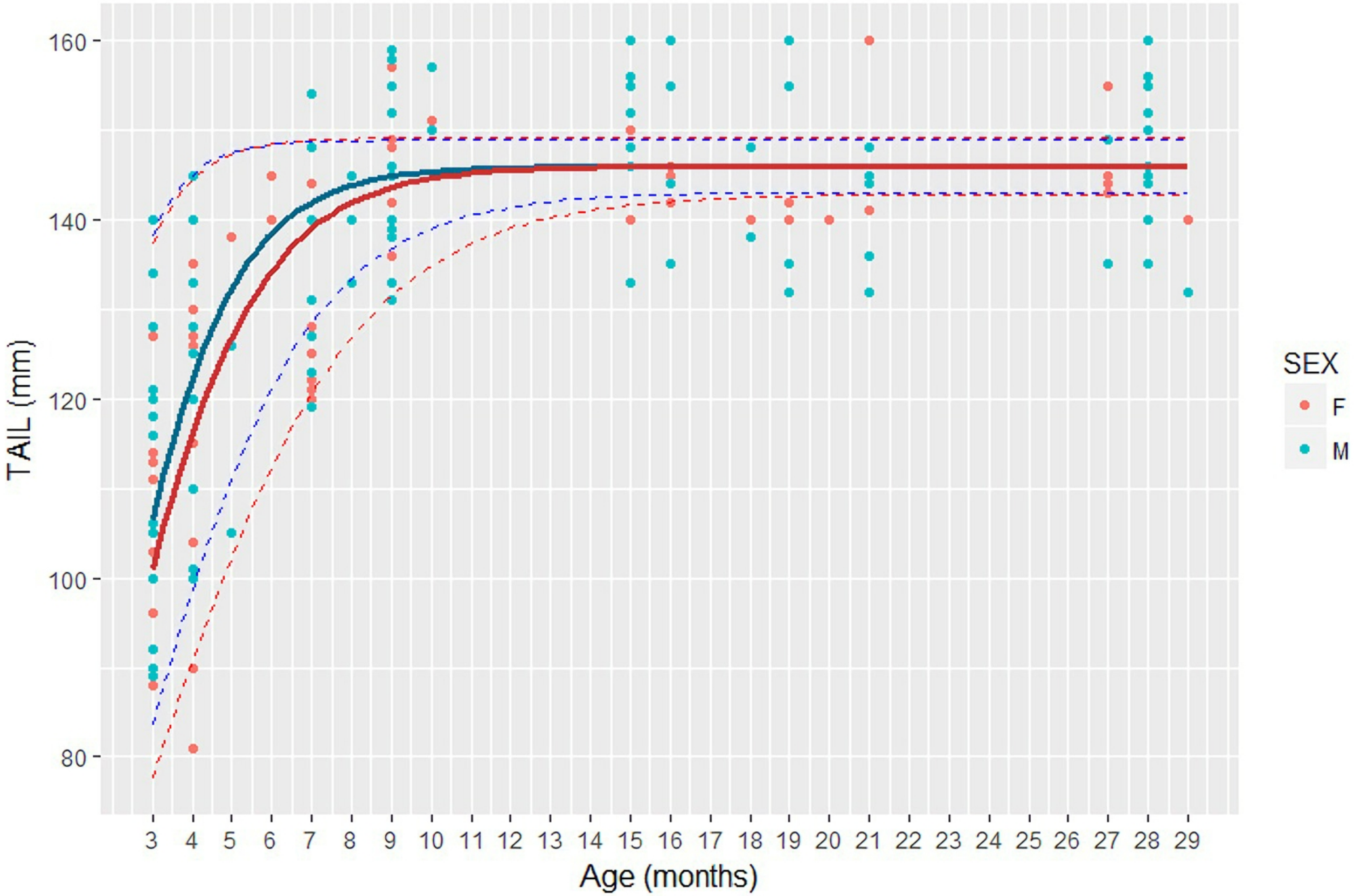

Radius-Ulna bone (mm)
120
100
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
SEX
F
M



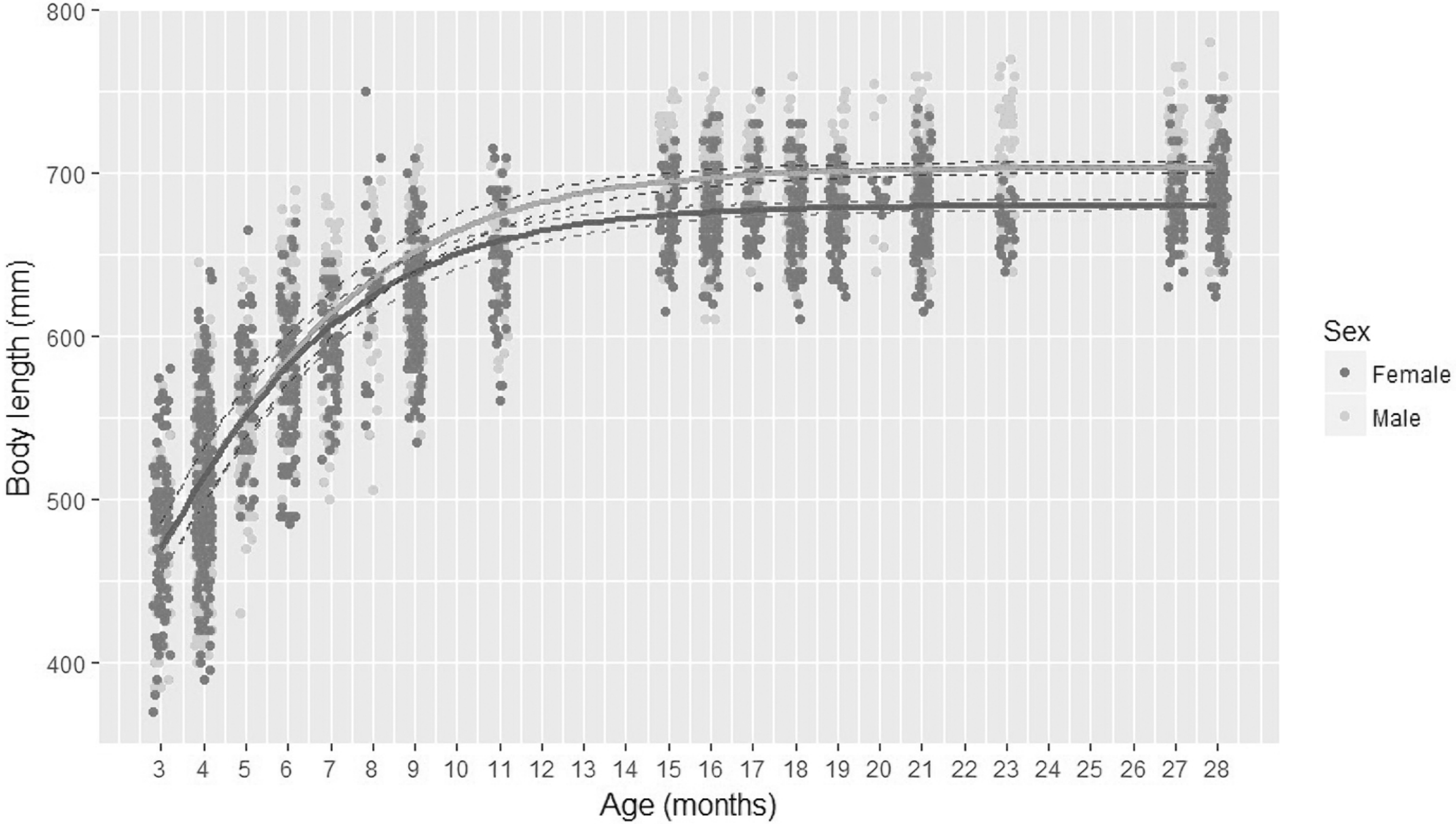
Humerus bone (mm)
120
100
80
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Age (months)
SEX
F
M

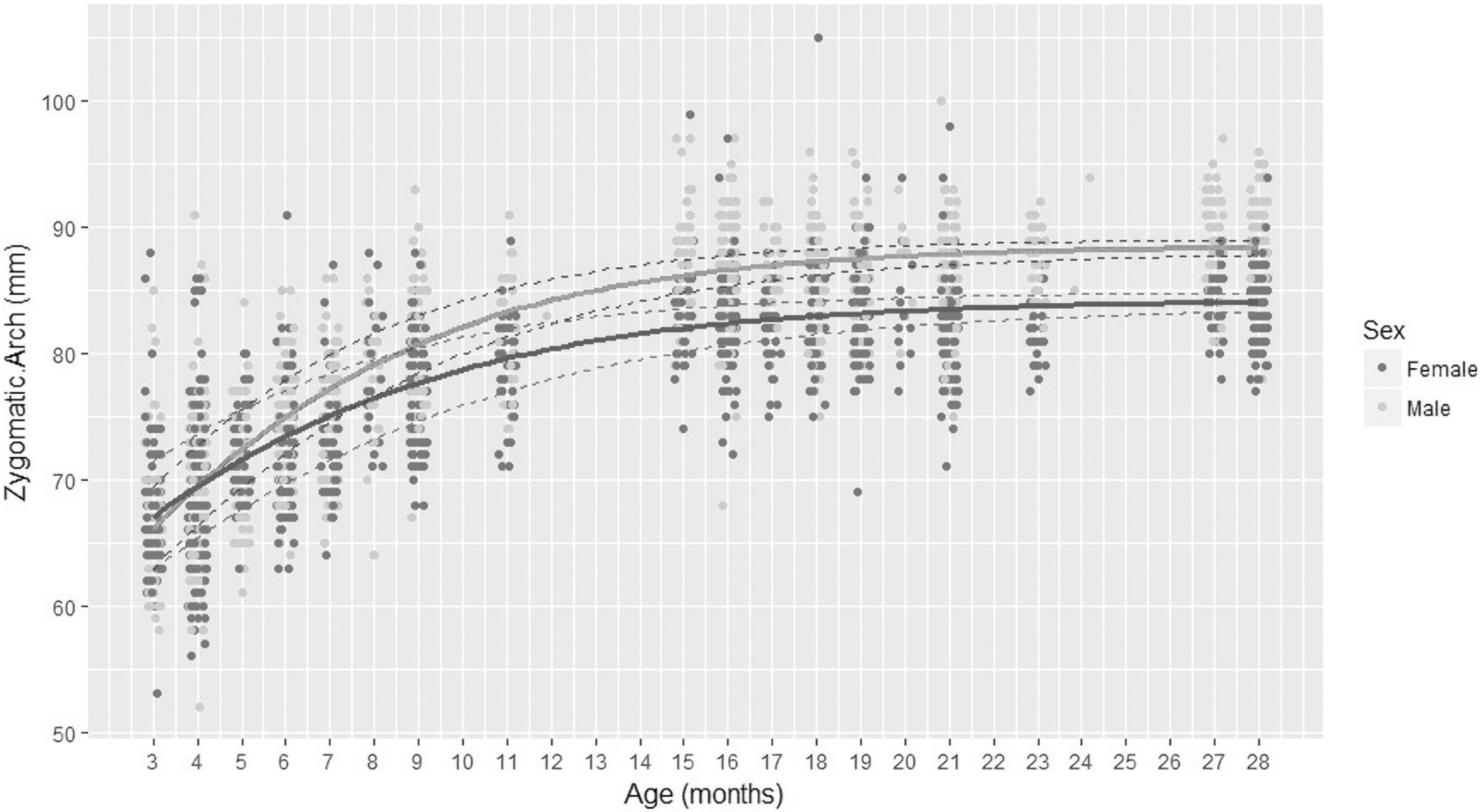

Patella-Femur bone (mm)
120
100
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
SEX
F
M

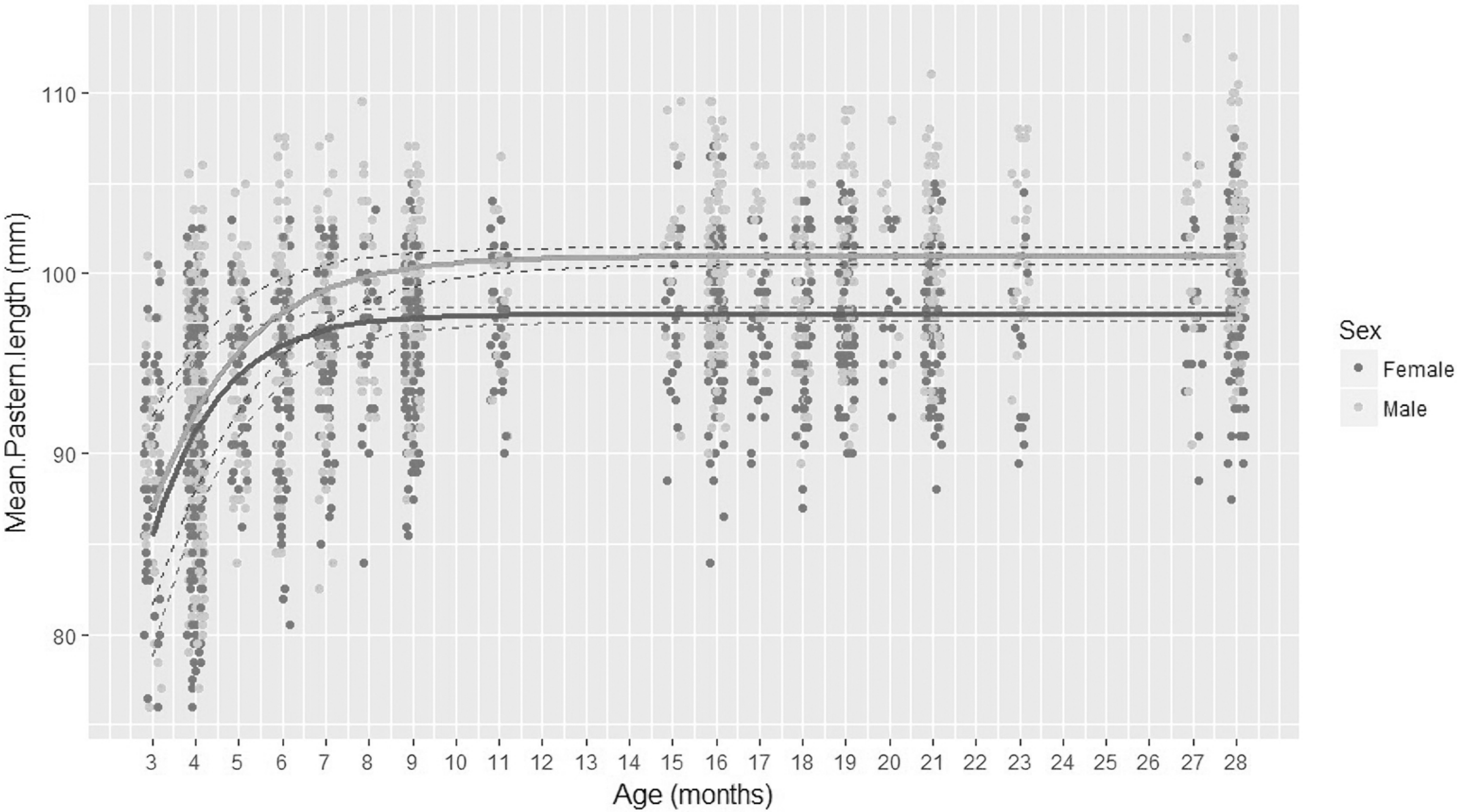

Tibia-Patella bone (mm)
120
100
80
60
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Age (months)
SEX
F
M

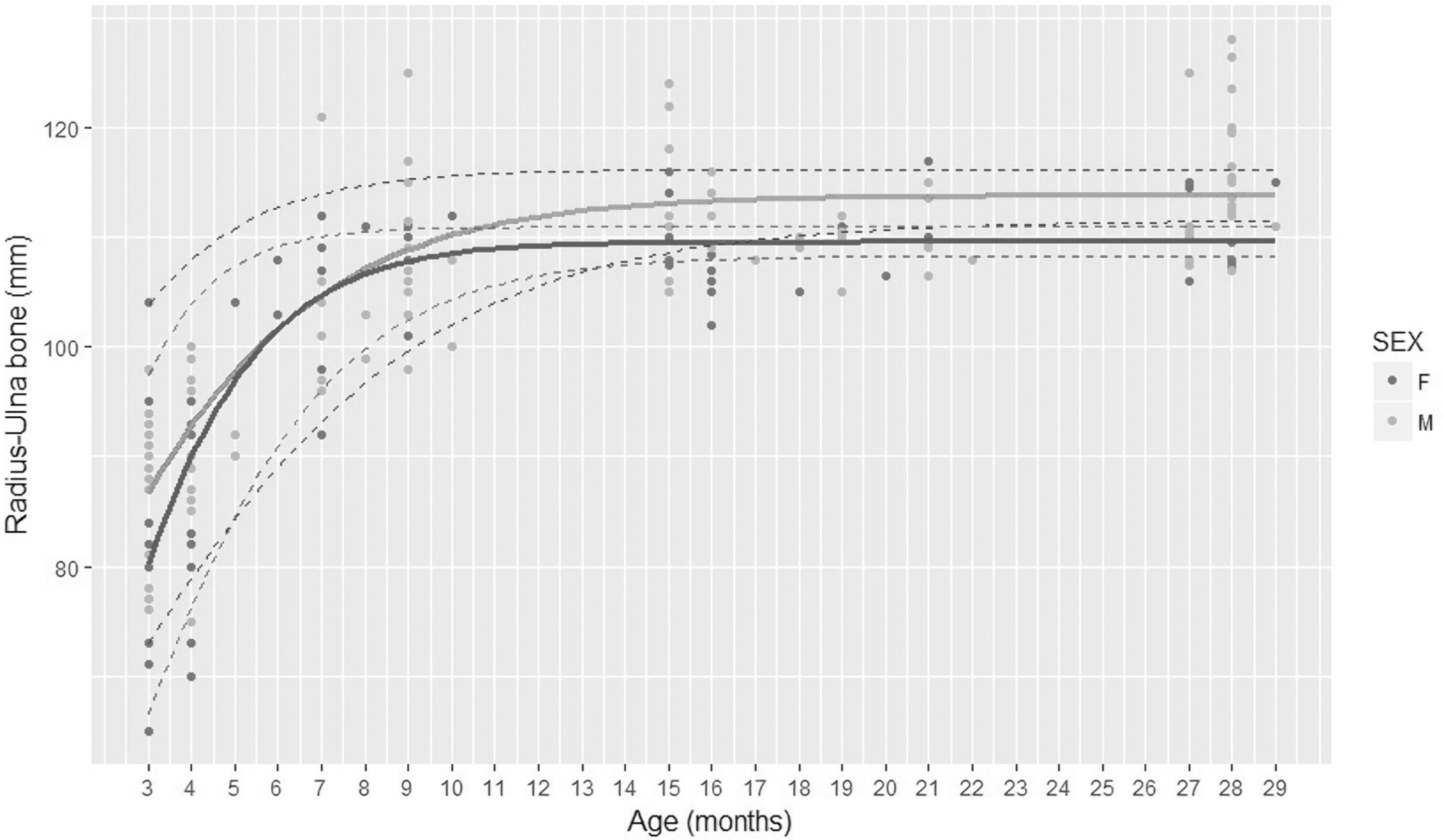


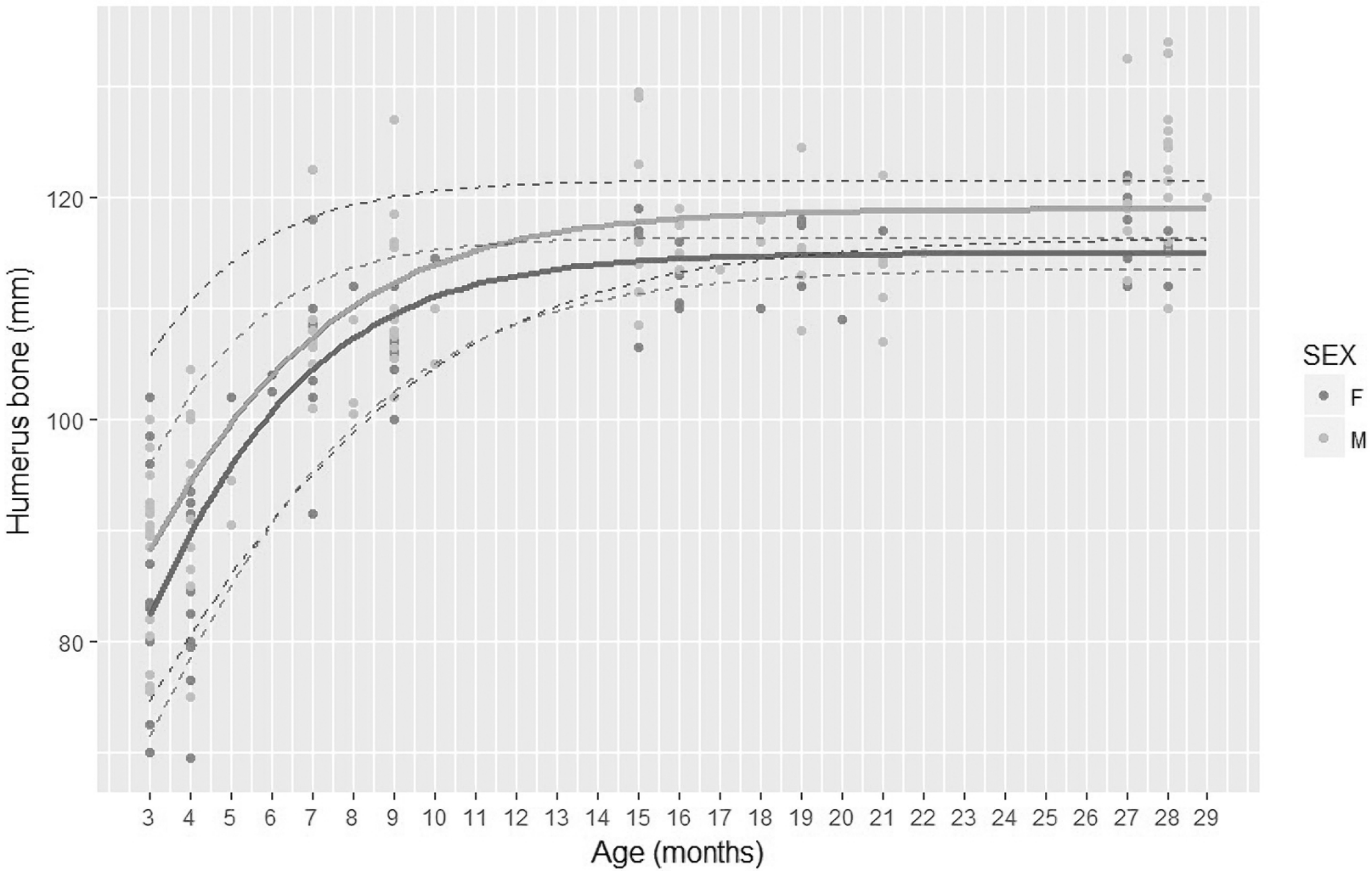
TAIL (mm)
160
140
120
100
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
SEX
F
M

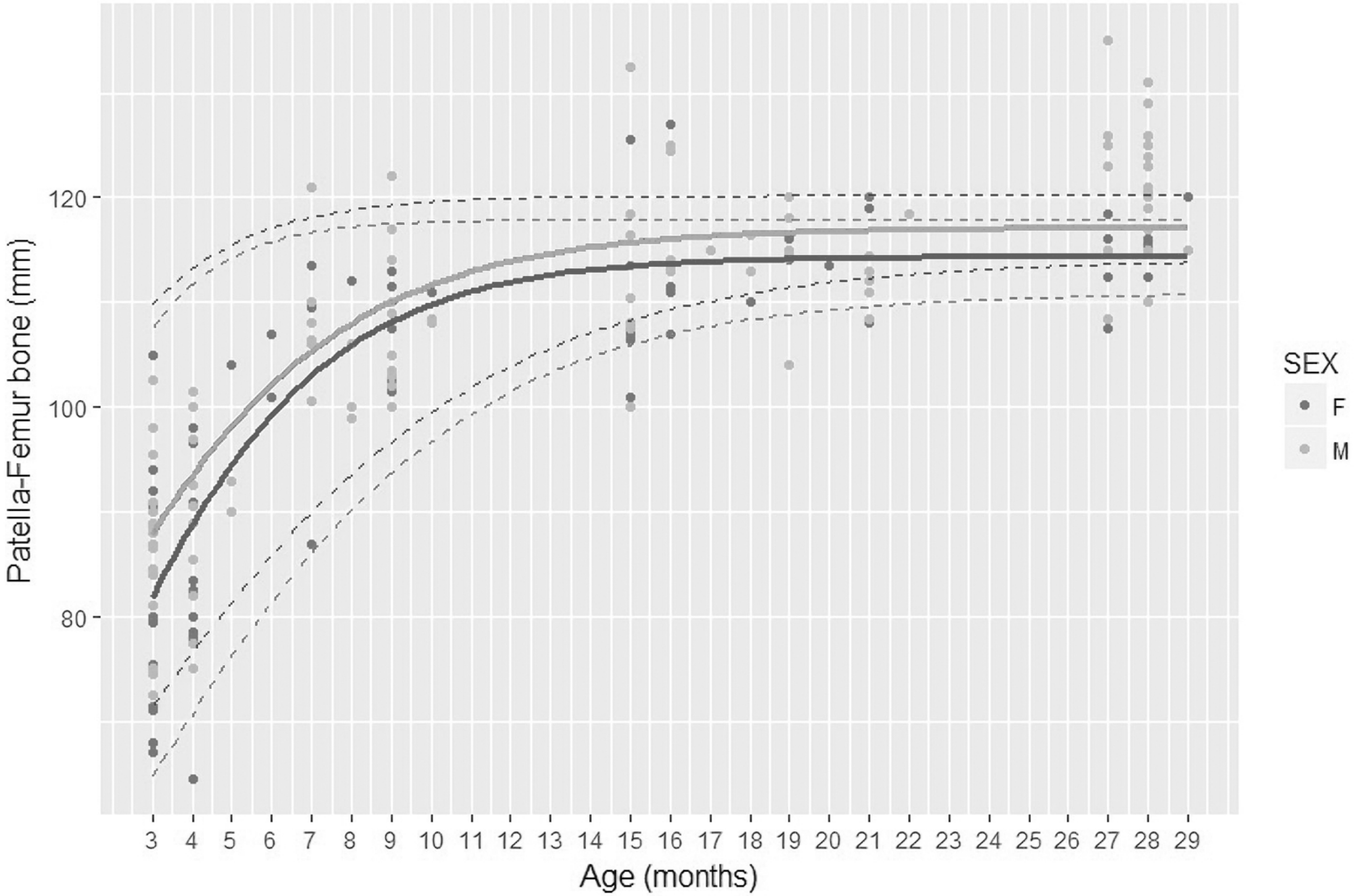

Body length (mm)
800
700
600
500
400
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Sex
Female
Male

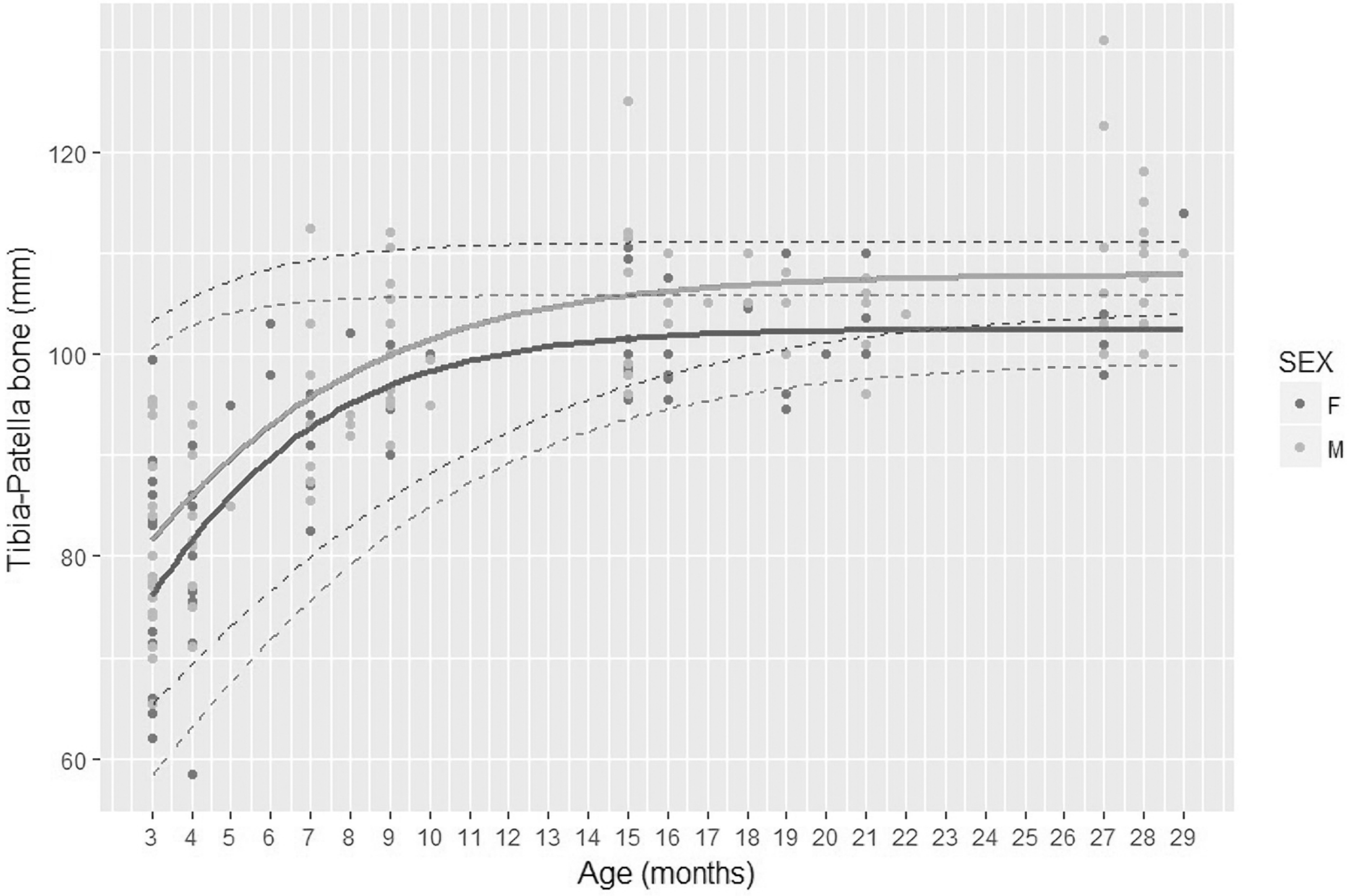

Zygomatic Arch (mm)
100
90
80
70
60
50
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Age (months)
Sex
Female
Male


Mean.Pastern.length (mm)
110
100
90
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
Sex
Female
Male

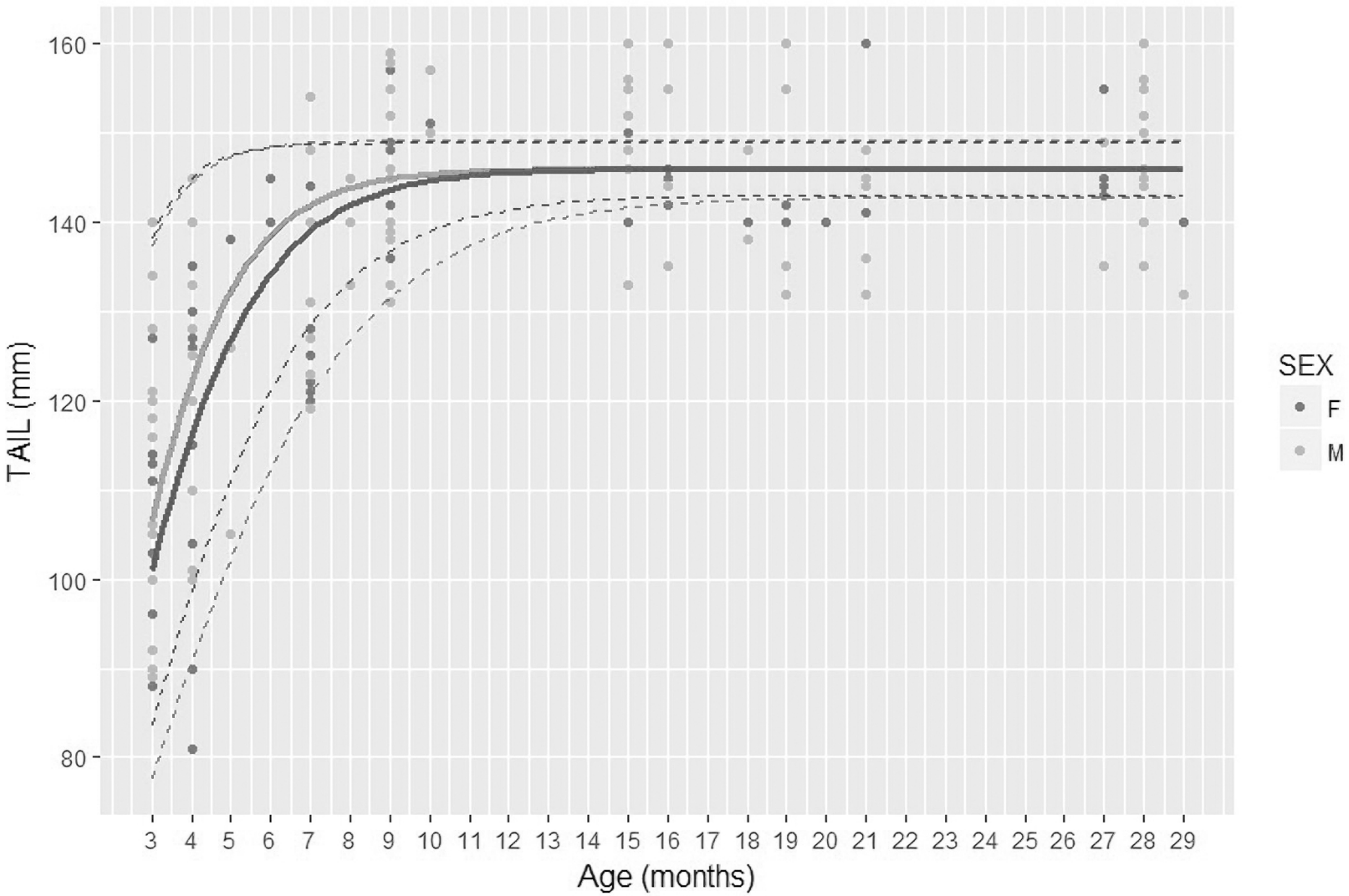

120
100
80
Radius-Ulna bone (mm)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Age (months)
SEX
F
M


Humerus bone (mm)
120
100
80
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Age (months)
SEX
F
M


Patella-Femur bone (mm)
120
100
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
SEX
F
M



Tibia-Patella bone (mm)
120
100
80
60
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
Age (months)
SEX
F
M



TAIL (mm)
160
140
120
100
80
Age (months)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
SEX
F
M