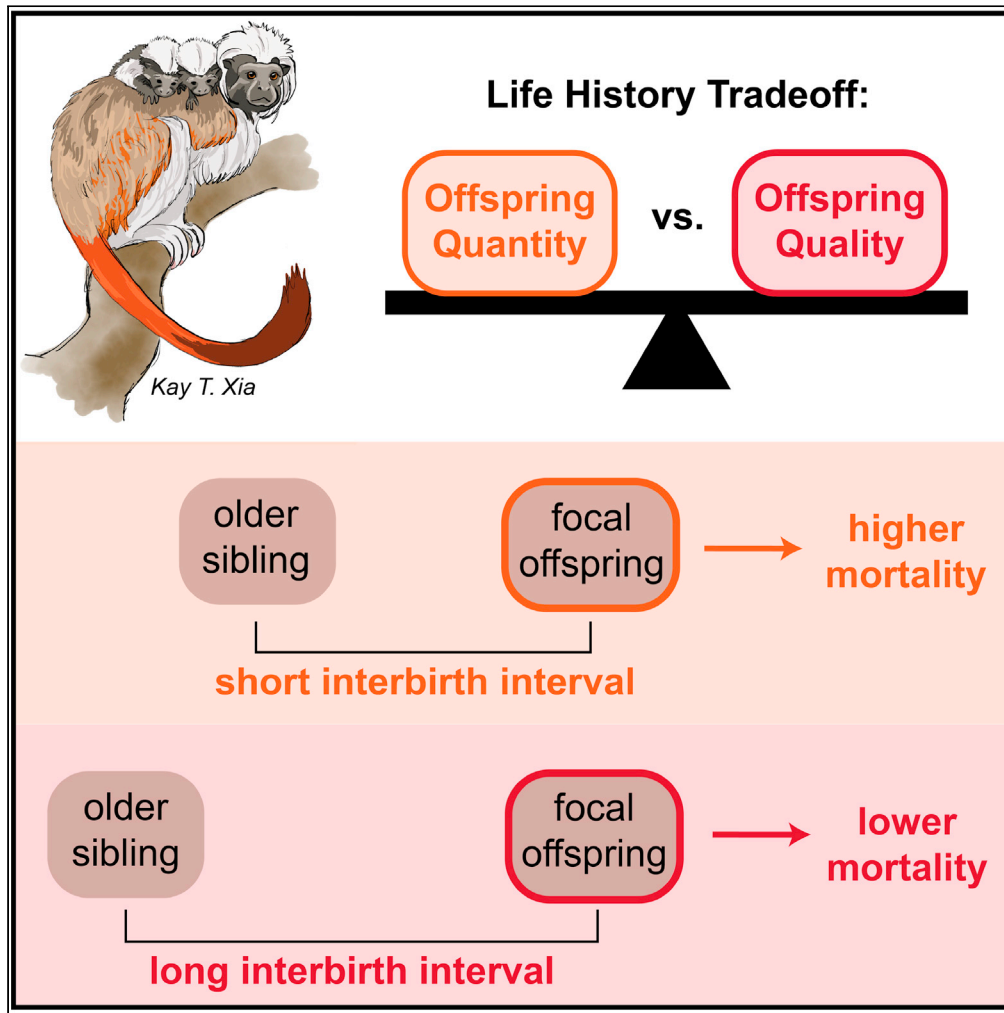


Article

After short interbirth intervals, captive callitrichine monkeys have higher infant mortality



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Highlights

Callitrichines are unusual primates; they breed cooperatively and birth litters

We analyzed 15,852 births with known interbirth intervals in captive callitrichines

Short interbirth intervals were associated with increased mortality risks

Callitrichines seem to face trade-offs between offspring quality and quantity

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Article

After short interbirth intervals, captive callitrichine monkeys have higher infant mortality

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SUMMARY

Life history theory predicts a trade-off between the quantity and quality of offspring. Short interbirth intervals—the time between successive births—may increase the quantity of offspring but harm offspring quality. In contrast, long interbirth intervals may bolster offspring quality while reducing overall reproductive output. Further research is needed to determine whether this relationship holds among primates, which have intensive parental investment. Using Cox proportional hazards models, we examined the effects of interbirth intervals (short, normal, or long) on infant survivorship using a large demographic dataset (n = 15,852) of captive callitrichine monkeys (marmosets, tamarins, and lion tamarins). In seven of the nine species studied, infants born after short interbirth intervals had significantly higher risks of mortality than infants born after longer interbirth intervals. These results suggest that reproduction in callitrichine primates may be limited by physiologic constraints, such that short birth spacing drives higher infant mortality.

INTRODUCTION

Life history theory predicts trade-offs between the quantity and quality of offspring (Stearns, 1992, 2000). Prolific parents may incur the costs of lower-quality offspring. Shorter interbirth intervals (IBIs)—the length of time between successive births—represent one strategy parents may use to increase their reproductive performance by increasing offspring quantity. In contrast, extended IBIs may allow for increased parental investment, thereby increasing offspring quality. Primates, a lineage typified by intensive parental investment (Jones, 2011), provide excellent opportunities to explore the consequences of reproductive trade-offs associated with IBI. In humans, unusually short or long IBIs are associated with increased risks of infant mortality (Conde-Agudelo et al., 2006). This pattern also has been observed in free-ranging rhesus monkeys—offspring born after short IBIs were more likely to die compared with offspring born after long IBIs (Lee et al., 2019). Broadly, short IBIs are thought to be risky for infants due to (i) divided parental attention (and resources) between dependent offspring; (ii) maternal resource limitations after recovering from a previous pregnancy; or (iii) maternal metabolic recovery post pregnancy (Stearns, 1992, 2000).

To better understand these reproductive processes across primates, we analyzed a large dataset (n = 15,852) of births with known IBIs in nine species of callitrichine monkeys—an American primate clade that routinely produces litters (of fraternal twins and triplets) and relies on cooperative care to raise offspring (Haig, 1999; Tardif, 1996; Tardif and Ross, 2009). We derived these data from demographic records of zoo and laboratory populations spanning 80 years (1938–2018 (McCoy et al., 2019)). Do callitrichine infants suffer higher mortality after extreme (shorter or longer) IBIs? We found that monkeys born after short IBIs had significantly higher mortality in seven of the nine species studied, suggesting that fundamental life history trade-offs may underlie the relationship between infant mortality and atypical pregnancy spacing in callitrichine primates.

Methods

To investigate the relationship between IBI and infant mortality, we studied nine species of callitrichine monkeys using demographic data from zoo and laboratory populations (Figure 1; Table 1; *Callithrix geoffroyi*, *Callithrix jacchus*, *Cebuella pygmaea*, *Saguinus imperator*, *Saguinus oedipus*, *Leontopithecus chrysomelas*, *Leontopithecus chrysopygus*, *Leontopithecus rosalia*, and *Callimico goeldii*). We compared the survivorship profiles of individuals

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Continued



born after short, normal, and long IBIs (Figure 2; see STAR Methods; Data S1) by constructing Cox proportional hazards models. In these models, we also included variables for litter size because singletons have higher survivorship than litters (McCoy et al., 2019) and litter number (i.e., what number litter it was for a given dam) to control for dam age and parity. We also controlled for dam identity (Figure 2; Data S1). We performed two statistical comparisons: first, whether models with IBI were a better fit than those without (Likelihood Ratio Tests); second, which categories of IBI significantly harmed survivorship (Cox Proportional Hazards; Figure 2; Data S1). Given the archival nature of our dataset, we did not perform an Institutional Animal Care and Use Committee review. However, these data were derived from institutions adhering to all national and international guidelines, including the American Society of Primatologists' guidelines for the ethical treatment of nonhuman primates.

RESULTS

Overall, births after short IBIs were significantly worse for infant survivorship than were for normal or late births (Figure 2; Data S1). The models with IBI (versus without) were a better fit in eight of nine species (Table 1; Data S1). In seven of these species, monkeys born after a short IBI had higher mortality than monkeys born after a normal IBI, and monkeys born after a short IBI had higher mortality than monkeys born after a long IBI for six species. It is worth noting that in the two species (*L. chrysopygus* and *S. imperator*) for which short IBI did not correlate with lower infant survivorship, sample sizes were relatively small and birth spacing did not follow a normal distribution (Figure 3; Data S2 and S3).

DISCUSSION

Short IBI is correlated with high infant mortality in captive callitrichine monkeys, a result that recapitulates data from human and macaque populations. Primates, a clade that invests heavily in offspring via gestation, lactation, and prolonged periods of offspring care (Charnov and Berrigan, 1993), provide excellent opportunities for studying the relationships between IBI and infant mortality. For example, in free-ranging rhesus macaques, offspring born after short IBIs had higher mortality risks, particularly if the older sibling survived (Lee et al., 2019). Chimpanzee offspring born after short IBIs were significantly smaller than their long IBI counterparts, which may have important implications for long-term health and survival (Emery Thompson et al., 2016). Given that our data support these patterns, it seems that short birth spacing imposes reproductive costs, including offspring mortality, in primates. Energetic constraints may underlie this pattern. Indeed, primate life history is characterized by an extended period of offspring dependency, during which parental investment remains high (Jones, 2011). Accelerated reproductive strategies characterized by short IBIs may limit the energies invested in any given offspring, resulting in higher risks of offspring mortality.

Our results also add to a growing body of knowledge about the complex reproductive strategies of callitrichine monkeys, particularly processes associated with sibling competition. Firstly, during callitrichine pregnancy, the intrauterine environment promotes cell swapping between siblings, resulting in whole-body chimeras (Patten, 2021; Ross et al., 2007; Silva et al., 2017; Wedi et al., 2016). That is, any given monkey likely has chimeric tissues composed of two or more individual genomes (even potentially including in the germline (Patten, 2021; Ross et al., 2007), but see (Wedi et al., 2016)). Such chimerism is predicted to alter the balance between cooperation to conflict among siblings (see (Haig, 1999; Patten, 2021) for detailed treatments). Secondly, family members other than the parents care for offspring (Tardif, 1996; Tardif and Ross, 2009). One therefore might expect that callitrichines have low infant mortality thanks to cooperative care, but it appears that frequently birthing twins and larger litters imposes the costs of higher infant mortality due to direct or indirect sibling conflict (McCoy et al., 2019). Relatedly, callitrichine mothers experience a postpartum estrus where they can ovulate and conceive soon after giving birth (unusual among primates (French et al., 2002)). Notwithstanding this remarkable trait, the reproductive rates of callitrichines seem to be constrained, given that conceiving too soon was associated with higher offspring mortality. Finally, callitrichines also have an unusually long gestation length given their small body and brain size (Hartwig, 1996); this is likely because callitrichines often give birth to litters of two or more (while most primates bear singletons), and longer gestations are required for fetal growth to a minimally viable size (Hartwig, 1996). Thus, sibling competition seems to represent an important factor shaping survival and reproduction within this clade.

Limitations of the study

We would like to note some potential limitations to this study. First, we compiled data from zoos and biomedical laboratories, settings in which husbandry mitigates many perinatal risks, including predators,

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Figure 1. Our dataset of captive marmosets, tamarins, and lion tamarins spanned nine species, pictured here.

- (A) Goeldi's marmoset (*Callimico goeldii*), photo credit Stefan Lippmann (stefan_photos@flickr.com).
 (B) White-headed marmoset (*Callithrix geoffroyi*), photo Tony Hisgett (CC BY 2.0 www.commons.wikimedia.org/w/index.php?curid=14621454).
 (C) Common marmoset (*Callithrix jacchus*), photo credit Emmanuel Keller.
 (D) Pygmy marmoset (*Cebuella pygmaea*), photo credit Emmanuel Keller.
 (E) Golden-headed lion tamarin (*Leontopithecus chrysomelas*), photo credit Emmanuel Keller.
 (F) Black lion tamarin (*Leontopithecus chrysopygus*), photo credit Roger Smith (www.flickr.com/photos/wodjamiff/).
 (G) Golden lion tamarin (*Leontopithecus rosalia*), photo credit Andrew Potter.
 (H) Emperor tamarin (*Saguinus imperator*), photo credit Emmanuel Keller.
 (I) Cotton-top tamarin (*Saguinus oedipus*), photo credit Andrew Potter.

infection, intraspecific aggression (Savage et al., 2021), and environmental stressors. Many of the species studied herein breed seasonally in the wild but more regularly in captivity (with artificial light cycles and constant humidity/food availability). Second, captive breeding programs often employ assistive reproductive technology and birth control techniques. We note that our results are consistent across these different

Table 1. Data sources and basic interbirth interval (IBI) statistics for each species

Species	Common name	Gestation length (days) ^{i,j}	Normal IBI range (Days) ^j	Analysis with complete dataset (N = 15,852)					Analysis eliminating IBIs < 92.5% of full gestation length (N = 15,527)				
				Individuals born (N)			LRT χ^2	LRTp	Individuals born (N)			LRT χ^2	LRTp
				Normal	Short	Long			Normal	Short	Long		
<i>Callimico goeldii</i> ^a	Goeldi's marmoset	150	[162–168]	444	259	1,665	91.5	<0.0005	495	177	1,665	64.9	<0.0005
<i>Callithrix geoffroyi</i> ^{b,c}	White-headed marmoset	144	[150–156]	339	223	1,308	12.3	0.0021	361	171	1,286	9.7	0.0078
<i>Callithrix jacchus</i> ^{d,e,f}	Common marmoset	144	[151–157]	1,379	560	1,892	52.5	<0.0005	1,540	298	1,892	42.4	<0.0005
<i>Cebuella pygmaea</i> ^a	Pygmy marmoset	142	[150–156]	45	51	84	8.3	0.016	46	49	81	6.6	0.037
<i>Leontopithecus chrysomelas</i> ^c	Golden-headed lion tamarin	125	[130–135]	394	112	1,158	42.4	<0.0005	394	76	1,158	26.5	<0.0005
<i>Leontopithecus chrysopygus</i> ^h	Black lion tamarin	125	[154–159]	24	51	182	1.5	0.46	24	45	182	1.7	0.42
<i>Leontopithecus rosalia</i> ^c	Golden lion tamarin	125	[132–138]	207	125	1,540	59.4	<0.0005	228	86	1,519	19	<0.0005
<i>Saguinus imperator</i> ^c	Emperor tamarin	152	[183–189]	23	120	168	10.6	0.005	20	115	168	8.6	0.014
<i>Saguinus oedipus</i> ^a	Cotton-top tamarin	184	[193–198]	532	232	2,735	47.4	<0.0005	498	251	2,702	9.2	0.01

IBI = interbirth interval. "Normal" IBI are the births located within 2.77 days of the peak IBI (see [STAR Methods](#)). We included only births with interbirth intervals less than 365 days because husbandry practices may have confounded patterns over longer periods of time. We report the results of Likelihood Ratio Tests (LRT) to evaluate whether removing the predictor variable of IBI significantly reduced the fit of the Cox proportional hazards model for each species.

^aWorld Association of Zoos and Aquariums.

^bEuropean Association of Zoos and Aquaria.

^cAssociation of Zoos and Aquaria.

^dUniversity of Zurich.

^eSouthwest National Primate Research Center.

^fMassachusetts Institute of Technology.

^gAustralasian Species Management Program.

^hInternational Studbook.

ⁱGestation lengths from (French et al., 2002; Hartwig, 1996). Specifically: *Callimico goeldii* (Hartwig, 1996), genus-level), *Callithrix geoffroyi* (Hartwig, 1996), genus-level), *Callithrix jacchus* (French et al., 2002), *Cebuella pygmaea* (French et al., 2002), *Leontopithecus chrysomelas* (French et al., 2002), *Leontopithecus chrysopygus* (average of the other two *Leontopithecus* species in our study from (French et al., 2002)), *Leontopithecus rosalia* (French et al., 2002), *Saguinus imperator* (average of 5 other *Saguinus* species from (Hartwig, 1996)), *Saguinus oedipus* (French et al., 2002; Hartwig, 1996).

^jRounded to the nearest integers, we recalculated these values for the analysis excluding IBIs < 92.5% gestation time.

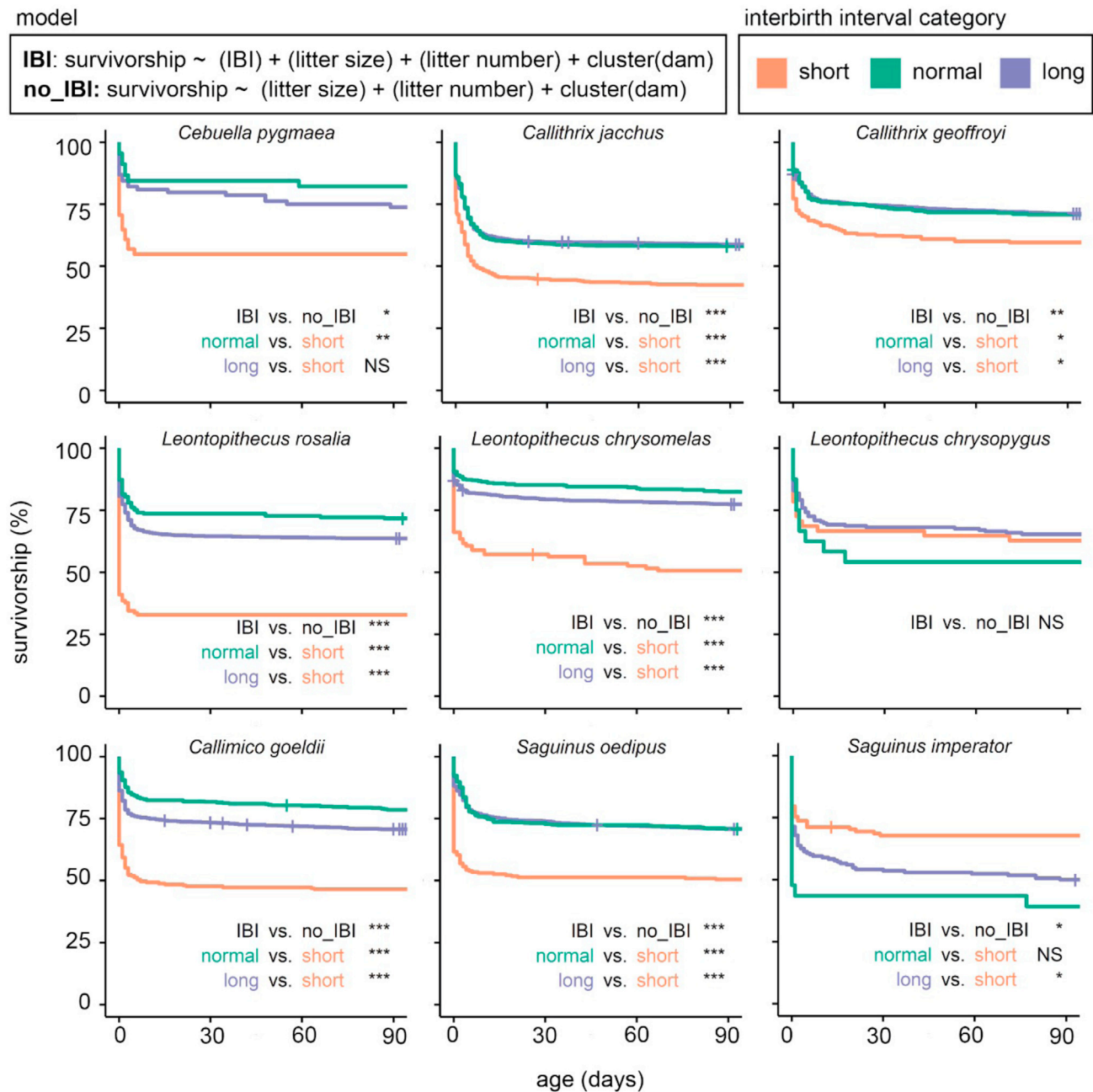


Figure 2. In most of the species studied, monkeys born after a short interbirth interval (IBI) had significantly higher risks of infant mortality than did monkeys born after longer IBIs.

In each panel, we report whether the Cox proportional hazards model including IBI was a better fit than one without (Likelihood Ratio Test) as well as whether short IBIs were associated with higher mortality compared to normal and long IBIs (Cox Proportional Hazards). For eight species, including IBI significantly improved the model fit. Of those models, short IBIs predicted worse survivorship than did normal IBIs for seven species and short IBIs predicted worse survivorship than long IBIs for six species. For the eighth species (*Saguinus imperator*), long IBI predicted significantly worse survivorship than did short. Censored data (animals still alive at an age less than 90 days and therefore their survivorship through infancy is not yet known) are indicated by vertical tick marks on the survival curves. Models also included litter size and litter number (what number litter it was for that dam) as predictors and controlled for dam identity by clustering by dam. We analyzed N = 15,852 total births; we also ran the same analysis removing inviable births—i.e., all IBIs < 92.5% the gestation time of a given species—and found comparable results (N = 15,527 births; Figure 2A; see STAR Methods). Full statistical results for both analyses are in Table 1. ***p ≤ 0.0005; **p ≤ 0.005; *p ≤ 0.05.

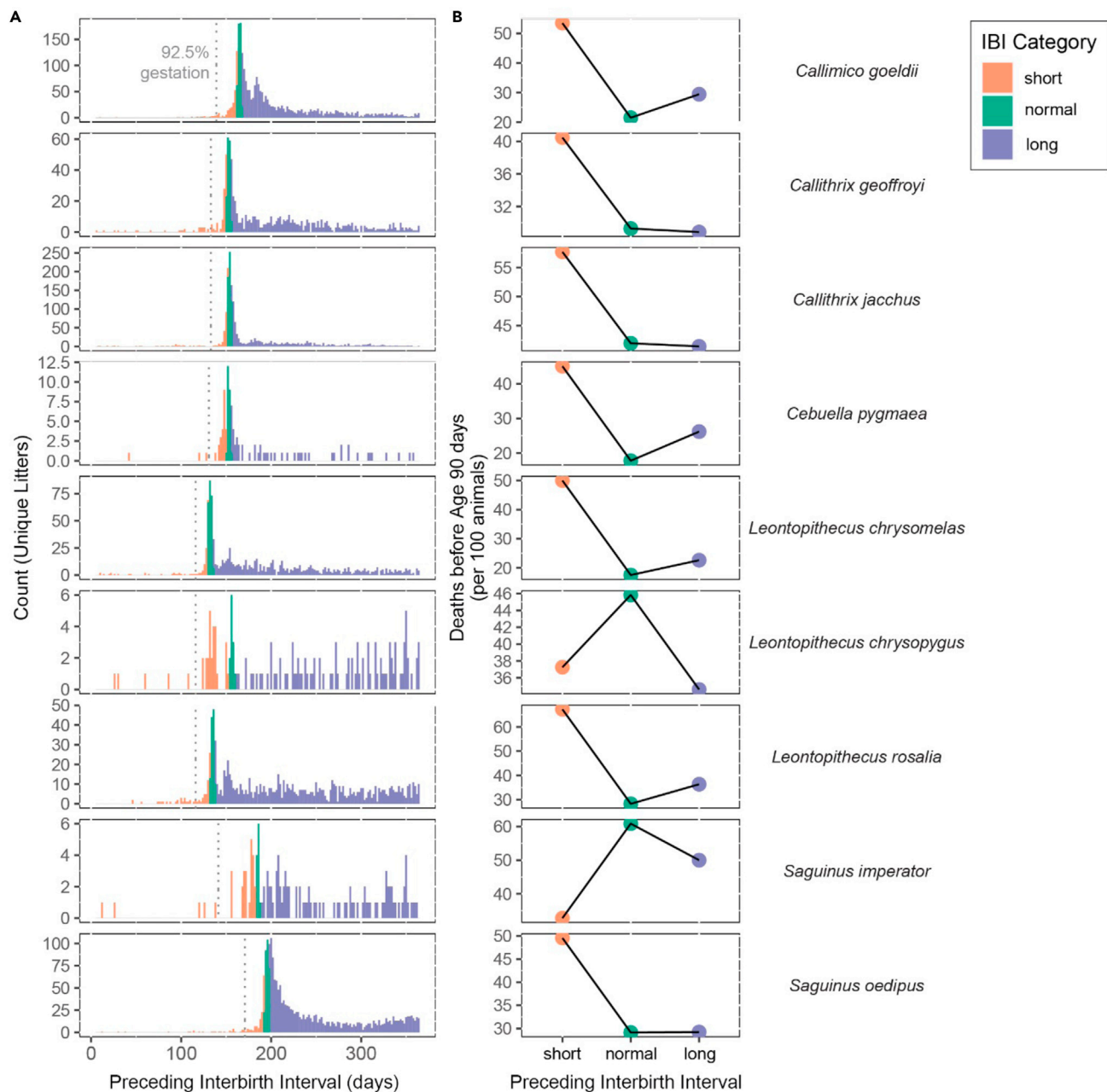


Figure 3. Distribution of interbirth intervals (IBI) and infant mortality data for nine species of callitrichine monkeys.

(A) Histogram of births falling into early, normal, or late interbirth interval (IBI) designations for each callitrichine species (N = 15,852). Dotted lines indicate the length of time required for 92.5% of a gestation length for each species—i.e., the minimal length of time required for a viable birth (Howson et al., 2012). We repeated the analysis excluding data left of the dotted line and found comparable results (N = 15,527).

(B) Number of deaths per 100 animals for infants assigned to short, normal, or long IBI groups.

captive conditions, indicating that the observed patterns are not entirely context-dependent. Third, some births within the short IBI category may have been pre-term births (but see discussion in STAR Methods). However, after eliminating these potentially unviable births, the patterns of infant survivorship were consistent with our original findings (see STAR Methods; Table 1). Fourth, we studied broad demographic trends. Coupling these findings with details of social behavior and physiologic profiles would provide important mechanistic insights into the factors underlying infant mortality in callitrichines.

Conclusions

We have shown that captive callitrichine monkeys, like humans and rhesus monkeys, have higher infant mortality after short IBIs. In addition to advancing the understanding of life history trade-offs and sibling competition, this work may have implications for the management of captive callitrichines, namely that captive breeding programs should favor longer IBI to increase infant survivorship. Future studies could consider how parent-offspring conflict shapes the evolution of IBI: in short, a longer interbirth interval may be better for a given infant's survivorship but worse for a parent's overall reproductive performance (Haig, 2014). Our work further reinforces the hypothesis that the elevated mortality risks associated with short birth spacing may result from fundamental biological constraints on reproductive rates of human and nonhuman primates—a basic trade-off between quality and quantity.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2021.103724>.

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AUTHOR CONTRIBUTIONS

Brett M. Frye and Dakota E. McCoy conceived the work and wrote the manuscript with support from Jennifer Kotler, David Haig, and Suzette Tardif. Amanda Embury, Judith M. Burkart, Monika Burns, Simon Eyre, Peter Galbusera, Jacqui Hooper, ArunI DOE, AgustínLópez Goya, Jennifer Mickelberg, Marcos Peromingo Quesada, Miranda Stevenson, Sara Sullivan, Mark Warneke, Sheila Wojciechowski, and Dominic Wormell provided the datasets. All authors reviewed the manuscript and contributed to the interpretation of the results.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Other		
Code to analyze survivorship using Cox Proportional Hazards Models	This paper	N/A

RESOURCE AVAILABILITY

This study did not generate new unique materials.

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Brett Frye (bfrye05@gmail.com).

Materials availability

Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Data and code availability

- Data: The data used in this study came from participating zoos and laboratories; authors interested in using this data must receive permission from those institutions for their specific research questions.
- Code: All original code is available in this paper's supplemental information ([Data S1](#), [S2](#), and [S3](#)).
- Art: Inquiries about photography should be directed to individual artists (contact information in [Figure 1](#)).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We studied nine species of callitrichine monkeys using demographic data from zoo and laboratory populations ([Figure 1](#); [Table 1](#); *Callithrix geoffroyi*, *Callithrix jacchus*, *Cebuella pygmaea*, *Saguinus imperator*, *Saguinus oedipus*, *Leontopithecus chrysomelas*, *Leontopithecus chrysopygus*, *Leontopithecus rosalia*, and *Callimico goeldii*). We included data from infants of all sexes.

METHOD DETAILS

To categorize interbirth intervals (IBIs) as short, normal, or long for each species, we (1) identified the peak interbirth interval on a density distribution, (2) labeled the births within 2.77 days of the peak in either direction as "normal", and (3) labeled births before and after that normal range as short and long ([Figure 3A](#); [Data S2](#) and [S3](#)). We chose the threshold of 2.77 days because it represented the one-fifth of births closest to the peak for our three most well-sampled species (2.77 is the average of the value for *Callithrix jacchus*, *Callimico goeldii*, and *Saguinus oedipus*). We eliminated IBIs longer than one year in duration on the assumption that those animals may have been subject to birth control practices (e.g., oral contraceptives or social separation). We excluded IBIs shorter than 5 days, because these may represent late-born littermates or errors in data entry. Our calculated values for normal IBI were similar to those reported in the literature ([French et al., 2002](#); [Hartwig, 1996](#)). We repeated all analyses using both (i) all IBI data and (ii) IBI data excluding inviable births, i.e., births that were less than 92.5% of a species' gestation time (see details in [STAR Methods](#)).

QUANTIFICATION AND STATISTICAL ANALYSIS

We constructed Cox Proportional Hazards models of survivorship using the "coxph" function in the R package "survival" ([Therneau and Grambsch, 2000](#)). We included litter size as a predictor variable, because singletons have higher survivorship than litters ([McCoy et al., 2019](#)), litter number (i.e., what number litter it was for a given dam) to control for parity, and the IBI category (short, normal, or long). We also clustered births by dams to account for non-independence of siblings born to the same mother. In each model, we right

censored the data of monkeys that were alive at the time of data collection and for those that survived past 90 days postpartum. All sample sizes, data distributions, and statistical information are available in [Figures 2 and 3](#) and [Table 1](#). See [Data S1](#), [S2](#), and [S3](#) for R Code.

We used Likelihood Ratio Tests (LRT) to evaluate whether removing the predictor variable of IBI significantly reduced the fit of the Cox proportional hazards model ([Table 1](#); [Data S1](#)). We then reported the Cox proportional hazard model output, that is, whether individuals with short IBIs had significantly higher mortality before age 90 days compared to individuals born after normal or long IBIs.

After visualizing the distribution of short, normal, and long IBIs, we determined that some of the births which fell into the short IBI category likely resulted from pre-term births (we note that some of the monkeys in the normal and long IBI categories were doubtless pre-term births as well, which is why we initially analyzed the data without removing any data points). We therefore re-analyzed the data, eliminating those births in which IBIs were less than 92.5% of the average gestation time for each species ([Table 1](#); [French et al., 2002](#); [Hartwig, 1996](#)). We selected this cut-off because this metric represents the designation between pre- and full-term pregnancies in humans ([Howson et al., 2012](#)). We report these findings in [Table 1](#). Overall, this more stringent analytic approach produced results that were consistent with our original analyses. That is, individuals belonging to the short IBI category had significantly higher risk of mortality during the period of infancy for seven of the nine species studied.

ADDITIONAL RESOURCES

All original code is available in this paper's supplemental information ([Data S1](#), [S2](#), and [S3](#)).