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RESEARCH ARTICLE

Food mobility and the evolution of grasping behaviour: a case study in strepsirrhine primates

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ABSTRACT

Manual grasping is widespread among tetrapods but is more prominent and dexterous in primates. Whether the selective pressures that drove the evolution of dexterous hand grasping involved the collection of fruit or predation on mobile insects remains an area of debate. One way to explore this question is to examine preferences for manual versus oral grasping of a moving object. Previous studies on strepsirrhines have shown a preference for oral grasping when grasping static food items and a preference for manual grasping when grasping mobile prey such as insects, but little is known about the factors at play. Using a controlled experiment with a simple and predictable motion of a food item, we tested and compared the grasping behaviours of 53 captive individuals belonging to 17 species of strepsirrhines while grasping swinging food items and static food items. The swinging motion increased the frequency of hand-use for all individuals. Our results provide evidence that the swinging motion of the food is a sufficient parameter to increase hand grasping in a wide variety of strepsirrhine primates. From an evolutionary perspective, this result gives some support to the idea that hand-grasping abilities evolved under selective pressure associated with the predation of food items in motion. Looking at a common grasping pattern across a large set of species, this study provides important insight into comparative approaches to understanding the evolution of the hand grasping of food in primates and potentially other tetrapod taxa.

KEY WORDS: Food properties, Grasping origin, Grip type, Hand, Predation, Nocturnal visual predation hypothesis

INTRODUCTION

Prehension, defined as the ‘application of functionally effective forces by any appendage to an object for a task’ (Sustaita et al., 2013, p. 381) is a fundamental behaviour in a large number of tetrapods. It is crucial in various behavioural contexts such as feeding, moving, and mating or other social interactions (Brunon et al., 2014; Karl and Whishaw, 2013; Pouydebat et al., 2014; Sustaita et al., 2013). Although prehensility exists in many vertebrates, precise manual dexterous grasping (i.e. reach and retrieve) and manipulation of objects is thought to be particularly developed in primates. It is even considered by many to be one of the defining features of the taxa (Bishop, 1964; Clark, 1959; Lemelin and Schmitt, 1998; Napier, 1956, 1960; Pouydebat et al., 2014; Wood, 1916).

The evolution of prehensility in general has been linked to arboreal habits (Fabre et al., 2013; Sustaita et al., 2013; Nyakatura, 2019) and the idea that prehensile hands are associated with an arboreal lifestyle has been widely accepted since the early 20th century. However, which specific selective pressures drove the development of primate manual prehensility remains an area of debate. Wood (1916) articulated the idea that the primate hand, in addition to serving as a prehensile organ like the foot, evolved for the manipulation of objects. His arguments were expanded by Cartmill (1972, 1974a,b), who rejected a simple general model of arboreal living to explain orbital convergence and prehensile clawless cheiredia. He argued instead that prehensile clawless hands, along with forward-facing eyes, evolved in association with insect predation in a terminal (fine-branch) environment, especially under low light conditions (Cartmill, 1992), an idea that became known as the nocturnal visual predation (NVP) hypothesis. Sussman and others challenged this view and proposed that grasping evolved in association with the evolution of angiosperms, arguing that primate hand prehensility was selected together with colour vision as an adaptation for exploiting fruits and flowers (Hellner-Burris et al., 2010; Rasmussen, 1990; Regan et al., 2001; Sussman, 1991; Sussman and Raven, 1978). Rasmussen (1990) synthesised the two hypotheses and proposed that grasping was primarily selected for harvesting fruits in the thin branch niche, whereas other primate features, such as orbital convergence, evolved subsequently as adaptations for insect predation (see Nityananda and Read, 2017, for a review).

Strepsirrhines are a monophyletic group of primates located near the base of the primate tree and are thought to be more representative of early primates than anthropoids. Nevertheless, they have their own evolutionary history, leading to broad diversification of hand morphology and function, with roughly 100 highly ecologically, morphologically and socially divergent species. Contrary to catarrhines, they seem to show a unique (i.e. one) whole-hand power grip with no digit individualisation (Bishop, 1962, 1964; Christel and Fragaszy, 2000; Peckre et al., 2019; Regan et al., 2001; Reghem et al., 2013; Schöneich, 1993). Nevertheless, all strepsirrhine species appear to be able to grasp with the hands, and significant variation seems to exist in the propensity of these species to use their hand to grasp static objects (Peckre et al., 2016). As a result, they represent an ideal group to test hypotheses about the factors driving the evolution of hand-grasping ability in primates.

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Whether the selective pressures that drove the evolution of dexterous hand prehensility involved the collection of fruit or predation on mobile insects remains an area of debate. One way to explore this question is to examine preferences for manual versus oral grasping of a moving object. Previous studies on strepsirrhines showed a preference for oral grasping when grasping static food items and a preference for grasping strategies involving the hand(s) when grasping living, mobile prey (Nekaris, 2005; Reghem et al., 2011; Scheumann et al., 2011; Siemers et al., 2007; Toussaint et al., 2013, 2015; Table 1). Interestingly, Toussaint et al. (2013) also showed that hand grasping was increased by both fast- and slow-living prey (cockroaches versus mealworms; Table 1). These results offer support for the NVP hypothesis, but little is known about the specific factors at play in this increased hand use.

First, while the mobile property of living prey is associated with increased hand use compared with oral prey capture, these tests compared food items that differ not only in their mobility but also in their size, Young's modulus and fracture toughness. These are properties that are known to influence grasping strategies (Nekaris, 2005; Peckre et al., 2019; Petter, 1962; Pouydebat et al., 2014; Scheumann et al., 2011; Toussaint et al., 2013, 2015). Toussaint et al. (2015) were the first to test the specific use of the hands to grasp a mobile version of an otherwise static food item by swaying a piece of banana on a string. This static-to-mobile approach reduces the confounding factors due to differences in food properties between the mobile and static food items tested in prior studies (Table 1). More importantly, we argue that this approach also allows testing whether such a simple, predictable movement is sufficient to increase hand use or whether this change in grasping strategy is associated with characteristics specific to living mobile prey that may move in more complex and unpredictable directions.

Second, most of the studies testing for the effect of food mobility on grasping strategies report observations in an arboreal environment. Yet, substrate characteristics are also known to influence grasping strategies (Fabre et al., 2017; Toussaint et al., 2015). Hence, though there is consensus on the importance of both the arboreal environment and predation for the evolution of manual-grasping abilities, the effects of substrate and predation on the evolution of grasping abilities still need to be better distinguished by being tested independently.

In this study, we quantitatively tested the effect of swinging food items on grasping behaviours in a broad sample of strepsirrhine species on a non-arboreal substrate while controlling for the effect of food properties. By doing so, we specifically aimed to identify the factors at play in the increased hand use observed and particularly to investigate whether a simple swinging motion is sufficient to increase hand use when grasping food items. The results of Toussaint et al. (2015) in the grey mouse lemur (*Microcebus murinus*) allow us to predict that food items will be grasped significantly more often with the hand(s) during simple, predictable swinging movements as compared with static food items.

MATERIALS AND METHODS

Animals and housing

We collected and analysed data for 53 individuals (30 males and 23 females) belonging to 17 species of strepsirrhines from six out of the seven extant families (excluding the Lepilemuridae; Table 2). All data were collected at the Duke Lemur Center (Durham, NC, USA), where housing conditions and enrichment are similar for all species (https://lemur.duke.edu/discover/for-researchers/facilities/). Animal handling was performed in compliance with the International Primatological Society (IPS) Guidelines for the Use of Nonhuman Primates in Research according to the protocol IACUC #A089-14-04 approved by the Duke University Institutional Animal Care and Use Committee (IACUC). For each individual, relative age was calculated by dividing the actual age of the individual by the longevity of the species in question (based on Zehr et al., 2014; Table 2).

Experimental setup

We first videotaped each individual in its home enclosure for 1–7 days during its usual feeding period. Next, we performed and videotaped 5–11 mobile food grasping trials per individual as follows. A food item was hung on a 70×0.5 cm sterilisable, lightweight metal bar that was then swung by a staff member in a linear, pendular motion 30 cm above the ground in front of the animal. Alternatively, for the smallest species, *Cheirogaleus medius*, *Nycticebus coucang* and *Nycticebus pygmaeus*, the food item was instead hung on a rope (the IACUC was concerned that larger species could trap and injure their fingers in the rope). The pendulum was pushed to reach an angle of 45 deg from its vertical rest position. Grasping events that occurred after the pendulum was slowed down by prior failed grasps were not included in the analyses. The rope and metal bar pendulum were sanitised after each recording session and sterilised after each recording day. We used digital video cameras (Sony HDR-PJ790V, full HD 1080, 24.1MP; Sony HDR-SR11, 10.2MP; Sony Handycam, HDR-PJ230, 8.9MP; Sony HDR-CX240E, full HD 1080, 9.2MP) for the diurnal species and a low light digital video camera (Sony HDR-SR11 10.2MP) for the nocturnal species.

Considering the variation of the natural diets between the species tested and in accordance with the protocols approved by the Duke Lemur Center and the IACUC, it was not possible to use identical food items across all species. For the static test procedure, the individuals were observed grasping food items included in their usual diet (Table S1). For the mobile test procedure, for each species, one food type was chosen from their usual diet in order to maximise the motivation of the species to participate in the experiment (Table 2).

Table 1. Summary of the items used and associated grasping strategies observed in precedent studies on strepsirrhine grasping strategies

	Mobile		Static		
Species	Food item used	Preferred grasping strategy	Food item used	Preferred grasping strategy	Reference
Loris lydekkerianus	Insects	Two hands	Gum	Mouth	Nekaris, 2005
Microcebus murinus	Insects	Hands	/	/	Siemers et al., 2007
	Mealworms	Hand–mouth combination	/	/	Scheumann et al., 2011
	Mealworms	One or two hands	Banana piece	Mouth	Toussaint et al., 2013
	Crickets	One or two hands	Banana piece	Mouth	Toussaint et al., 2013
	Cockroaches	One or two hands	Banana piece	Mouth	Toussaint et al., 2015
	Banana piece swaying on a string	One or two hands	Banana piece	Mouth	Toussaint et al., 2015

Table 2. List of individuals included in the different datasets

Species (taxonomic authority)	Family	Activity pattern	Item used for mobility test	Duke Lemur Center ID	Sex	Relative age	Datasets[1]	No. events full dataset		Average no. failures		No. events restricted dataset	
								Static	Mobile	Static	Mobile	Static	Mobile
Cheirogaleus medius É. Geoffroy 1812	Cheirogaleidae	Nocturnal	Mealworm	Aucklet	M	0.31	1, 2, 3	9	6	0	0.7	1	6
				Francolin	M	0.22	1, 2	12	5	0	1.2	–	–
				Ibis	M	1.18	1, 2, 3, 4	18	5	0	0.2	5	5
				Tananger	M	0.19	1, 2	15	5	0.2	0.8	–	–
Daubentonia madagascariensis Gmelin 1788	Daubentoniidae	Nocturnal	Peanut	Merlin	M	1.39	1	4	5	0	1.2	–	–
				Morticia	F	0.50	1	2	6	0	1.2	–	–
				Nozy	M	1.16	1, 2	7	6	0	1.2	–	–
				Ozma	F	1.23	1, 2	5	6	0	0.8	–	–
Eulemur collaris É. Geoffroy 1817	Lemuridae	Diurnal	Grape	Giscard	M	1.34	1, 2	31	5	0.1	0	–	–
				Martine	F	1.39	1, 2	13	5	0	0.2	–	–
				Pascal	M	1.08	1, 2, 3	8	5	0	1	2	5
Eulemur coronatus (Gray 1842)	Lemuridae	Diurnal	Grape	Aria	F	0.09	1, 2, 3	17	5	0	0.6	2	5
				Geb	M	1.14	1, 2, 3	13	5	0	0.6	3	5
Eulemur flavifrons Gray 1867	Lemuridae	Diurnal	Grape	Hemsworth	M	0.09	1, 2, 3	46	7	0	0.3	1	7
				Margaret	F	0.25	1, 2	23	5	0	0	–	–
				Olivier	M	1.23	1, 2, 3, 4	20	5	0	0.8	9	5
				Presley	M	0.25	1, 2, 3, 4	20	5	0	0	7	5
Eulemur macaco (Linnaeus 1766)	Lemuridae	Diurnal	Grape	Harmonia	F	1.77	1	15	4	0	1	–	–
				Hesperus	M	1.78	1, 2	30	5	0	0.8	–	–
Eulemur mongoz Linnaeus 1766	Lemuridae	Diurnal	Grape	Flor	F	1.44	1, 3	142	4	0	0.2	1	4
				Julio	M	1.09	1, 2, 3	97	10	0	0.3	2	10
				Pedro	M	1.08	1, 2, 3	20	5	0	0	1	5
Eulemur rubriventer I. Geoffroy 1850	Lemuridae	Diurnal	Grape	Cheyenne	F	1.34	1, 2, 3	15	6	0.1	0	1	6
				Hopi	F	1.25	1	10	3	0	2	–	–
				Iroquois	M	1.14	1, 2, 3, 4	20	5	0.1	0	14	5
Eulemur rufus (Audebert 1799)	Lemuridae	Diurnal	Grape	Cardinal	M	1.00	1, 2, 3	23	7	0	0.1	1	7
Hapalemur griseus Link 1795	Lemuridae	Diurnal	Grape	Beavis	M	0.89	1, 2, 3	70	7	0	0	1	7
				Beeper	F	0.82	1, 2, 3	41	6	0	0	1	6
				Beware	F	0.99	1	35	4	0	0.2	–	–
Lemur catta Linnaeus 1758	Lemuridae	Diurnal	Grape	Aracus	M	1.43	1, 2, 3, 4	14	6	0	0	5	6
				Gretel	F	0.17	1, 3	19	4	0	0.8	13	4
				Licinius	M	0.29	1, 3	4	4	0	0	1	4
				Liesl	F	0.40	1, 3	22	2	0	0	10	2
				Schroeder	F	1.38	1, 2, 3, 4	17	8	0	1.8	7	8
				Tellis	F	0.64	1	4	6	1.2	0	–	–
Nycticebus coucang (Boddaert 1785)	Lorisidae	Nocturnal	Mealworm	Dharma	F	1.60	1, 2, 3	9	7	0	0.3	3	7
Nycticebus pygmaeus Bonhote 1907	Lorisidae	Nocturnal	Mealworm	Flea	F	1.53	1	3	6	0	0.3	–	–
				Junebug	F	0.73	1, 3	35	4	0	0	17	4
				Moth	M	0.50	1, 3	3	5	0	0	3	5
Otolemur crassicaudatus É Geoffroy 1812	Galagidae	Nocturnal	Grape	Pretoria	F	0.91	1, 2, 3, 4	13	9	0	0	5	9
Propithecus coquereli A. Grandidier, 1867	Lemuridae	Diurnal	Cucumber	Antonia	F	1.43	1, 2	65	7	0	0.3	–	–
				Bertha	F	0.34	1, 2, 3	28	6	0	0	1	6
				Gordian	M	1.62	1, 2	23	10	0	0.1	–	–

Continued

Table 2. Continued

Species (taxonomic authority)	Family	Activity pattern	Item used for mobility test	Duke Lemur Center ID	Sex	Relative age	Datasets[1]	No. events full dataset		Average no. failures		No. events restricted dataset	
								Static	Mobile	Static	Mobile	Static	Mobile
				Pompeia	F	0.51	1, 2	62	5	0	0.4	–	–
				Tiberius	M	2.30	1, 2	17	6	0	0.2	–	–
Varecia rubra (É. Geoffroy 1812)	Lemuridae	Diurnal	Grape	Borealis	M	1.23	1, 2, 3, 4	13	5	0	2.4	8	5
				Hunter	M	0.86	1, 2	18	6	0	1.3	–	–
Varecia variegate Kerr 1792	Lemuridae	Diurnal	Grape	Amor	M	0.09	1, 2, 3, 4	21	6	0	1	7	6
				Hershel	M	0.09	1, 2, 3, 4	19	5	0	0.2	6	5
				Kizzy	F	0.51	1, 2, 3	32	8	0	0.2	2	8
				Krok	M	0.29	1, 3	24	4	0	0.5	13	4
				Magellan	M	0.24	1, 2, 3	14	9	0	0.1	1	9
				Rees	M	0.09	1, 2, 3	30	7	0	0.7	4	7

[1] Datasets in which the individual was included with: (1) full dataset (n=53 individuals, N=17 species), (2) restricted dataset including only the grips of static food items when these items were of the same nature as the one provided in the mobile food trials (n=33 individuals, N=15 species), (3) full dataset excluding individuals that were not observed for at least five item grasping events in each condition (n=39 individuals, N=16 species), (4) restricted dataset including only the grips of static food items when these items were of the same nature as the one provided in the mobile food trials and excluding individuals that were not observed for at least five item grasping events in each condition (n=10 individuals, N=7 species).

A prior study showed that the size, Young's modulus and fracture toughness of the food significantly impact the grasping strategies adopted by strepsirrhines (Peckre et al., 2019). In particular, small items were associated with an increase in mouth grasping compared with strategies involving the hand(s). However, Young's modulus and fracture toughness did not significantly impact the grasping strategy associated with small items (whereas they did when considering big items). To account for size as a factor of variation, we only consider grasping of small items. In accordance with Peckre et al. (2019), we considered an item as 'small' when it was narrower than one hand width of the focal species. Choosing a relative measure of the size of the item allowed us to control for the high variability of body size across the species tested. As Young's modulus and fracture toughness did not impact small item grasping strategy (Peckre et al., 2019), we examined 21 different small items across a broad range of Young's modulus and fracture toughness values (Table S1). Published data for Young's modulus (median 1.4 MPa, range 0.2–50.4 MPa) and fracture toughness (median 308.6 J m^{-2}, range 20.0–1030.6 J m^{-2}) in a sub-sample of the small items (N=12) indicate a significant positive correlation (r=0.71, P=0.01) between the two material properties (raw data and citations provided in Table S1). The nine small food items for which there are no published data are almost certainly within the range reported here as they consist of similar fruits and vegetables.

As the diameter and the orientation of the support also significantly impact grasping behaviours (Fabre et al., 2017; Toussaint et al., 2015), we tested both food conditions while the individuals were sitting on the floor of the enclosure or a large wooden board, thus simulating the terrestrial environment. These conditions correspond to the usual surfaces where these individuals receive their daily food ration.

Data analysis

We reviewed the videotapes and noted every instance of identifiable small food item grasping using Avidemux 2.6.8 (Free Software Foundation, Inc.). Grasping strategies were characterised by the first body part(s) to hold onto the object to be lifted from the substrate or pendulum. Grasping strategies were thereby defined as 'oral' when only the mouth was used, 'unimanual' when one hand only was used, 'bimanual' when both hands were used simultaneously, and combined 'oral–unimanual' or combined 'oral–bimanual' when the mouth and the hand(s) were used simultaneously. We also noted, for each item grasped, the number of non-successful attempts preceding the successful grip. The resulting dataset is provided as supplementary material (Table S2).

Statistical analyses

Statistical analyses were performed using R version 3.5.2 (http://www.R-project.org/). The effect of the mobility of the food on grasping strategies was first tested using Fisher's exact tests based on the proportion of grips involving each strategy. These proportions were first averaged for each individual and then per species. These tests were run on: (i) the full dataset and (ii) a restricted dataset including only the grips of static food items when these items were of the same nature as the one provided in the mobile food trials for a given species (Table 2). For these tests, we excluded individuals that were not observed for at least five item grasping events in each condition (Table 2) as we considered that the calculated proportions were not informative enough when n<5. As a result, these tests were run on a full dataset of 39 individuals (16 species) and a restricted dataset of 10 individuals (7 species) (respectively, datasets 2 and 4 in Table 2). Using the above-described full dataset (dataset 2 in Table 2), we ran permutation tests for paired samples on the individual proportions for each grasping strategy independently to test for an effect of the mobility of the food on the grasping strategy adopted. The average number of failures preceding a successful grip per individual (based on the same full dataset, dataset 2 in Table 2) when grasping mobile and static food items was compared using a permutation test for paired data.

To further investigate the effect of mobility, relative age, sex and pendulum type on the grasping strategies adopted, we also ran a multinomial mixed model using the R package 'MCMCglmm' (Markov Chain Monte Carlo generalised linear mixed models; Hadfield, 2010; with the following parameters: burnin=15,000 and nitt=40,000). In this model, we expressed the probability of adopting one of the grasping strategies as a function of our variables of interest. To account for repeated measures and cluster-specific correlations, we included species and individual identity random intercepts. Because both bimanual and combined oral–bimanual strategies were used in less than 5% of the observed grips, we only used three broader grasping categories, namely oral, hand(s) (unimanual or bimanual) and oral–hand(s) (combined oral–unimanual or combined oral–bimanual). The sample for this model consisted of 1592 grips performed by 53 individuals belonging to 17 species (dataset 1 in Table 2). Because two individuals were the only representatives of their species, we grouped them with the individuals of their phylogenetically closest sister species to allow treatment of the species-specific effect as a random factor. Hence, we grouped the *Otolemur crassicaudatus* (*n*=1) and the *N. coucang* (*n*=1) with the *N. pygmaeus* (*n*=3). Given that the effect of the phylogenetic history on these behavioural traits is not straightforward, we also ran the models while grouping the three individuals that were the only representatives of their species under the same fictive species. The results obtained with both grouping methods were similar; therefore, we chose to present the results of only the first method. Stability of the model was assessed by calculating the 95% credible intervals for posterior means based on 100 model calculations (Table 3; Fig. S1).

To explore how the unimanual grasping strategy was influenced by the different variables of interest, a generalised linear mixed model (GLMM; Baayen et al., 2008) with a binomial response distribution, a logit link function and a 'bobyqa' optimiser was fitted using the glmer function of the 'lme4' R package (version 1.1-21; Bates et al., 2015). As in the multinomial model described previously, mobility, relative age, sex and pendulum type were included as fixed effects, and individual identity and species as random effects. To keep the rate of type I errors at the level of 5% (Barr et al., 2013; Schielzeth and Forstmeier, 2009), we included all possible random slope components (mobility, sex and age within species and mobility within individual identity). We manually dummy coded and centred mobility and sex before including it as a random effect. Age was *z*-transformed before being included as a random effect. Initially, we also included the corresponding correlations among random intercepts and slopes. The correlation between intercepts and slopes of mobility within individual identity seemed to be unidentifiable as indicated by absolute correlation parameters being essentially one (Matuschek et al., 2017); in consequence, we excluded it from the model.

We assessed model stability by comparing the estimates obtained from the model based on all data with those obtained from models, excluding levels of the random effects one at a time (Nieuwenhuis, 2012; Fig. S2). To check for potential collinearity issues, we determined variance inflation factors (VIF) for a standard linear model excluding the random effects (Field, 2005). This revealed a VIF of 1.0 for the four fixed effects, showing that the results are not distorted by collinearity.

We compared the full model with a null model lacking the fixed effect of mobility but comprising the same random effects structure as the full model (Forstmeier and Schielzeth, 2011), using a likelihood ratio test (Dobson and Barnett, 2008). Confidence intervals were obtained using the function 'bootMer' of the package 'lme4', using 1000 parametric bootstraps. Tests of the individual fixed effects were derived using likelihood ratio tests with the function 'drop1' and its argument test set to 'Chisq' (Barr et al., 2013). We determined the effect sizes (R^2) using the function 'r.squaredGLMM' of the package 'MuMIn' (https://CRAN.R-project.org/package=MuMIn). The sample for this model consisted of 1592 grasping events (549 unimanual grips), performed by 53 individuals belonging to 17 species (dataset 1 in Table 2).

As an additional analysis, we ran these two models on the restricted dataset described above. The sample for these models consisted of 350 grips (220 unimanual grips) performed by 33 individuals belonging to 15 species (dataset 3 in Table 2). For the GLMM on this restricted dataset, the correlation between intercepts and slopes of mobility within individual identity seemed to be unidentifiable. Consequently, we excluded it from the model (Matuschek et al., 2017). Model stabilities are presented in Fig. S3 for the multinomial model and Fig. S4 for the GLMM.

Strepsirrhine species share a phylogenetic history and, therefore, cannot be considered as independent data points (Felsenstein, 1985). Previous studies showed that there is a significant phylogenetic signal in grasping behaviour associated with large items but not with small ones (Fabre et al., 2018; Peckre et al., 2016, 2019). We tested the presence of a phylogenetic signal in the coefficients of the effect of food mobility on grasping behaviour using the multivariate *K*-statistic using the R 'physignal' function included in the 'geomorph' package (Adams, 2014; https://CRAN.R-project.org/package=geomorph). The coefficients were extracted from GLMMs run on the full dataset for the two main strategies used in both conditions (i.e. unimanual and oral grips). The *K*-value is a scaling parameter for the correlations between species traits, relative

Table 3. Fixed effects of the multinomial model based on the full dataset (dataset 1)

		95% credible interval			Estimate		
	Posterior mean	Lower	Upper	Effective sample size	Min. (2.5%)	Max. (97.5%)	*P*-value
Intercept: oral	−15.45	−19.89	−10.26	14.88	−37.66	−10.91	**<0.001*****
Intercept: oral+hand(s)	1.28	−1.90	4.01	10.47	−8.69	18.17	0.455
Sex – male	1.14	−0.81	3.05	101.13	−1.14	3.00	0.230
Relative age	−1.47	−3.13	0.37	82.44	−4.02	0.18	0.101
Pendulum – rope	1.52	−2.44	4.81	154.03	−2.48	5.43	0.389
Oral: mobility – static	19.17	14.28	22.49	6.85	15.09	41.78	**<0.001*****
Oral+hand(s): mobility – static	11.70	8.15	15.17	5.39	8.43	28.49	**<0.001*****

Significant results are in bold. Asterisks indicate significance level: ****P*<0.001.

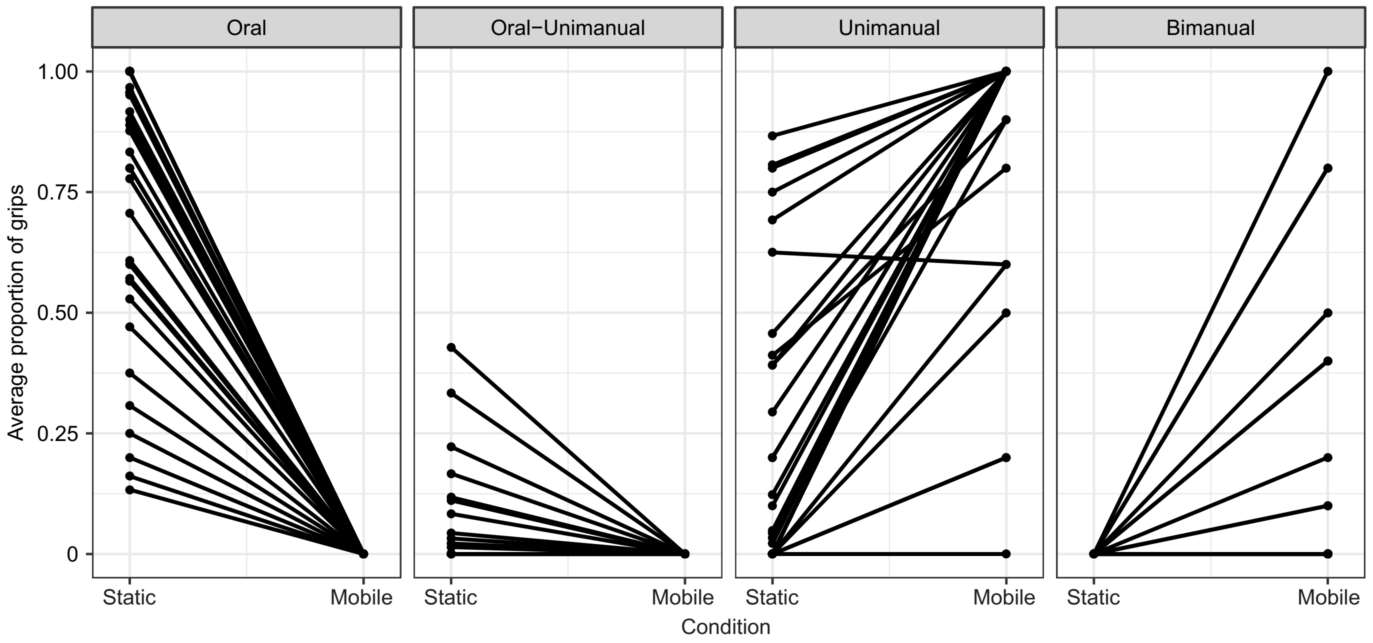

Fig. 1. Average proportion of usage of the four different grasping strategies per individual for mobile and static conditions (dataset 2). *n*=39 individuals.

to the correlation expected under a Brownian motion model of trait evolution. Values of *K*<1.0 correspond to traits being less similar among species than expected based on their phylogenetic relationships. We also tested independently the presence of a phylogenetic signal in the coefficients of the effect of food mobility on the probability of using a unimanual grip only using the R 'phylosig' function included in the 'phytools' package (Revell, 2012). We used a consensus phylogenetic tree in version 3 of the 10kTrees Project (Arnold et al., 2010).

RESULTS

Grasping strategies differed significantly according to the mobility of the food at both the species and individual level and for both grip subsets (Fisher's exact tests: $P<0.001$; Figs 1 and 2). When grasping mobile food items compared with grasping static food items, the individuals used on average significantly more unimanual (89.0±4.1% versus 18.6±4.5%; $Z=5.61$, $P<0.001$; Fig. 1) and bimanual grips (11.0±4.1% versus 0%; $Z=2.52$, $P=0.004$; Fig. 1) and significantly fewer oral (0% versus 77.2±4.5%; $Z=-5.88$, $P<0.001$; Fig. 1) and oral–unimanual grips (0% versus 4.0±1.5%; $Z=-2.46$, $P=0.001$; Fig. 1). No significant difference was found when comparing the average proportion of oral–bimanual grips for both food item categories (0% versus 0.2±0.2%; $Z=-1$, $P=1$).

Grasping was more stereotyped for mobile food items and was limited to only three grasping strategies (unimanual, bimanual and oral–unimanual) compared with five grasping strategies used when the item was static. Significantly more failed attempts preceding a successful grasp were observed when grasping mobile versus static food items (0.48±0.09 versus 0.01±0.01; $Z=4.03$, $P<0.001$; Fig. 3).

The multinomial model revealed significant effects of the food item mobility on the grasping strategy adopted (Table 3). When the item was static, the relative probability of choosing the oral strategy

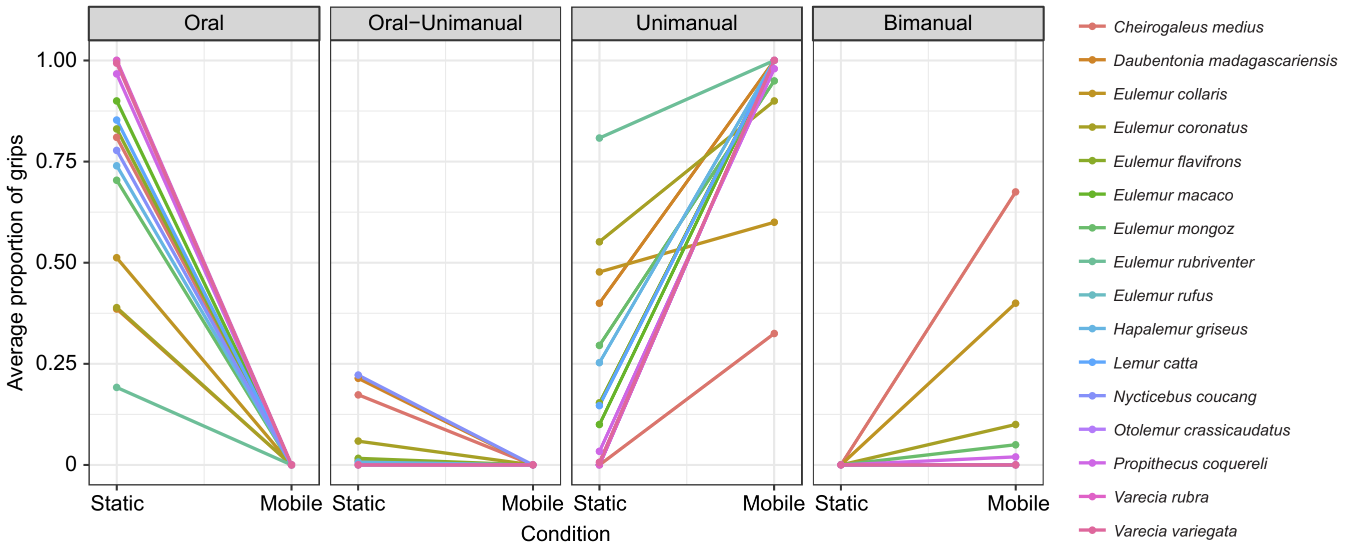

Fig. 2. Average proportion of usage of the four different grasping strategies per species for mobile and static conditions (dataset 2). *N*=16 species.

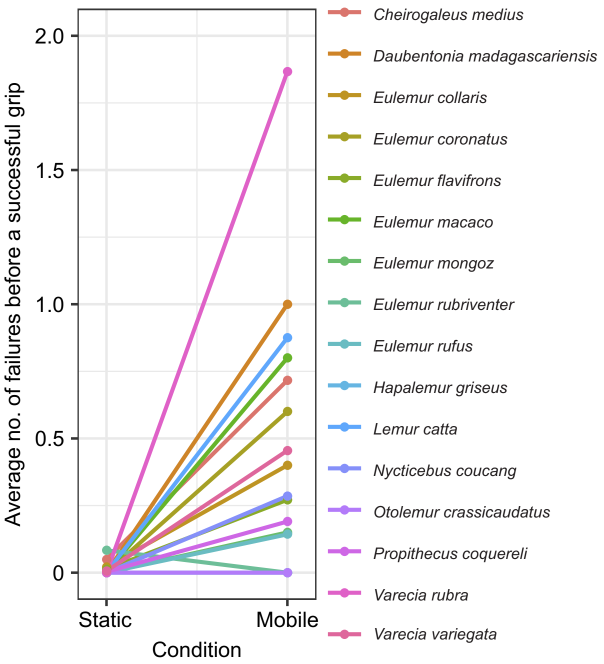

Fig. 3. Average number of failures preceding a successful grasp per species for mobile and static conditions (dataset 2). *N*=16 species.

to grasp the item increased dramatically versus choosing a manual strategy (β=19.17, 95% credible interval: 14.28–22.49; $P<0.001$; Table 3) or choosing a mouth–hand(s) combined strategy (β=11.70, 95% credible interval: 8.15–15.17; $P<0.001$; Table 3). Similar results were obtained for the multinomial model on the restricted dataset (Table 4). These multinomial models did not reveal any effect of the sex, the age of the individuals nor the pendulum type used on their grasping strategies (Tables 3 and 4).

The mobility of the food item significantly influenced the probability of unimanual grips (likelihood ratio test comparing full and null model: $\chi^2=24.23$, d.f.=1; $P<0.001$; marginal $R^2=0.49$, conditional $R^2=0.90$). The probability of using a unimanual grip to grasp a static item , as compared with the probability of using another grasping strategy, was significantly lower compared with when grasping a mobile food item (β=−9.99±1.84; $P<0.001$; Table 5; Fig. 4A). This effect was confirmed when using the more restricted dataset (likelihood ratio test comparing full and null model: $\chi^2=24.61$, d.f.=1; $P<0.001$; marginal $R^2=0.45$, conditional $R^2=0.98$; β=−17.38±6.14; $P<0.001$; Table 6; Fig. 4B). The linear models did not reveal any effect of age, sex or pendulum type used on this relative probability of grasping with one hand (Tables 5 and 6).

The effect of mobility on the probability of grasping with one hand varied considerably across individuals (s.d.=4.26) and species (s.d.=3.24). No correlation was observed between the random intercept of species and the random slope of the effect of mobility on the probability of grasping with one hand ($r=0.08$). There was no significant phylogenetic signal ($K_{\mathrm{mult}}=0.14$, $P=0.462$ and $K=0.14$, $P=0.482$ for unimanual strategy only) in the model coefficients of the effect of mobility on grasping strategy.

DISCUSSION

In this study, we quantified and compared the proportions of the different grasping strategies used by 53 captive individuals belonging to 17 species of strepsirrhines grasping static and swinging food items on a non-arboreal substrate, while controlling for the effect of three food properties (size, Young's modulus and fracture toughness). We observed increased hand use in comparison to mouth grasping in all of the 53 tested individuals. In most cases, the proportion of unimanual grips increased. However, in the few cases where this was not the case, the proportion of bimanual grips increased (Fig. 2). This result generalises previous observations made for strepsirrhines (Table 1) to a much broader range of species and simpler (predictable) food item motions. Indeed, it supports our prediction that even stereotypic, rhythmic, simple mobility of an otherwise static item induces a manual versus oral grasping pattern.

As mentioned in Materials and Methods, several factors could not be fully controlled for because of the diversity of the species tested and the associated protocols approved by the Duke Lemur Center and the IACUC. The pendulum device consisted of either a metal bar or a rope and the food items presented varied. In this study, we addressed the general pattern observed across species rather than species differences, and within a given species, all the mobility trials were performed with the same pendulum device and the same food items. Moreover, the directionality of the observed pattern (increased hand use) was similar for all species. Additionally, the type of pendulum used in the experiment was considered as a fixed effect and was not observed to significantly impact the grasping strategies across species. The presence of the effect was also not dependent on whether we considered the full dataset or the restricted dataset, which included only the grips of static food items when these items were the same as the items provided in the mobile food trials.

Our results provide evidence that the swinging motion of the food is a sufficient parameter to increase hand grasping in a wide variety of strepsirrhine primates. Previous studies have described an increase in hand use in strepsirrhines when performing more complex tasks (Jolly, 1964; Santos et al., 2005; Schöneich, 1993). Interestingly, our results also show that grasping mobile food items appears to be a more challenging task, with more failures preceding a successful grasp than when grasping a static food item. One could argue that our pendulum task is more complex simply because of its novelty and/or irrelevance for the individual tested. However,

Table 4. Fixed effects of the multinomial model based on the restricted dataset (dataset 3)

		95% credible interval			Estimate		
	Posterior mean	Lower	Upper	Effective sample size	Min. (2.5%)	Max. (97.5%)	*P*-value
Intercept: oral	−23.49	−34.82	−13.54	33.49	−48.93	−12.15	**<0.001*****
Intercept: oral+hand(s)	1.74	−4.86	8.54	5.59	−6.71	23.25	0.743
Sex – male	3.23	−4.38	11.03	74.49	−3.32	10.91	0.403
Relative age	−6.30	−14.54	1.28	24.66	−15.87	0.75	0.104
Pendulum – rope	−2.65	−14.53	7.86	67.02	−14.61	6.65	0.623
Oral: mobility – static	33.49	24.56	41.00	5.22	20.59	57.68	**<0.001*****
Oral+hand(s): mobility – static	25.90	18.40	32.48	5.48	10.71	39.80	**<0.001*****

Significant results are in bold. Asterisks indicate significance level: ***$P<0.001$.

Table 5. Results of the effects of mobility, sex, age and pendulum type on the probability of grasping with one hand only based on the full dataset (dataset 1)

			95% confidence interval					Estimate[5]	
	Estimate	s.e.	Lower	Upper	χ^2	d.f.	*P*-value	Min.	Max.
Intercept	8.01	1.86	5.20	13.02	–		–	6.32	8.80
Mobility[1] – static	−9.99	1.84	−15.40	−7.34	24.23	1	**<0.001*****	−10.90	−8.25
Relative age[2]	0.58	0.45	−0.41	1.63	1.66	1	0.198	0.36	0.74
Sex[3] – male	−0.89	1.01	−3.37	1.27	0.83	1	0.363	−1.50	−0.33
Pendulum type[4] – rope	−0.04	1.62	−3.59	3.02	0	1	1.000	−6.53	2.70

Significant results are in bold. Asterisks indicate significance level: ****P*<0.001. (1) Dummy coded with mobile being the reference category. (2) *z*-transformed to a mean of 0 and a standard deviation of 1. (3) Dummy coded with female being the reference category. (4) Dummy coded with rope being the reference category. Sample size is 1592 grasping events (549 unimanual grips), performed by 53 individuals belonging to 17 species. (5) Minimum and maximum model estimates derived by dropping levels of random effects one at a time.

compared with studies in captivity, increased proportions of hand use have also been reported in the wild where the presence of compliant substrates such as thin branches and wind may favour food mobility (Alexander, 1991; Schmitt, 1999).

From an evolutionary perspective, our results give some support to the idea that hand-grasping ability evolved under selective pressures associated with the predation of food items in motion. This is consistent with the ideas posited by Cartmill (1972, 1974a,b) and further elaborated by him (Cartmill, 1992) as the NVP hypothesis. However, our results also show that a simple repetitive swinging motion of the experimental setup, which undoubtedly confers a more predictable trajectory to the food item than that expected for a living insect, is sufficient to explain increased hand use. Hence, it also provides some support for the idea that primates would use a manual prey capture strategy in association with moving fruits. Indeed, a swinging motion such as the one used in this study may also be consistent with the movement of flowers or fruits located in the terminal branches and moving under the effect of the wind or other animal movements in the same tree. The fact that this effect was persistent across all species present in our dataset, including both nocturnal and diurnal species as well as insectivorous and non-insectivorous species, also supports this idea. Further experiments may be able to tease apart predation on live prey versus grasping of moving fruits and flowers using terminal branches in motion.

The absence of a significant phylogenetic signal on the effect of food mobility on grasping behaviour suggests that in the conditions considered here, closely related species of strepsirrhines do not have a more similar behavioural pattern compared with distantly related species. The absence of this type of phylogenetic signal was

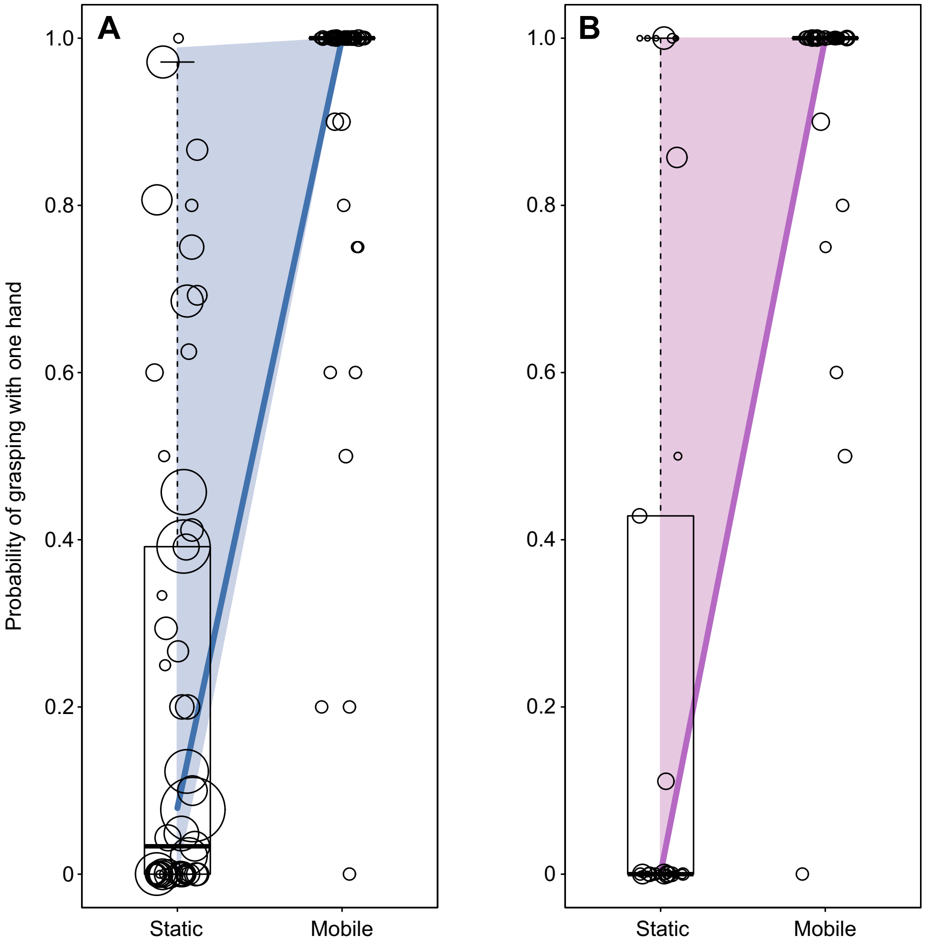

Fig. 4. Estimated and observed probability of grasping food items with one hand for mobile and static conditions (datasets 1 and 3). Fitted model (conditional on age being an average, and based on sex and pendulum type manually dummy coded and then centred) for (A) the full model (dataset 1; blue; *N*=1592 grips performed by 53 individuals from 17 species) and (B) the reduced model (dataset 3; pink; *N*=350 grips performed by 33 individuals from 15 species), and 95% confidence intervals. The individual proportion observed for each category is also indicated, with the size of the dot corresponding to the number of events considered. Please note that lines are drawn for illustrative purposes; continuity between the two conditions is not assumed.

Table 6. Results of the effects of mobility, sex, age and pendulum type on the probability of grasping with one hand only based on the restricted dataset (dataset 3)

			95% confidence interval					Estimate^5	
	Estimate	s.e.	Lower	Upper	χ^2	d.f.	*P*-value	Min.	Max.
Intercept	13.09	5.00	8.31	31.20	–	–	–	9.64	15.74
Mobility^1 – static	−17.38	6.14	−43.31	−11.55	17.70	1	**<0.001*****	−20.87	−12.55
Relative age^2	2.77	1.92	−1.92	8.81	0.76	1	0.384	0.95	3.31
Sex^3 – male	−2.95	3.03	−15.72	4.64	0.26	1	0.608	−5.62	−1.08
Pendulum type^4 – rope	−3.08	3.39	−13.89	5.63	−0.28	1	1	−8.13	5.37

Significant results are in bold. Asterisks indicate significance level: ***$P<0.001$. (1) Dummy coded with mobile being the reference category. (2) z-transformed to a mean of 0 and a standard deviation of 1. (3) Dummy coded with female being the reference category. (4) Dummy coded with rope being the reference category. Sample size is 350 grasping events (220 unimanual grips), performed by 33 individuals belonging to 15 species. (5) Minimum and maximum model estimates derived by dropping levels of random effects one at a time.

expected considering the fact that previous studies did not show any significant phylogenetic signal in grasping behaviour associated with small items (Fabre et al., 2018; Peckre et al., 2016, 2019).

Because probabilities cannot exceed one, we expected to find a negative correlation between the random intercept of species and the random slope of the effect of mobility on the probability of grasping with one hand. Indeed, because of this ceiling effect, the probability of grasping mobile food with one hand cannot increase as much in species where the probability of grasping a static food item with one hand is already high. The observed absence of a correlation is probably due to the increased use of the bimanual strategy in some species (Fig. 2). A correlation between the random intercept of species and the random slope of the effect of mobility on the probability of grasping with the hands (unimanual or bimanual grip) is then suspected.

The relatively low sample size per species does not allow discussion of the species-level patterns in detail. The identification of potential primitive characters (manual grasping of mobile food in this case) is suggested by the presence of common grasping patterns in a large number of morphologically diverse species. Considering that strepsirrhines are thought to be more representative of early primates than anthropoids, even though they have their own evolutionary history leading to broad diversification of hand morphology and function, this study provides a comparative approach to understanding the evolution of hand grasping of food items in primates and potentially other tetrapod taxa (Fragaszy and Crast, 2016; Pouydebat et al., 2008).

Hand use for feeding is indeed present in many extant animal orders and is even thought to have been present in the first terrestrial vertebrates (Whishaw and Karl, 2019). However, most of the current studies only provide data on a restricted number of species, preventing discussion of evolutionary continuity in a comprehensive evolutionary framework (Iwaniuk and Whishaw, 2000; Whishaw and Karl, 2019). Interestingly, the two comparable studies that have been carried out in other tetrapod taxa point to the same result of an increase in hand use when grasping mobile food items (*Monodelphis domestica* and *Rattus norvegicus*: Ivanco et al., 1996; *Xenopus laevis*: Anzeraey et al., 2017). Expansion of our tests to include additional tetrapod species would allow the observations on primates to be evaluated more broadly from a functional and evolutionary perspective.

Conclusions

Looking across a broad set of species within a clade to identify common grasping patterns is important for the identification of potential primitive characters. Our results show that even a simple repetitive swinging motion of the food was sufficient to initiate a profound change in food acquisition strategies by increasing hand grasping in a wide variety of strepsirrhine primates. The swinging motion of our experimental setup undoubtedly conferred a more predictable trajectory to the food item than the motion expected for a living insect, providing some support for the idea that early primates used a manual prey capture strategy in association with both living insects and moving fruits.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: E.P., A.-C.F.; Methodology: L.R.P., A.L., C.W., E.P., A.-C.F.; Software: L.R.P.; Validation: L.R.P., A.-C.F.; Formal analysis: L.R.P., A.L., A.-C.F.; Investigation: D.B., E.E., K.W., E.S., A.-C.F.; Resources: D.B., E.E., K.W., E.S., C.W., E.P., A.-C.F.; Data curation: L.R.P., A.L.; Writing - original draft: L.R.P., A.L., A.-C.F.; Writing - review & editing: L.R.P., A.L., C.W., E.P., A.-C.F.; Visualization: L.R.P., A.L.; Supervision: C.W., E.P., A.-C.F.; Project administration: C.W., A.-C.F.; Funding acquisition: C.W., A.-C.F.

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Supplementary information

Supplementary information available online at
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