Chapter 20
The Evolutionary Morphology of Tree Gouging in Marmosets

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Abstract The marmosets, *Callithrix* spp. and *Cebuella pygmaea*, are unique among anthropoids in their habitual biting of trees with their anterior teeth to elicit exudate flow. This tree-gouging behavior is thought to offer certain ecological benefits to marmosets, such as routine access to an under-exploited resource, as well as have specific influences on their behavioral ecology.

In order to better understand morphological adaptations for tree gouging in the marmoset masticatory apparatus, we characterized the mechanics of this behavior in a laboratory setting and compared these data to field observations of common marmosets (*Callithrix jacchus*) in northeast Brazil. Common marmosets generate biting forces up to eight times their body mass when biting simulated tree substrates in the laboratory. When gouging, however, marmosets are not biting as forcefully as they can. Comparisons of the mechanical properties of laboratory substrates with trees gouged in the wild suggest that gouging forces observed in the laboratory are comparable to those that marmosets use during gouging in the wild. Moreover, marmosets use relatively wide jaw gapes during gouging both in the laboratory and in the wild. These wide jaw gapes during gouging approach the maximum structural capacity for jaw opening in common marmosets.

Morphological comparisons of masticatory apparatus form between gouging marmosets and nongouging tamarins corroborate these laboratory and field data. Marmosets do not exhibit morphologies that offer increased force generation or load resistance abilities. Furthermore, marmosets exhibit several morphologies of their masticatory apparatus that facilitate increased jaw opening. Previous suggestions that marmoset gouging involves relatively large bite forces likely misrepresent the nature of this behavior. Instead, marmosets need only to score the tree bark to elicit the tree's defense response of exudate flow.

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Resumen Los marmosets *Callithrix spp*. y *Cebuella pygmea*, son únicos entre los antropóides en su habitual mordisco en árboles con sus dientes anteriores para sacar corrientes exudadas. Este comportamiento de excavación de árboles se cree ofrece a ellos ciertos beneficios ecológicos, tal como el acceso rutinario a recursos poco utilizados, asi como tener influencias específicas en su comportamiento ecológico.

Con el propósito de entender adaptaciones morfológicas para excavar árboles en el aparato masticatorio de los marmoset, caracterizamos los mecanismos de dicho comportamiento en un laboratorio y comparamos nuestros datos de laboratorio con las observaciones de campo de *Callithrix jacchus* en el noreste de Brazil. Los *Callithrix jacchus* generan al morder hasta ocho veces su masa corporal al ser estimulados por substancias de árboles en el laboratorio. Sin embargo, al cavar, los *C. jacchus* no mordieron tan fuerte como ellos pueden. Comparaciones de las propiedades mecánicas de los substratos de laboratorio con árboles excavados en estado salvaje sugiere que las fuerzas de excavación observadas en el laboratorio son comparables con aquellos que los marmosets usarian durante la excavación en la selva. Alternativamente, los marmosets usan aperturas de mandíbulas relativamente amplias, medidas como la distancia entre las puntas incisivas superiores e inferiores, durante la excavación tanto en el laboratorio como en lo salvaje. Dichas aperturas de mandíbulas durante la excavación se acercan la capacidad máxima estructural de apertura de mandíbula en los marmosets comunes.

Comparaciones morfológicas de la forma de los aparatos masticatorios entre los marmosets excavadores y los tamarins no excavadores corroboran los datos de laboratorio y de campo. Los marmosets no muestran morfologías que ofrecen incremento en la generación de fuerza o habilidades de resistencia de carga. Alternativamente, los marmosets exhiben variadas morfologías en su aparato masticatorio que facilitan las habilidades de apertura de mandibula. Sugerencias anteriores de que la excavación marmoset muestra fuerzas de mordiscos relativamente grandes es probable que no representa la naturaleza de este comportamiento; los marmosets simplemente proponen marcar árboles para sacarle a los árboles su reacción de defensa.

Resumo Os sagüis, *Callithrix* spp. and *Cebuella pygmaea*, são únicos entre os antropóides no hábito de morder as árvores com seus dentes anteriores para induzir o fluxo de exsudados. Este comportamento de perfurar o tronco das árvores é concebido como algo que ofereceria benefícios ecológicos aos sagüis, tais como o acesso rotineiro a recursos sub-explorados, assim como traria influências específicas na sua ecologia comportamental.

Para entender melhor estas adaptações morfológicas para perfuração de árvores no aparato mastigação dos sagüis, nós caracterizamos a mecânica deste comportamento em laboratório e comparamos estes dados à s observações de campo de sagüis (*Callithrix jacchus*) no nordeste do Brasil. Sagüis geram forças de mordida de até oito vezes as suas massas corporais quando mordem substratos de árvores simulados no laboratório. Quando perfuram o tronco, entretanto, os sagüis não

mordem tão forte quanto poderiam. Comparações das propriedades mecânicas dos substratos de laboratório com as árvores perfuradas no campo sugerem que as forças de mordida observadas em laboratório são comparáveis aquelas que os sagüis devem empregar na perfuração dos troncos no campo. Ademais, os sagüis fazem aberturas da boca relativamente amplas durante a perfuração tanto no laboratório como no campo. Estas aberturas amplas durante a perfuração dos troncos se aproximam da capacidade de abertura máxima estrutural da mandíbula nos sagüis.

Comparações morfológicas do aparato de mastigação entre micos e sagüis que perfuram e que não perfuram troncos corroboram com estes dados de laboratório e do campo. Sagüis não apresentam morfologias que permitam um aumento na geração de força ou na capacidade de resistência à carga. Além disso, sagüis exibem várias morfologias do aparato de mastigação que facilitam um aumento da abertura da boca. Sugestões prévias de que a perfuração dos troncos nos sagüis envolvem forças de mordidas relativamente grandes foram provavelmente fruto de uma má interpretação da natureza deste comportamento. Ao invés disso, os sagüis precisam somente raspar a casca das árvores para estimular su a resposta de defesa sob a forma de um fluxo de exsudado.

20.1   Introduction

Feeding on tree exudates, such as gums or saps, is common among primates[1]. Primatologists have observed at least 37 primate species eating tree exudates (Coimbra-Filho and Mittermeier 1977; Garber 1984; Nash 1986 and references therein). Additionally, this feeding behavior is widely dispersed among primates with most superfamilies having at least one exudate-eating member. A much smaller subset of exudate-eating primates actively elicits exudate flow by mechanically damaging trees with their anterior teeth. We define this type of biting behavior as tree gouging (Stevenson and Rylands 1988). Among anthropoids, the marmosets are the only habitual tree gougers (Nash 1986).

The development of this unusual feeding behavior in marmosets raises numerous questions related to how and in what context tree gouging evolved, whether there are essential morphological adaptations for gouging and if so, how these morphological features might be integrated during the adaptive evolution of this behavior. To begin to address these questions related to marmosets and gouging, we initially need to think about this behavior in the context of marmoset behavioral ecology. We also need to understand how this behavior works from a mechanical perspective in order to speculate what various morphological components do during gouging. In this chapter, we review data on laboratory experiments simulating tree gouging, field work studying both gouging and the mechanical properties of

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[1]The terms gummivory and exudativory have both been used to describe feeding on tree exudates. Nash (1986) discusses differences in these terms. We use them synonymously to include references applying either term as our interest is primarily related to the associated feeding behavior.

trees as well as comparative morphometric analyses to discern possible morphological adaptations for tree gouging in marmosets. Finally, we combine these data with our current understanding of callitrichid phylogeny and evolution to speculate on the evolution of tree gouging in marmosets.

20.2 The Prevalence and Importance of Tree Gouging in Marmoset Behavioral Ecology

Before we examine the functional morphology of tree gouging, we need to ask how this behavior relates to marmoset ecology. Without some indication that gouging plays an important role in the behavioral ecology of marmosets, we cannot advance robust arguments for any derived morphologies being adaptations for this behavior.

We have already noted that eating exudates is common throughout primates. This is also true of callitrichids where most species have been observed to feed on gums opportunistically, seasonally or continually throughout the year (e.g., Izawa 1975; Kinzey et al. 1975; Coimbra-Filho and Mittermeier 1977; Ramirez et al. 1977; Garber 1980, 1984; Rylands 1981, 1984; Maier et al. 1982; Soini 1982, 1987; Lacher et al. 1981, 1984; Sussman and Kinzey 1984; Stevenson and Rylands 1988). The marmosets are the most frequent exudate feeders within the callitrichids. Additionally, field reports state that several marmoset species (including both the common marmoset, *Callithrix jacchus,* and the pygmy marmoset, *Cebuella pygmaea*) habitually gouge holes in trees with their anterior teeth to stimulate exudate flow (e.g., Kinzey et al. 1975; Coimbra-Filho and Mittermeier 1977; Ramirez et al. 1977; Rylands 1981, 1984; Maier et al. 1982; de Faria 1983; Soini 1982; Lacher et al. 1981, 1984; Fonseca and Lacher 1984; Sussman and Kinzey 1984; Stevenson and Rylands 1988; Yepez et al. 2005). Field data also indicate that marmosets spend a significant portion of their daily activity cycle gouging trees, sometimes in excess of 70% of their day, and that exudates comprise a major component of their diet (Ramirez et al. 1977; Coimbra-Filho et al. 1981; Lacher et al. 1981; Maier et al. 1982; Fonseca and Lacher 1984; Sussman and Kinzey 1984; Melo 2001; Yepez et al. 2005) (Fig. 20.1).

Exudates are hypothesized to provide marmosets several ecological benefits, including a dietary source of calcium and other minerals, a rich source of carbohydrates, a seasonally-stable food supply, and a means of "avoiding" interspecific competition by feeding on this under-exploited food source (e.g., Coimbra-Filho and Mittermeier 1977; Maier et al. 1982; Sussman and Kinzey 1984; Nash 1986; Stevenson and Rylands 1988; Garber 1992; Ferrari 1993; Power 1996). Additionally, certain aspects of their behavior including home range size, daily path length, and group sizes may be related to exudate feeding (Maier et al. 1982; Rylands 1984; Ferrari and Ferrari 1989; Garber 1992; Rylands and de Faria 1993; Harrison and Tardif 1994; Kinzey 1997). Collectively, the frequency of exudate feeding, the potential benefits, and the behavioral correlates suggest that exudate eating is important to callitrichid behavioral ecology.

Fig. 20.1 Gouge marks left in a Tambor tree (*Enterolobium contorticilicum*, Leguminosae) by common marmosets at Estação Ecológica do Tapacurá, Pernambuco, Brasil. Trees with similar numbers of gouging marks are common throughout the home ranges of various marmoset groups. Note the individual near the base of the tree for scale

20.3   Determining Masticatory Apparatus Function During Gouging

Several morphological features of callitrichids such as small body size, claw-like nails, robust lower incisors lacking lingual enamel, canine height reduction, reduced condylar height, longer jaw-muscle fibers, and/or expansion of the stomach or large intestines are suggested to be functionally and/or adaptively linked to exudate feeding and gouging in callitrichids (Kinzey et al. 1975; Hershkovitz 1977; Rosenberger 1978; Chivers and Hladik 1980; Coimbra-Filho et al. 1980;

Garber 1980; Martin 1990; Power 1996; Hamrick 1998; Vinyard et al. 2003; Taylor and Vinyard 2004, 2008; Taylor et al. Chap. 19 this volume). Furthermore, multiple researchers hypothesize that tree gouging involves relatively large jaw forces (Szalay and Seligsohn 1977; Rosenberger 1992; Dumont 1997; Spencer 1999) or jaw gapes (Vinyard et al. 2003; Taylor and Vinyard 2004; Taylor et al. Chap. 19 this volume). In most of these cases, there is little in vivo data demonstrating how these specific morphologies function during tree gouging and/or exudate feeding. Given that we cannot routinely determine function in primate skulls from simply observing skull form (e.g., Daegling 1993), we need empirical data demonstrating how the masticatory apparatus functions during gouging before we can make realistic interpretations of morphology in gouging marmosets.

With respect to the masticatory apparatus, both the forces required to indent, fracture, and peel barks during gouging as well as the jaw movements involved in this behavior must be considered from a mechanical perspective. We developed a simulated gouging apparatus (Vinyard and Schmitt 2004) that allows animals to freely gouge while we record the magnitude and timing of forces passing through the jaw to the gouging substrate. We use lateral-view video of jaw movements to capture the time and maximum amount of jaw opening, measured as a maximum linear gape between the upper and lower incisors, during gouging. We can use these data characterizing gouging mechanics in a laboratory setting to explore hypothesized morphological adaptations for tree gouging in marmosets.

To date, we have collected jaw force and movement data during several hundred gouges by four common marmosets (*Callithrix jacchus*) on our gouging apparatus (Vinyard et al. 2001, unpub. data). We only present summary data for the 25 gouges with the largest peak forces from the lower jaws because most adaptive hypotheses focus on the largest forces produced during gouging. The peak resultant force for the lower jaw averaged 28.0 N (SD = 3.1) for these largest gouges. Thus, these marmosets produced peak gouging forces that were up to eight times their body mass. Lower jaw forces lasted, on average, 121 ms (SD = 29) during a gouge. Peak superoinferior (SI) forces of 22.8 N (SD = 3.6) were significantly larger than peak anteroposterior (AP) forces of 11.9 N (SD = 3.5) (Paired *t*-test; $p < 0.001$). SI forces peaked significantly earlier than AP forces (Paired *t*-test; $p = 0.003$).

We can apply these results to build a preliminary, qualitative sketch of how marmosets produce jaw forces during gouging (Fig. 20.2). Marmosets anchor their upper jaws in the gouging substrate by pushing downward and into the substrate. Lower jaw forces begin as the animal pushes with its lower teeth both into and upwardly on the substrate. Figure 20.2 illustrates this as SI forces typically start when the AP force trace is briefly positive. The AP force trace changes direction and becomes negative, signifying the animal pulling away from the substrate with its incisors (Fig. 20.2). SI forces are often, but not always, larger than AP forces showing that the animal pushes harder upwardly as opposed to outwardly on the substrate (Fig. 20.2). Peak vertical (SI) forces usually occur as AP forces are declining. In summary, these marmosets appear to gouge by anchoring their upper jaws, then using their lower jaws to first penetrate the substrate and then "scoop" pieces of the
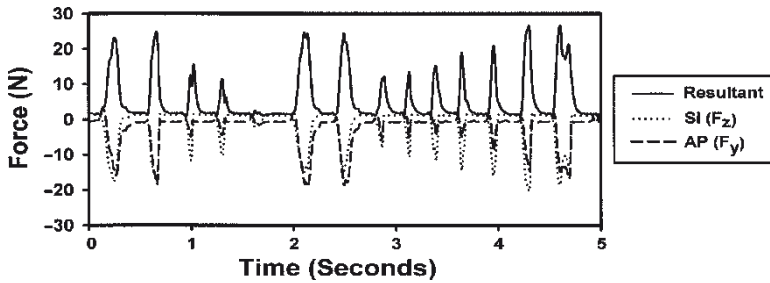
Fig. 20.2 Force traces for a typical gouging sequence of 13 gouges. These traces show the force (N) for the resultant (solid), AP (dashed) and SI (dotted) components. (The ML force was omitted to facilitate observation of the AP and SI forces). We arbitrarily represent the resultant force trace rising above zero and the AP (dashed line) and SI (dotted) forces extending down from zero. An increased negative value for the AP and SI forces represent the marmoset pulling away from the gouging block and pushing upwardly on the block, respectively

substrate by pushing up and pulling out. This final movement helps to propagate cracks during the isolation of a piece of tree substrate. Isolated pieces are often clamped between the teeth and pulled off the block in a subsequent event.

With respect to linear jaw gapes, we also focus on the largest 25 maximum linear gapes during gouging. The average of the largest 25 maximum jaw gapes during a gouge was 23.8 mm (SD=1.1). On average, jaw movements lasted 364 ms (SD=140) during a gouge. One novel finding from this work is that marmosets often use large gapes when gouging (Fig. 20.3). Marmosets gouged with gapes as large as 25.8 mm. These gapes are nearly as large as the maximum passive gape estimate of 29.5 mm, a measure of the structural capacity for jaw opening taken on several wild and laboratory-reared marmosets while they were anesthetized.

20.4   Evaluating the Relative Nature of Gouging Performance

We need comparative datasets to interpret the relative significance of jaw forces and movements during gouging. Towards this end, we compare peak gouging forces to peak vertical bite forces during anterior tooth biting in marmosets to test the hypothesis that gouging involves relatively high forces in the masticatory apparatus. Similarly, we compare maximum gapes during gouging to those during insect chewing to test the hypothesis that gouging involves relatively large gapes.

The comparison of gouging and transducer bite forces clearly shows that these marmosets were not gouging as hard as they could bite (Fig. 20.4a). The largest 25 vertical bite forces averaged 45.3 N (SD=6.4). These bite forces are significantly larger than the average peak force of 28.0 N (SD=3.1) from the 25 largest gouges (Mann-Whitney U-test; $p<0.001$) (Fig. 20.4a). This result offers no support for the hypothesis that gouging involves relatively high forces in the masticatory
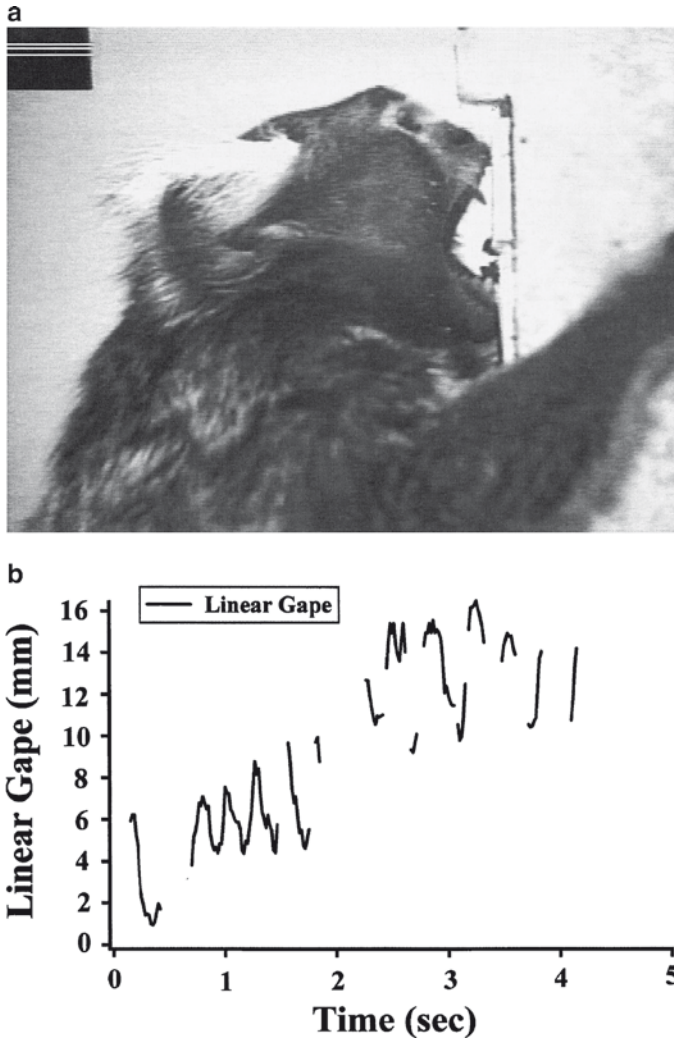
Fig. 20.3 Linear gapes during gouging. (**a**) Marmosets use large gapes when gouging. (**b**) Plot of linear gapes during a gouging sequence. Maximum gapes tend to increase across the sequence. Gape estimates are interrupted because incisor landmarks were not visible in every frame

apparatus (Vinyard et al. 2001). We remain cautious in concluding that marmosets do not generate relatively large forces during gouging because we are uncertain how closely transducer biting mimics behaviors that marmosets routinely perform in their natural habitat.

Comparison of maximum jaw gapes for gouging and cricket chewing shows that marmosets use much larger gapes when gouging (Vinyard et al. 2001) (Fig. 20.4b). The largest 25 maximum chewing gapes averaged 9.6 mm (SD=2.0). The average maximum gape during gouging, 23.8 mm (SD=1.1), was significantly larger (M-W U-test; $p < 0.001$). The hypothesis that gouging involves relatively large gapes is
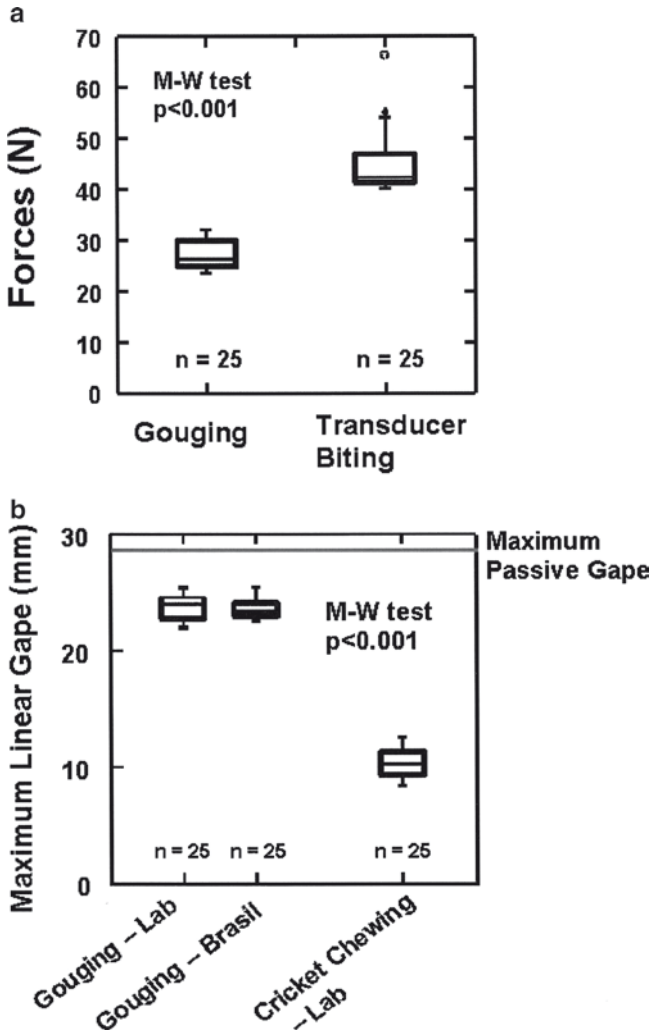
Fig. 20.4 (**a**) Maximum vertical bite forces were significantly larger than peak gouging forces. Transducer biting occurred at a gape of 12–15 mm. This gape is within the range of gapes during gouging. (**b**) Comparison of maximum jaw gapes during gouging in the laboratory, gouging in the field and cricket chewing. Mann-Whitney U-tests indicate that the largest maximum gapes during gouging in the laboratory and/or in the field are significantly larger than jaw gapes during cricket chewing. Furthermore, jaw gapes during gouging approach the average maximum passive gape estimate of 29.0 mm for marmosets (i.e., the line near the top of the figure). This result suggests that marmosets are approaching their maximum structural ability for jaw opening during gouging. This maximum passive gape is based on a sample of 32 individuals including an approximately equal number of laboratory-reared and wild individuals

supported by these data. Because the largest gapes during gouging approach the average maximum passive gape of *C. jacchus* (Fig. 20.4b), marmosets appear to be approaching their maximum structural capacity for jaw opening during gouging.

20.5 Linking Laboratory Data to Natural Environments: Giving the Laboratory a Biological Role

One of our key assumptions in determining morphological adaptations for tree gouging is that the laboratory setup accurately replicates the gouging environment marmosets normally experience in the wild. If the laboratory setup differs significantly from field conditions, then our interpretation of gouging performance may have little relevance to marmoset adaptations because of a lack of an appropriate environmental context. In other words, if our laboratory setup does not present a reasonable analog then it is unlikely that the mechanical events we observed during simulated gouging match the biological role of the masticatory apparatus in their environment.

We attempt to address this issue by comparing simulated gouging to tree-gouging behavior in free-ranging common marmosets at two sites in northeast Brazil: 1) Estação Ecológica do Tapacurá and 2) the campus of the Universidade Federal Rural de Pernambuco (Vinyard et al. 2004, unpub. data). Based on our behavioral observations, gouging in the laboratory appears qualitatively similar to marmoset behaviors in their natural environment. Thus, we conclude that we are eliciting a reasonable behavioral analog of tree gouging in the laboratory.

We cannot record jaw forces during gouging in the wild. However, because the properties of the trees that marmosets gouge influence the jaw forces elicited, we compared mechanical properties of trees gouged in the wild to those of laboratory substrates. Specifically, we compared four laboratory substrates, manufactured blocks of pine and red oak as well as fresh-cut pieces of sweetgum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*), to properties of 17 trees gouged by common marmosets at these sites. We assessed the hardness and friction, as they relate to the initial indentation of the gouged substrate, the stiffness and toughness linked to the initial fracture, and the work to peel pieces of substrate from the tree or block. In general, the two fresh laboratory substrates (sweetgum and red maple) always fell within the range of properties from wild trees (Fig. 20.5a). Alternatively, the manufactured pine block often fell slightly outside the natural range while oak blocks were clearly different from naturally-gouged tree properties. Interestingly, laboratory marmosets showed little interest in gouging the oak substrate and typically used very low forces when they did.

We were able to estimate maximum gapes during gouging in the field by measuring the distance between the anchoring site of the upper teeth and the beginning of the lower jaw's scrape during single gouging sequences (Fig. 20.5b). The largest 25 maximum gapes measured in the field averaged 22.9 mm (SD = 1.1) and are significantly larger than those during insect chewing (Fig. 20.4b). Furthermore, these gapes are similar to maximum jaw gapes measured in the laboratory. This similarity validates our jaw movement data during gouging in the laboratory. In summary, the laboratory data (other than that on red oak) appear to provide a reasonable analog for marmoset gouging in the wild.
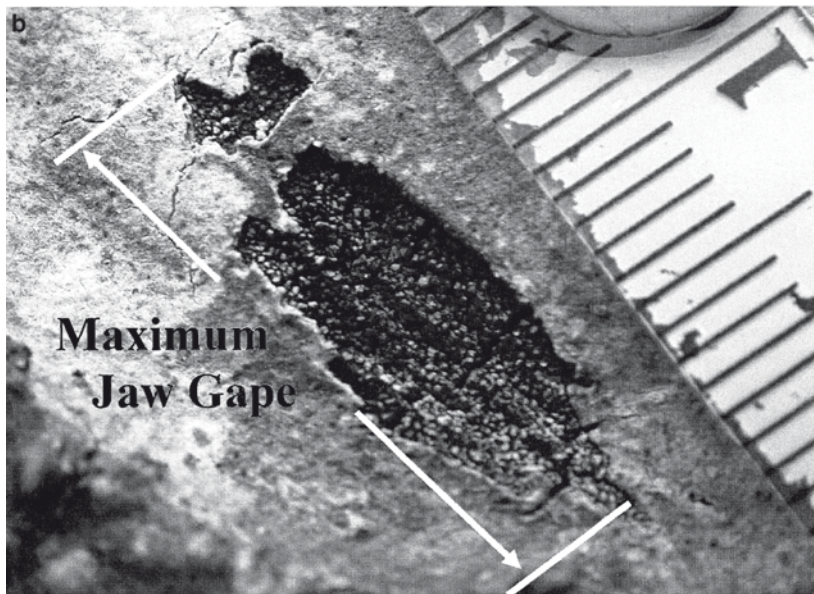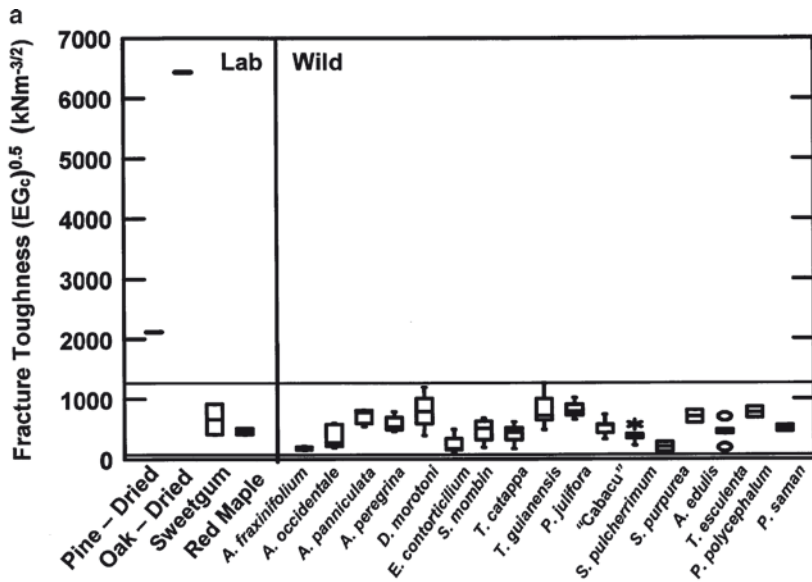
Fig. 20.5 (**a**) Fracture toughness for the experimental substrates used in the laboratory and 17 species of trees gouged by marmosets in their natural environment (Vinyard et al. 2004; unpub. data). Fracture toughness is a material constant measuring the critical stress for a given crack length at which fast fracture begins (Ashby and Jones 1980). We estimate fracture toughness as the square root of the product of stiffness (E) and toughness (G_c). The two manufactured substrates, pine and oak, require significantly more stress per unit crack length to generate fast fracture. Alternatively, the fracture toughness of sweetgum and red maple fall within the range of trees that are gouged in the field suggesting that these laboratory substrates have mechanical properties that mimic those of trees that marmosets gouge in the wild. (**b**) Measurement of maximum jaw gape during a gouge in the field

20.6 Morphology of the Marmoset Masticatory Apparatus and Tree Gouging

The combined laboratory and field data suggest that common marmosets use relatively large jaw gapes but do not necessarily generate relatively large bite forces during gouging. These results offer little support for hypotheses that marmosets generate large jaw forces during gouging and/or have morphological adaptations in the masticatory apparatus for creating or resisting large forces. Recent morphometric analyses comparing masticatory apparatus form in marmosets to nongouging tamarins support this conclusion in showing that marmosets likely do not have increased force generation or load resistance abilities in their bony skull or jaw muscles (Vinyard et al. 2003; Taylor and Vinyard 2004, Vinyard and Ryan 2006, Taylor et al. Chap. 19 this volume). We speculate that modifications of the lower anterior dentition such as increased labiolingual incisor thickness and the loss of lingual enamel help to increase the wedging ability and sharpness of these teeth, respectively, and thereby facilitate removing tree pieces with reduced bite forces.

Alternatively, morphological comparisons of the bony masticatory apparatus and jaw muscles indicate multiple features related to increasing jaw gapes as compared to nongouging tamarins. Specifically, marmoset jaws tend to have anteroposteriorly elongated glenoid articular surfaces and condyles (as a measure of the condylar radius of curvature) along with a condyle positioned closer to the toothrow. Along with a relatively longer mandible, these features all facilitate increased jaw gape (Vinyard et al. 2003). Similarly, the fiber architecture of marmoset jaw-closing muscles facilitate increased stretching and hence larger jaw gapes as compared to nongouging tamarins (Taylor and Vinyard 2004, 2008; Taylor et al. Chap. 19 this volume). We hypothesize that these morphological differences are linked to tree-gouging in marmosets (Vinyard et al. 2003). Furthermore, these modifications may provide functional and/or adaptive advantages related to an optimal alignment of the incisal cutting edge during gouging, increased jaw excursion during a gouge and/or increased bite force production at very large gapes when these jaw muscles are highly stretched.

20.7 Evolution of the Marmoset Masticatory Apparatus for Tree Gouging

It is fairly clear that features, such as claw-like nails and small body size, shared by gouging and nongouging callitrichids are unlikely to be adaptations specifically for tree gouging. It is possible that these morphological changes and their concomitant behavioral shifts acted as preadaptations for tree gouging in marmosets (Garber et al. 1996). Based on our in vivo and field data, we speculate that two components of the masticatory apparatus have adapted to this gouging behavior. The first component, which many researchers have recognized for some time, involves the

anterior lower dentition. Morphological changes in the lower teeth that align the canine and incisal occlusal surfaces at the same level, increased the labiolingual thickness of the incisors and hypertrophied the labial enamel while reducing the lingual enamel (creating a sharp dentoenamel wear gradient), all appear functionally related to tree gouging (Rosenberger 1978). We speculate that these changes increased the mechanical efficiency of gouging and reduced the amount of force required to remove a given piece of substrate. The second component involves changes in the masticatory muscles and temporomandibular joint (TMJ) related to increasing jaw gapes. Changes in muscle and TMJ position theoretically reduce stretching of the jaw muscles when opening the jaw widely. These changes facilitate both increased gape and the ability to generate greater bite forces at these larger gapes (Vinyard et al. 2003). Additional changes in the TMJ facilitate joint rotation and translation that increase the ability to open the jaw widely (Vinyard et al. 2003). Finally, longer jaw-muscle fibers provide increased muscle stretching capacity for wide jaw opening (Taylor and Vinyard 2004, Taylor et al. Chap. 19 this volume). These observations linking tree gouging to morphological changes for increased jaw movements offer one of the first observed instances where jaw movements, rather than bite forces, appear to be the target of evolutionary change in a primate biting behavior.

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