Use of zygodactylous grasp by *Caluromys philander* (Didelphimorpha: Didelphidae)

Dionisios Youlatos

Aristotle University of Thessaloniki, School of Biology, Department of Zoology, University Campus, GR-54124 Thessaloniki, Greece

Received 13 April 2009; accepted 24 October 2009

Abstract

The present report aims to quantify the use of zygodactylous (opposability of digits II to III) grasping in relation to positional modes and support size and orientation, in the highly arboreal, walking/climbing woolly opossum, *Caluromys philander*. For this purpose, four captive adult *C. philander* were intensively video-recorded and their positional behavior, hand grasp, and support size and orientation use were analyzed frame-by-frame. Overall, *C. philander* used a zygodactylous grasp in 81.3 ± 1.2% of bouts. In terms of support features, this grasp was particularly common on (a) supports that could be wholly and partly held by the animals' hand and (b) vertical supports in particular. In a comparable manner, zygodactyly dominated during above-support positional modes, but was significantly less used during bridging and suspension. The results show that zygodactylly provided an above-support secure and steady grasp on relatively unstable arboreal supports, by aligning the hand with the main axis of the support. This very likely assisted in controlling over the applied torques during cautious quadrupedal and climbing activities with extended hand contact that characterizes the locomotor strategy of *C. philander*. These observations need to be further tested by more detailed kinetic studies and on a larger sample of arboreal didelphids.

© 2009 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

*Keywords:* *Caluromys philander*; Didelphidae; Zygodactylous grasp; Locomotion; Postures

Introduction

Within the discontinuous, unstable, three-dimensional arboreal context, prehensile feet, opposing the hallux to the lateral toes, are crucial in securing reliably an animal upon arboreal supports (Cartmill, 1974, 1985; Szalay, 1984, 1994; Szalay and Dagosto, 1988; Sargis, 2001; Sargis et al., 2007). Additionally, prehensile hands further contribute to holding and maintaining the firm contact with one or multiple arboreal supports promoting safe and secure movement and postures (Cartmill, 1985). In arboreal mammals, prehensile hands are characterized by different grasping patterns: most primates variably oppose the pollex to the lateral digits, forming a grip between digits I and II or I and III, when digit II is reduced to a stub (Napier, 1961). However, most arboreal metatherians and some primates are reported to use a zygodactylous or schizodactylous grasp (sensu Haines, 1958), establishing a powerful grip between digits II and III. This grip most likely contributes to a more palms-turned-toward-the-midline posture of the hand, stabilizing the forearm upon the branch and assisting body progression during quadrupedal activities (Grand, 1968; Grand and Barboza, 2001). The zygodactylous grasp is clearly visible in the
anatomical arrangement of the hand of certain forms (e.g. *Phascolarctos* Young, 1879), but has been implied by the digital osteo-muscular arrangement in most others (Coues, 1869; Jouffroy, 1962; Landsmeer, 1979; Jouffroy et al., 1991; Youlatos, 1999; Argot, 2001; Abdala et al., 2006; Voss and Jansa, 2009). All these forms are usually referred to as “zygodactylous”, mainly based on anecdotal reports. However, to what extent or in which context this grasping mode is actually employed by these forms, remains largely unknown, and the lack of such data weakens any potential morpho-functional associations towards this direction.

In this context, the present report quantified the use of zygodactylous grasp in relation to positional mode and support features in the woolly opossum, *Caluromys philander* (Didelphimorphia, Didelphidae) in captivity. *Caluromys philander* is a proficient canopy, fine-branch, walking and climbing “zygodactylous” marsupial (Rasmussen, 1990; Lemelin et al., 2003; Delciellos and Vieira, 2006, 2009). This renders the species a suitable model for investigating potential relationships of frequencies of zygodactylous grasp to specific locomotor and postural modes and support diameter and orientation. Similar data, extended in other allegedly “zygodactylous” didelphids, and applied to meticulous morpho-functional investigations, could be essential in elucidating the adaptive significance of this grasping mode in arboreal didelphimorph marsupials.

Material and methods

Study animals and housing

The data of the present study derive from the analysis of video recordings of two adult male and two adult female captive *Caluromys philander* from French Guiana. The animals were housed in enclosures (2.5 m high × 2 m deep × 2.5 m wide), topped by wire mesh and fronted by glass window in the Laboratoire d’Ecologie Générale at Brunoy, France, under a 12:12 light:dark regime. Each enclosure contained a variety of branches of various diameters and orientations whereupon the animals were moving freely. However, provided supports in a cage were expected to limit locomotor and postural options of the animals. The estimate of their availability would allow for a controlled test of support preference or avoidance. For these reasons, I calculated the availability of different support size and orientation categories (see below for definitions). In terms of support size, S1 supports represented 29.2%, S2, 48.1%, and S3, 22.7%, of all available supports (n = 137). Similar observations were applied to support orientation, where horizontal supports represented 24.8%, moderately inclined ones 27%, steep ones 24.8%, and vertical ones 23.4% (n = 137). Preference or avoidance of these categories was then evaluated by the Jacobs’ D value (Jacobs 1974): D = U–A/U + A–2UA, where U is proportion of use, and A is proportion of availability. Values of the index range from −1, depicting strong avoidance, to +1, showing strong preference, whereas values around 0 are considered as neutral.

Data collection

The animals moved freely on the available supports within the enclosure. Each animal was filmed using a SONY Hi-8 CCD-TR705E camcorder at 24 frames/sec and at a shutter speed of 1/500th for a single day (9:00-17:00) within the enclosures from the glass window. The original Hi-8 tapes were transcribed to DVDs that were subsequently analyzed frame by frame for data collection using VirtualDubMod (http://virtualdubmod.sourceforge.net). I used the ‘bout method’ for recording behavioral observations and a bout ended when one of the recorded variables changed. For each bout the following variables were recorded: (a) hand grasp type, (b) locomotor or postural mode, (c) support size, and (d) support orientation.

A hand grasp was identified as (i) *zygodactylous*, when the hand was placed in a neutral position on the substrate and there was an evident firm grasp or an evident cleft between digits II and III, the main axis of the support passing between these two digits (Fig. 1), and (ii) *convergent*, when all digits appeared to converge to the median axis of the hand, the latter grasping in a position of evident ulnar deviation compared to the main axis of the support.

In terms of locomotor and postural modes, only those that actually involved hand grasps were considered in this study. These were: (i) *diagonal-sequence walk*, that involved body displacement along single horizontal or oblique supports using quadrupedal diagonal sequence diagonal couplets walking gait; (ii) *clamber*, that involved body displacement towards various directions using multiple supports and an irregular quadrupedal gait and limb movements; (iii) *climb*, that involved upward or downward body displacement along single steep or vertical supports using a regular quadrupedal gait, with digital grasping; (iv) *bridge*, when crossing short gaps keeping at least three limbs anchored; (v) *suspension*, that involved below support quadrupedal locomotion on single or multiple supports; (vi) *stand*, an above-support quadrupedal posture with semi-extended or crouched limbs; and (vii) *vertical cling*, a posture with the body held mainly vertical onto a steep or vertical support.

Support size categories were based on published metrics of the hands of adult *C. philander* (Lemelin,
1999; Argot, 2001). Thus (i) S1 corresponded to supports that could be fully grasped by a single hand (diameter <1 cm); (ii) S2, to supports that could be partly embraced by a single hand (diameter 1-4 cm); and (iii) S3, to supports that could be, in no way, embraced and whereupon the hand posed gently curved (diameter >4 cm).

Finally, support orientation involved (i) horizontal, with an inclination within ±22.5° to horizontal, (ii) moderate, inclination between 22.5-45°, (iii) steep, inclination between 45-67.5°, and (iv) vertical, inclination within ±22.5° to vertical.

Data analysis

A total of 2,036 hand grasp bouts were collected deriving from four individuals. Initially, I calculated frequencies for each individual by dividing the number of bouts each behavior was observed by the total number of bouts, and then, I computed means ±1 SD. Subsequently, the goal was to test separately mean frequencies of different types of recorded variables that derived from the small number of the sampled individuals. In this case, where multiple individuals are to be compared in multiple interdependent categorical variables, multivariate tests can be used to calculate significance of differences. Thus, in the present case, where one wants to test whether a set of observations within a group are more similar to each other than to sets of observations of different groups, Wilk’s lambda (λ) is the preferred test. It is a multivariate test that estimates unexplained variance, and its advantage lies in the fact that it takes into account effects among the tested variables. All statistical tests were performed by SPSS 11.0 (S.P.S.S. Inc., Chicago, U.S.A.). Tests yielding \(P\) values of 0.05 or less were considered statistically significant and only those are reported in the results section.

Results

Prior to reporting frequencies of use of zygodactylous grasp in the different behavioral and support contexts it is necessary to identify the most common locomotor and postural modes and the nature of supports utilized by woolly opossums during the present study in captivity. These results have been presented elsewhere (Youlatos, 2008) and will be briefly stated here. Of the locomotor modes considered here, diagonal-sequence walk was the dominant one (52.0±2.4%), followed by clamber (24.0±2.2%) and climb (11.9±1.2%). Bridging and suspension were infrequent (5.2±1.2% and 4.5±1.2% respectively), while claws were never used. Of all the postures that involved hand grasp, quadrupedal stand was particularly common (42.5±3.3%), whereas vertical cling was infrequent (2.8±0.7%). In terms of support size, S1 supports were frequently used (31.8±1.7%) but according to availability (\(D=0.06\)), while the use of S2 largely dominated (63.4±1.2%) and slightly preferred (\(D=0.31\)). Finally, S3 supports were seldom used (2.4±0.6%) and strongly avoided (\(D=-0.84\)). Horizontal and moderately inclined supports were frequently used and slightly preferred (37.0±0.8%, \(D=0.32\) and 42.4±0.9%, \(D=0.33\), respectively). Steep supports were not commonly used (12.7±0.9%) and slightly avoided (\(D=-0.39\)), while vertical ones were generally avoided (7.9±1.5%, \(D=-0.55\)).

Considering all activities, the hand held with a zygodactylous grasp in 81.3±1.2% of bouts, while in the rest of the bouts a convergent grasp was used. Rates of zygodactylous grasp were especially high upon both S1 and S2 supports (Table 1a). In these cases, digits I/II and digits III-V composed, respectively, the opposing radial and ulnar pincer arms, that surrounded either

![Fig. 1. Zygodactylous grasp of Caluromys philander on S2 (top) and S3 supports (bottom).](image-url)
Table 1. Means ± SD of percentages of use of zygodactylous grasp on the different support size and orientation categories.

<table>
<thead>
<tr>
<th>Support size</th>
<th>(a) Support orientation</th>
<th>%</th>
<th>(b) Support orientation</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>Horizontal</td>
<td>94.3 ± 0.9</td>
<td>80.0 ± 1.2</td>
<td></td>
</tr>
<tr>
<td>S2</td>
<td>Moderate</td>
<td>81.8 ± 1.4</td>
<td>81.3 ± 1.9</td>
<td></td>
</tr>
<tr>
<td>S3</td>
<td>Steep</td>
<td>14.4 ± 0.7</td>
<td>81.6 ± 1.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vertical</td>
<td></td>
<td>87.4 ± 0.7</td>
<td></td>
</tr>
<tr>
<td>Sampled animals</td>
<td></td>
<td>4</td>
<td>Sampled animals</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 2. Means ± SD of percentages of use of zygodactylous grasp in the different locomotor and postural modes.

<table>
<thead>
<tr>
<th>Locomotion</th>
<th>%</th>
<th>(b) Postures</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diagonal-Sequence</td>
<td>86.1 ± 1.6</td>
<td>Stand</td>
<td>66.1 ± 1.9</td>
</tr>
<tr>
<td>Walk</td>
<td>Climb</td>
<td>91.5 ± 1.9</td>
<td>Vertical Cling</td>
</tr>
<tr>
<td></td>
<td>Clamber</td>
<td>85.5 ± 2.2</td>
<td>Bridge</td>
</tr>
<tr>
<td></td>
<td>Suspension</td>
<td>43.2 ± 1.3</td>
<td>Sampled animals</td>
</tr>
</tbody>
</table>

Discussion

Many arboreal metatherians – more particularly didelphimorphs and phalangeriforms (with few exceptions like *Trichosurus*) – are allegedly classified as “zygodactylous”, reportedly using a hand grasp between digits II and III. This classification has been mainly based on anecdotal reports, with no attempts to actually quantify this type of grasp in either free ranging or captive animals. The current study is the first quantified description of the use of zygodactylous grasping in a metatherian. The highly arboreal, fine-branch walker/climber *C. philander* presented a good model to test potential functional-adaptive associations between zygodactylly, positional behavior and support characteristics. In effect, the study showed that *C. philander* extensively used the zygodactylous grasp during arboreal activities. Zygodactylly dominated in above support locomotion and postures, being especially frequent in vertical modes, but was significantly less common in suspensory ones. In terms of support characteristics, the zygodactylous grasp was extensively used upon supports that could be fully or partly embraced by the hand, and was particularly frequent upon vertical supports. Although the present study occurred in a captive setting, which is expected to limit positional options, the comparison between availability and use of support characteristics along with locomotor and postural diversity, provided a reliable context to study the utilization of zygodactly in *C. philander*.

The extended use of zygodactylous grasping was mainly associated with relatively slender and vertical arboreal supports. Such arboreal supports are usually difficult to handle by most arboreal mammals.
Non-vertical small-diameter supports require powerful and firm holds of the extremities to counteract the gravitational force, the medio-lateral reaction forces, and branch swaying torques developed during pronograde postures and locomotion respectively (Grand, 1984; Cartmill, 1985). Recent observations have demonstrated that C. philander exhibits relatively slow traveling speeds on thinner supports, whereupon it moves with long strides (Delciellos and Vieira, 2006). This locomotor strategy, along with the relatively reduced stride frequency (Delciellos and Vieira, 2007) and longer support phases (Lemelin et al., 2003) should promote safer body displacement by minimizing unnecessary branch sway on thinner supports. This dynamic stability is very likely assisted by the common use of the zygodactylous grasp. In this way, the placement of the hand in a relatively neutral position, at a minimal angle compared to the long axis of the support, would transmit the compressive forces to the line of movement (Preuschoft et al., 1993). This would eventually align them with the reaction forces of the support minimizing potential torques that would tend to rotate the hand (Preuschoft et al., 1995). In addition, the maintenance of a pronated position in the forearm would aid the powerful long flexors to exert more efficiently their tensile force on the relatively long digits, contributing to a more powerful and firm hold around the support (Preuschoft et al., 1993; Lemelin, 1999; Lemelin and Schmitt, 2007). These behavioral observations on the importance of zygodactylous grasping on small supports need to be further substantiated by detailed kinetic studies, but some biomechanical reports partly support these assumptions (Schmitt and Lemelin, 2002; Larson and Stern, 2006).

On the other hand, the negotiation of vertically oriented supports raises different problems (Cant, 1992). The forelimbs are mainly under tension that is counteracted by the compressive forces exerted by the hind limbs (Cartmill, 1974, 1985). Powerful hand prehension is essential for assuring a vertical posture or assisting the pull of the body towards a higher point. This may be particularly important for C. philander, which tends to climb relatively slowly, especially on thinner vertical supports, and employs relatively long strides (Delciellos and Vieira, 2009). This locomotor strategy implies lengthy periods when the hand may support wholly or a major part of the animal’s body weight while the rest of the limbs move suspended towards higher reaches (Delciellos and Vieira, 2009). In this case, the frequent use of zygodactylly would provide the necessary powerful grasp for the body to pivot around the holding hand. In effect, the neutral position of the hand, aligned or in a minimal angle with the long axis of the support may contribute to a better opposition of the resistance forces of the support, and impose lower active fore-aft and medio-lateral torques, modulated by both the intrinsic hand, and extrinsic forelimb musculature (Preuschoft et al., 1993, 1995). Although these assumptions are partly supported by biomechanical studies (Stalheim-Smith, 1989), more detailed research towards this direction would help elucidate this statement.

On the other hand, bridging and suspensory locomotion were infrequent, but were both characterized by significantly lower proportions of zygodactylous grasping. Suspensory quadrupedalism that C. philander was observed to perform appeared to apply unidirectional tensile forces to the hands imposed by gravity. In this case, if the hand was placed relatively aligned to the support via a zygodactylous grasp, the extrinsic flexor muscles would have required higher compressive forces to withstand gravity over a radially diverted hand. Conversely, a hand holding the support with a convergent grasp operating as a single functional hook-like unit would be better suited to overcome similar stresses (Preuschoft et al., 1993). Finally, bridging was a different case, as safety and stability was mainly required in the trailing limbs. In this case, the hind limbs needed to grasp firmly and securely through the extensive use of a powerful pedal grasp (Youlatos, 2008). The role of the forelimbs was limited to check available supports at the reaching point, and therefore, establishing stable, above support grasps may had been of reduced importance.

The results show that zygodactylous grasping provides safe and secure hand holds that appear to facilitate and promote cautious above-branch movements on supports that can be wholly or partly embraced and of variable inclinations but particularly vertically oriented. In contrast, it might not be well suited for below support positional activities. The present model, C. philander can therefore be considered as zygodactylous (without quoting), and as that, should be compared to other reportedly “zygodactylous” closely related didelphid species. The basal position of Caluromyys, in the phylogenetic tree of didelphid metatherians (Meredith et al., 2008; Voss and Jansa, 2009), is further ideal for understanding evolutionary trends of grasping and climbing behavior within the group. Unfortunately, there are no comparable detailed quantitative behavioral studies on other didelphids in order to evaluate similar trends. However, detailed gait metrics among didelphids have shown that arboreality and climbing have evolved early in the diversification of didelphids and continued throughout their history (Delciellos and Vieira, 2009). If this holds true and given that zygodactyly was mainly associated with similar above-branch behaviors, it is very likely that this grasping mode may have followed the same evolutionary trend within the family.

To support such a statement, the interaction of both detailed behavioral and anatomical studies is required. On one hand, occasional observations of zygodactylous grasps in the other arboreal didelphids may provide
such evidence for other “zygodactylyous” arboreal species. This would lend support to this assumption, but the question remains largely speculative due to lack of detailed work. On the other hand, anatomical studies of the hand in the genus (Grand, 1983; Lemelin, 1999; Argot, 2001; Abdala et al., 2006), in other didelphids (Coues, 1869; Young, 1879; Landsmeer, 1979; Stein, 1981; Szalay and Sargas, 2001), and in other metatherians (Szalay, 1994; Weisbecker and Warton, 2006; Weisbecker and Archer, 2008), have only traced from the 3rd to the 4th digit and the intrinsic flexors, shows that the functional axis of the hand has shifted the other intrinsic muscles of the other digits (Young, 1879; Weisbecker and Warton, 2006). The latter muscular arrangements have been also detected in other reportedly “zygodactylyous” metatherians (Landsmeer, 1979) and primates (Youlatos, 1999), but these functional convergences are based on partial information and should be considered with caution. In the case of zygodyactyly, the lack of this bulk of information renders all suggestions largely conjectural. Therefore, more detailed research on both behavior and anatomy in other arboreal didelphids and other phylogenetically distant arboreal diprotodontians (that are reportedly “zygodactylyous”) is needed in order to identify the functional-adaptive significance of zygodactyly within metatherian evolutionary history.

Acknowledgements

I am particularly grateful to Drs. M. Perret and M. Atramantowicz of the Laboratoire d’Ecologie Générale (CNRS/MNHN USM 301- UMR 5176) in Brinouy, France who authorized permission to study captive Caluromys philander under their care. The manuscript benefited from suggestions provided by Dr. C. Argot and Dr. V. Weisbecker. Special thanks also go to the two anonymous reviewers, whose instructive remarks greatly improved the manuscript, as well as editor Dr. M. Sanchez-Villagra, whose editorial work and aid had been more than beneficial to this contribution. The present study was partly financed by the Aristotle University of Thessaloniki and Socrates/Erasmus, facilitating faculty mobility.

References


