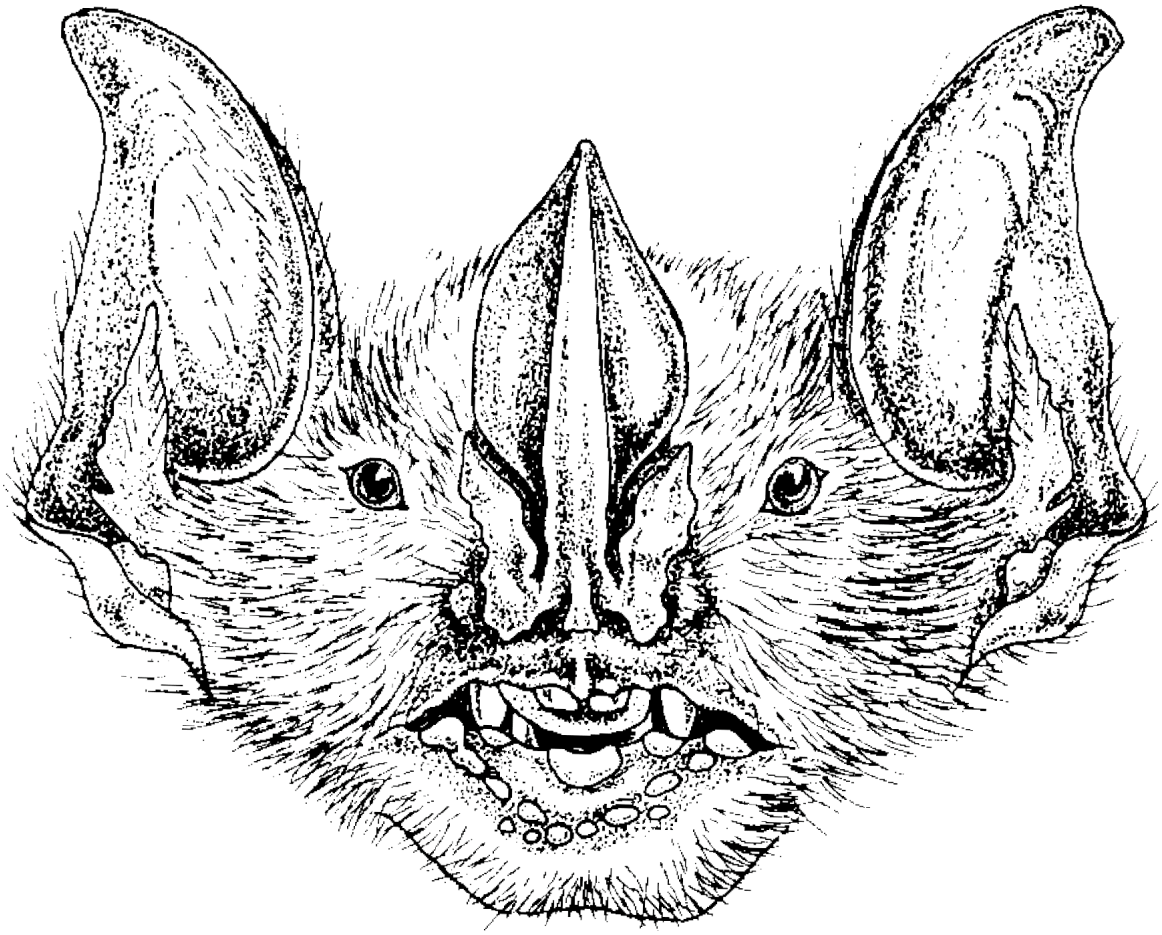


Cover Picture
D. L. Harrison

Sensory Ecology of Foraging Behavior in the Long-Legged Bat, *Macrophyllum macrophyllum*, in Panamá

DISSERTATION

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Für meine beiden Eltern Clarissa und Eduard

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Wir lassen vom Geheimnis uns erheben
Der magischen Formelschrift, in deren Bann
Das Uferlose, Stürmende, das Leben
Zu klaren Gleichnissen gerann.

Hermann Hesse

Zusammenfassung

Neotropische Fledermausgemeinschaften zeichnen sich durch eine außerordentlich hohe Diversität aus, bei der mehr als 100 Arten in lokalen Gemeinschaften zusammenleben können. Insbesondere die endemischen Neuwelt-Blattnasenfledermäuse (Phyllostomidae) weisen eine unter den Säugetieren einzigartige Vielfalt in ihrer Nahrungsökologie auf. Sie ernähren sich von Früchten, Nektar, Pollen, Arthropoden, kleinen Vertebraten und Blut. Trotz dieser Nahrungsvielfalt suchen sie in ähnlichen Habitaten in oder in der Nähe von Vegetation nach Nahrung, die sie von der Vegetation oder dem Boden absammeln ("gleaning"). Die kleine insektivore Phyllostomidenart *Macrophyllum macrophyllum* Schinz (1821) unterscheidet sich jedoch von allen anderen Blattnasen in mehreren morphologischen Besonderheiten, einem relativ großen Nasenblatt, einer mächtigen Schwanzflughaut, sowie langen Beinen mit großen Füßen und starken Krallen, die zu der Annahme führten, daß diese Art vorwiegend im hindernisfreien Raum über Wasser nach Beute jagt.

Innerhalb der Phyllostomiden ist die Nahrungssuche über Wasser einzigartig. Ansonsten kommt sie nur bei einer kleinen Gruppe von Wasserfledermäusen[1] aus verschiedenen Familien (Noctilionidae, Emballonuridae und Vespertilionidae) vor, die ihre Beute direkt von ("trawling" Modus) oder in der Luft dicht über der Wasseroberfläche ("aerial hawking" Modus) fangen. Während bei diesen Arten bereits gut bekannt ist, wie sie ihre Beute finden, gibt es von *M. macrophyllum* lediglich anekdotenhafte Berichte, wo und wie diese Art ihre Beute sucht und aufnimmt. In meiner in vier Kapitel gegliederten Dissertation untersuchte ich daher die Raumnutzung und Aktivitätsmuster von *M. macrophyllum* und bestimmte die sinnesökologischen Aufgaben, die sie beim Finden von Beute über Wasser leisten muß.

Die differentielle Nutzung des Raumes ist ein wichtiger Faktor, der zur Bildung von Diversität und zur Strukturierung lokaler Fledermausgemeinschaften beiträgt. Allerdings wissen wir insbesondere in den Tropen über Raumgrößen und -nutzung, wie auch über die Aufteilung des Raumes zwischen sympatrischen Fledermausarten noch sehr wenig. Jüngste Fortschritte in der Telemetrie ermöglichten es jedoch, Freilanduntersuchungen mit Miniatursendern an Fledermäusen durchzuführen und dabei die Aktionsraumgrößen für die Arten zu berechnen und Raumnutzungsmuster abzuschätzen. Während bislang vorwiegend frugivore Phyllostomiden das Ziel von Telemetriestudien waren, wurden Untersuchungen zur Raumnutzung insektivorer Arten erst in neuerer Zeit durchgeführt.

In Kapitel I untersuchte ich daher Raumgröße und Raumnutzungsmuster der insektivoren Fledermausart, *M. macrophyllum*, im Barro Colorado Nature Monument in Panamá von April bis Juli 2002. Ich fand, daß die vier Männchen und fünf Weibchen, die jeweils über 4–7 Nächte telemetriert wurden, große (Median: 24 ha, Bereich: 7–151 ha) Aktionsräume nutzten. Alle Tiere suchten ihre Nahrung ausschließlich über Wasser und begrenzten ihre Jagdaktivität auf die

[1] Ich entlehne diesen Begriff dem Englischen "trawling bat" und verwende ihn synonym. Der Begriff "Wasserfledermaus" ist hier nicht mit der temperaten "Wasserfledermaus" im engeren Sinne, *Myotis daubentonii* (Vespertilionidae), gleichzusetzen.

unmittelbare Nähe zum Ufer des Gatún-Sees. Die mittelgroßen Nahrungssuchgebiete (12 ha, 3–96 ha) wurden mit einer hohen Stetigkeit jede Nacht aufgesucht. Die kleinen Kerngebiete, in denen die Hauptjagdaktivität der Tiere stattfand, umfaßten rund 35% der entsprechenden Nahrungssuchgebiete (4 ha, 1–54 ha). Die weiteste, vom Tageshangplatz geflogene Entfernung variierte stark zwischen den Individuen und reichte von 0.5 km bis zu 7.5 km. Im Mittel flog *M. macrophyllum* jede Nacht eine Strecke von rund 35–47 km.

Weitere, die Diversität von Fledermäusen fördernde Faktoren, stellen die zeitlichen Aktivitätsmuster dar, die unter Einbeziehung unterschiedlicher Nahrungssuchstrategien die große Bandbreite und Flexibilität von Fledermäusen bezüglich morphologischer, sensorischer, und Verhaltensanpassungen an Habitate und Nahrung widerspiegeln.

Um den Einfluß von Habitat und Beuteverfügbarkeit auf Aktivitätsmuster abzuschätzen, untersuchte ich in Kapitel II die nächtliche Aktivität von *M. macrophyllum* in Panamá. Da diese Art, ebenso wie andere Wasserfledermäuse, kleine Insekten (vor allem Diptera und Lepidoptera) im hindernisfreien Raum über Wasser jagt, stellte ich die Hypothese auf, daß auch *M. macrophyllum* große Teile der Nacht damit verbringt, Beute von und über der Wasseroberfläche in raschem und kontinuierlichem Flug zu fangen. Diese Annahme wurde in meiner Studie bestätigt. Vier männliche und fünf weibliche telemetrierte *M. macrophyllum* suchten auf Flügen variabler Dauer (Mittel: 7 min, Maximum: 1 h), unterbrochen durch längere Hangphasen (15 min, 3 h) und einer nächtlichen Gesamtflugzeit von rund 3 h nach Nahrung. Die Aktivität wurde durch mehrere Faktoren beeinflußt. Ausflugs- und Einflugszeiten am Tageshangplatz waren mit Sonnenauf- und -untergangszeiten korreliert, während Mondlicht einen geringen Einfluß auf die Flugaktivität der Tiere hatte. Die maximale Aktivität fiel mit der Zeit höchster Insektenverfügbarkeit während der Dämmerung zusammen. Bei starkem Regen unterbrachen die Tiere ihren Flug.

Ein weiterer wesentlicher Faktor, der den Zugang zum großen Angebot nächtlicher Ressourcen ermöglicht und damit maßgeblich zur beobachteten hohen Diversität beiträgt, ist das komplexe Echoortungssystem der Fledermäuse, das ein breites Spektrum von Lauttypen umfaßt. Dabei spiegeln das Design der Laute, die aus charakteristischen funktionellen Elementen bestehen, sowie die typische Abfolge von Echoortungslauten die sensorischen Aufgaben der Detektion, Klassifizierung und Lokalisation von Beute wider. Echoortungssequenzen von Fledermäusen, die im offenen Luftraum nach Insekten jagen, folgen einem charakteristischen Schema. Suchlaute werden in regelmäßigen Abständen, meist ein Ruf pro Flügelschlag, bis zur Detektion von potentieller Beute ausgestoßen. Anschließend beginnt die Fledermaus mit der Verfolgung der Beute, was mit einer typischen Änderung der Lautstruktur einhergeht. Während der Annäherung an die Beute ermöglicht dies den Erhalt detaillierter Informationen über deren Art und Ort. Schließlich stößt die Fledermaus kurz vor Ergreifen der Beute eine Terminalgruppe aus, die aus

vielen, sehr kurzen, und mit hoher Wiederholrate abgegebenen Lauten besteht und maximale Lokalisationsgenauigkeit für den Fang bewegter Beute erlaubt. Im offenen Luftraum jagende insektivore Fledermäuse nutzen primär Echoortung zum Finden ihrer Beute.

Im Gegensatz zu Fledermäusen, die im offenen Luftraum Insekten jagen, findet man bei den Phyllostomiden, trotz ihrer hohen ökologischen Diversität, sehr einheitliche Ruftypen. Zudem verändern sie die Rufparameter bei der Annäherung an ihre jeweilige Nahrung nur geringfügig. Insbesondere produzieren sie keine ausgeprägte Terminalgruppe. Dies ist vermutlich darauf zurückzuführen, daß Blattnasenfledermäuse hauptsächlich unbewegte Nahrung von Oberflächen absammeln, was keiner komplexen Verfolgungsmanöver im dreidimensionalen Raum bedarf. Darüber hinaus sind gleanende Phyllostomiden mit der Schwierigkeit konfrontiert, daß Störechos des nahen Hintergrundes die eindeutige Nahrungsdetektion mit Hilfe der Echoortung erschweren und zum Teil ganz verhindern, da sie in Abhängigkeit der Beuteposition die Echos derselben maskieren können. Daher nutzen viele Phyllostomiden andere Sinnesmodalitäten (Geruch, Sicht und passives Hören auf von der Beute erzeugte Laute) zum Finden ihrer Nahrung.

Im Vergleich zu Fledermäusen, die ihre Nahrung von rauhen Oberflächen wie der Vegetation oder dem Boden absammeln, sind Fledermäuse, die ihre Beute über Wasser jagen, mit anderen sinnesökologischen Herausforderungen konfrontiert. Die akustischen Eigenschaften des Raumes über Wasser entsprechen weniger dem eines störechoreichen Raumes als vielmehr denen eines Rand- und Lückenraumes ("edge space"), da eine glatte Wasseroberfläche einen Großteil der Rufenergie niedrig fliegender Fledermäuse von den Tieren weg reflektiert. Folglich sind Wasserfledermäuse nur geringen oder überhaupt keinen Störechos ausgesetzt. Beute auf der Wasseroberfläche verursacht hingegen, abhängig von ihren akustischen Eigenschaften und ihrem Verhalten, charakteristische Änderungen in der Frequenz und Amplitude der Echos von Suchlauten, die von den Fledermäusen zur Beutedetektion genutzt werden. Dementsprechend stoßen Wasserfledermäuse aus den zwei bisher untersuchten Familien Echoortungslaute hoher Intensität aus und produzieren eine distinkte Terminalgruppe. Dies ist ein Indiz dafür, daß bei diesen Fledermäusen Echoortung eine bedeutende Rolle zum Suchen und Finden von Beute spielt.

Da bei den Blattnasenfledermäusen Echoortung zum Erkennen von Nahrung generell eine untergeordnete Rolle spielt, untersuchte ich in Kapitel III in Verhaltensexperimenten unter kontrollierten Bedingungen in einem Flugkäfig auf Barro Colorado Island (BCI) in Panamá die Bedeutung von Echoortung und anderen Sinnesmodalitäten für das Finden von Beute bei *M. macrophyllum*. Aufgrund seiner Nahrungssuchstrategie, Insekten über Wasser zu jagen, nahm ich an, daß *M. macrophyllum* im Gegensatz zu anderen Blattnasenfledermäusen ähnlich wie die anderen Wasserfledermäuse, primär Echoortung zum Erkennen von Beute nutzt. Da sich dies auch im Muster der Echoortungslaute zeigen sollte, erwartete ich, daß *M. macrophyllum* charakteristische Such- und Annäherungslaute, sowie eine distinkte Terminalgruppe ausstößt.

Dazu führte ich fünf Verhaltensexperimente mit neun Individuen durch, die ich in der Zeit vom 6. Januar bis 13. Juni 2003 einzeln für jeweils vier Nächte im Flugkäfig hielt. Diese Versuche zeigten, daß *M. macrophyllum*, wie angenommen, seine Beute auf der Wasseroberfläche primär mit Echoortung findet. Dabei nutzten die Tiere die für Phyllostomiden charakteristischen multiharmonischen, steil frequenzmodulierten Laute, die jedoch mit einer für Blattnasenfledermäuse ungewöhnlich hohen Intensität ausgestoßen wurden. Die wichtige Rolle der Echoortung beim Beutefang wurde noch bekräftigt durch das Ergebnis, daß die Annäherung an Beute von stereotypen, charakteristischen Änderungen im Lautmuster der Echoortung begleitet wurde, die denen von Fledermäusen entsprechen, die im offenen Luftraum Insekten jagen. Damit konnte ich zum ersten Mal im Echoortungsverhalten einer Blattnasenfledermaus eine eindeutige Terminalgruppe belegen.

Neben der Beuteerkennung durch Echoortung erlaubt Flexibilität im Nahrungssuchverhalten einigen Fledermäusen den Zugang zu mehr Ressourcen als anderen, die auf einen bestimmten Fangmodus und damit vermutlich auch auf bestimmte Nahrung beschränkt sind. In Kapitel IV untersuchte ich daher die Flexibilität des Nahrungssuchverhaltens und seinen Einfluß auf das Echoortungsverhalten von *M. macrophyllum*. In Verhaltensexperimenten im Flugkäfig testete ich die Fähigkeit von neun Individuen, über der Wasseroberfläche aufgehängte Beute zu fangen. Dabei verglich ich insbesondere das Echoortungsverhalten zwischen Experimenten, in denen Beute in der Luft und auf der Wasseroberfläche angeboten wurde. In Übereinstimmung mit anderen Wasserfledermäusen fand ich, daß das Nahrungssuchverhalten von *M. macrophyllum* eine hohe Flexibilität aufweist. Die Verhaltensexperimente zeigten, daß *M. macrophyllum* gleichsam Beute in der Luft als auch von der Wasseroberfläche fangen kann und der Fangmodus dabei keinen Einfluß auf das Echoortungsverhalten hat. Daraus schließe ich, daß die sensorische Aufgabe für die Fledermäuse in beiden Situationen vergleichbar ist. Die Möglichkeit, Insekten von und über der Wasseroberfläche zu fangen, ermöglicht dieser Art, Zugang zu einer Vielzahl von Insekten über Wasser zu erlangen und führt damit wahrscheinlich zu einer besseren Habitatnutzung.

Während des Beutefangs von oder über einer glatten Wasseroberfläche ist *M. macrophyllum* nur geringen oder keinen Störechos ausgesetzt. Im Gegensatz dazu wurde *M. macrophyllum* jedoch über dem Gatún-See häufig beim Jagen in der Nähe und über treibenden Matten der Wasserpflanze *Hydrilla verticillata* (Hydrocharitaceae) beobachtet, deren Blattspitzen die Wasseroberfläche brachen und dadurch für in der Nähe jagende Fledermäuse Störechos erzeugten, die die Echos potentieller Beute maskieren können. Störecho-produzierende Unebenheiten auf der Wasserfläche können, wie es für die temperate Wasserfledermaus, *Myotis daubentonii* (Vespertilionidae), gezeigt wurde, zu einer Reduzierung des Fangerfolgs führen, da die Beute nicht mehr eindeutig vor dem Hintergrund erkannt wird. Um den Einfluß von Hintergrund-Störechos auf das Echoortungs- und Nahrungssuchverhalten von *M. macrophyllum* zu untersuchen, führte ich Verhaltensexperimente an neun Individuen im Flugkäfig auf BCI durch, in denen ich

Beute in unterschiedlichen Abständen zu störecho-produzierendem Hintergrund auf und über der Wasseroberfläche anbot. Ich stellte die Hypothese auf, daß *M. macrophyllum* Beute nur dann findet, wenn die Beuteechos nicht oder nur geringfügig von Störechos maskiert werden. Zunehmende Maskierung der Beuteechos durch Störechos sollte die Erkennung von Beute erschweren und ein vollständiger Überlapp der beiden Echos sollte sie unmöglich machen. In den Experimenten war *M. macrophyllum* in der Lage, ein bestimmtes Maß an Maskierung der Beuteechos durch Störechos zu tolerieren. Sobald jedoch die Beuteechos komplett mit Störechos überlagert wurden, sank der Fangerfolg drastisch ab.

Fazit.— Zusammenfassend konnte ich in meiner Dissertation zeigen, daß *M. macrophyllum* ausschließlich über Wasser jagt. In ihrem Jagd- und Echoortungsverhalten entspricht diese Blattnasenfledermaus anderen Wasserfledermäusen, unterscheidet sich jedoch in vielerlei Hinsicht wesentlich von anderen Phyllostomiden. Die Größe der Aktionsräume spiegelt den Fang weiträumig verteilter Insekten von und über der Wasseroberfläche in ausgedehnten und kontinuierlichen Flügen wider. Dabei ermöglicht die Kombination zweier Jagdmodi *M. macrophyllum* hohe Flexibilität und Effizienz beim Beutefang und ermöglicht den Zugang zu reichhaltigen Nahrungsressourcen sowohl auf als auch über der Wasseroberfläche. Bei der Erkennung von Beute auf der Wasseroberfläche und in der Luft spielt die Echoortung eine zentrale Rolle. Dies zeigt sich auch in der Verwendung einer deutlichen Terminalgruppe, die es *M. macrophyllum* ermöglicht, bewegte Beute in der Luft zu fangen. Die Struktur der im Vergleich zu anderen Blattnasenfledermäusen lauten Echoortungssignale von *M. macrophyllum* ist dabei an die akustischen Eigenschaften des störecho-armen Habitats über Wasser angepaßt. Durch die hohe Bandbreite der kurzen, frequenzmodulierten Laute kann *M. macrophyllum* ein hohes Maß an Störechos bei der Beutedetektion tolerieren und ist daher in der Lage, Insekten auch in der Nähe von störecho-produzierendem Hintergrund zu finden.

Introduction

Neotropical bat communities are characterized by extraordinarily high diversity, where more than 100 species may coexist (Kalko 1998, Voss & Emmons 1996). In particular, the very diverse New World leaf-nosed bats (Phyllostomidae) are unparalleled in their foraging ecology, including food such as fruit, nectar, pollen, arthropods, small vertebrates, and blood (Findley 1993). Yet, despite this high dietary diversity, they typically forage in rather similar, narrow-space habitat close to or within forests, where they glean food from the vegetation or ground (Kalko 1998). However, the small insectivorous long-legged bat, *Macrophyllum macrophyllum* Schinz (1821; Phyllostomidae), differs from all other leaf-nosed bats in a variety of morphological characteristics, such as a relatively large noseleaf, a large tail membrane, long legs, and large feet with powerful claws. These attributes led to the suggestion that *M. macrophyllum* may primarily forage in unobstructed space above water (Harrison 1975).

Foraging above water is unique within the Phyllostomidae, and is otherwise only found in a few species of trawling bats of different families, including Noctilionidae, Emballonuridae, and Vespertilionidae, which catch prey directly from (trawling mode) or just above water surfaces (aerial mode; Kalko 1995a, Kalko *et al.* 1998, Jones & Rayner 1988, Siemers *et al.* 2001). Whereas it is well understood how these trawling bats find their prey on and above the water surface, only anecdotal information exists about where and how *M. macrophyllum* finds and acquires its food (Harrison 1975). In the four chapters of this study, I therefore investigated patterns of spatial use and activity, as well as the perceptual tasks, which have to be performed by *M. macrophyllum* while foraging over water, either trawling prey from the water surface or hawking it in the air.

Differential use of space has been discussed as one of the factors promoting diversity and structuring local bat communities (Findley 1993, Kalko *et al.* 1996). However, knowledge about range size and use, as well as partitioning of space between sympatric bat species is still limited, particularly in the tropics. Here, recent advances in radio tracking techniques have opened up new fields, in particular, the study of patterns of spatial use. Whereas to date mostly frugivorous phyllostomid species have been the target of radio tracking studies, investigation of spatial use in insectivorous species has just begun (Kalko *et al.* 1999, Weinbeer & Kalko 2004). In chapter I, I thus investigated range size and use of *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá, to understand patterns of spatial use in this unique insectivorous phyllostomid bat.

Another factor influencing bat diversity are temporal patterns of foraging activity combined with different foraging modes, which reflect the wide variety and flexibility of bats regarding behavioral, morphological, and sensory adaptations to foraging habitats and prey types (Aldridge & Rautenbach 1987, Neuweiler 1989, Fenton 1990, Schnitzler & Kalko 1998). For instance, some perch-hunting bats wait for prey to pass by or to produce specific, prey-generated sounds. Few, often large prey items per night are then taken in short sally flights mostly from the ground or

other surfaces (gleaning; Kalko *et al.* 1999). In contrast, aerial and trawling insectivorous bats, which forage in unobstructed space, spend up to several hours per night in pursuit of generally small insects, captured in the air or from the water surface (Chruszcz & Barclay 2003, Kalko *et al.* 1998, Jones & Rayner 1988), and often correlate their foraging activity with dusk and dawn peaks in prey abundance (Rydell *et al.* 1996).

In chapter II, I therefore assessed how foraging habitat and changes in prey availability affect patterns of foraging activity in *M. macrophyllum* in Panamá. Apart from some occasional mist net captures, there is no information about temporal aspects of foraging activity in this species (Harrison 1975). However, in accordance with other trawling bats, *M. macrophyllum* forages for similar prey (small insects, like Lepidoptera or Diptera) in unobstructed space over water (Harrison 1975). Therefore, I hypothesized that *M. macrophyllum* likewise spends large parts of the night pursuing its prey on and above water surfaces in fast and continuous flight.

Another key factor that grants access to a wide range of resources at night and ultimately lead to the high diversity of bats is the development of a complex echolocation system (Arita & Fenton 1997, Fenton 1995, Schnitzler & Kalko 1998). Overall, a broad spectrum of echolocation call types has evolved, where signal design, comprising distinct functional elements, and patterns of echolocation behavior reflect sensorial tasks in detection, classification, and localization of prey (Fenton 1990, Neuweiler 1990, Schnitzler & Kalko 1998). Echolocation sequences of bats foraging for insects in open space consist of characteristic call patterns (Griffin *et al.* 1960). Search calls are emitted at a regular rhythm, mostly one call per wing beat, until detection of potential prey. Thereafter, bats start pursuit with a distinctive change in call structure and pattern to obtain detailed information about type and location of prey during approach. Finally, prior to capture, bats produce a terminal group composed of many very short calls emitted at a high repetition rate that provides maximum localization accuracy for successful capture of moving prey (Griffin *et al.* 1960, Schnitzler & Kalko 1998). In aerial insectivores, echolocation is the prime cue for prey perception.

In contrast to open-space insectivores, narrow-space gleaning phyllostomid bats emit rather uniform calls with few changes in call parameters when approaching food. In particular, they do not produce a distinct terminal group. This is likely to be connected with the fact, that these bats mainly glean stationary food, which does not require complex pursuit maneuvers in three-dimensional space (Schnitzler & Kalko 2001). Furthermore, gleaning bats face the difficulty that clutter echoes from nearby background hamper detection of food by echolocation alone, as they may mask prey echoes depending on the position of prey (Arlettaz *et al.* 2001, Schnitzler & Kalko 2001). Therefore, many leaf-nosed bats also use other sensory cues to find food (Belwood & Morris 1987, Kalko & Condon 1998, Thies *et al.* 1998).

Compared to bats gleaning food in narrow-space from vegetation or ground, the sensorial challenge to bats foraging over water differs remarkably (Kalko & Schnitzler 1989, Rydell *et al.* 1999). In fact, acoustic properties above water are rather similar to background cluttered or edge space, since a smooth water surface reflects most of the signal energy away from a low-flying bat. Hence, trawling bats are exposed to little or even no clutter echoes (Boonman *et al.* 1998). Depending on its acoustic properties, prey on the water surface causes characteristic changes in frequency and amplitude (acoustic glints) in the echoes of search calls (Siemers *et al.* 2001). Consequently, similar to aerial insectivores, the few trawling bats that have been studied so far, emit species-specific, loud echolocation calls with a distinct terminal group (Britton *et al.* 1997, Jones & Rayner 1988, Schnitzler *et al.* 1994), indicating that echolocation plays an important role for finding and acquiring food (Schnitzler & Kalko 2001).

As echolocation for prey perception usually plays a minor role in phyllostomid bats, in chapter III, I assessed the role of echolocation and other sensory cues for finding prey in *M. macrophyllum* in behavioral experiments under controlled conditions in a flight cage on Barro Colorado Island (BCI), Panamá. Due to its foraging behavior, catching insects in edge space above water, I hypothesized that sensory ecology of *M. macrophyllum* corresponds to other trawling bats, which use echolocation as the prime cue for prey perception. This should be reflected in its pattern of echolocation signals, which I expected to consist of characteristic search and approach calls as well as a distinct terminal group.

In addition to perception of prey using echolocation, flexibility in foraging behavior permits some bats access to more resources than others, which are restricted to a certain foraging mode and hence a limited type of prey. For instance, trawling bats take advantage of the insect-rich space on and above water bodies (Boonman *et al.* 1998, Jones & Rayner 1988, Kalko *et al.* 1998). Similarly, many evening bats (Vespertilionidae) glean and aerial hawk insects to exploit prey that is distributed in space and time (Arlettaz *et al.* 2001, Chruszcz & Barclay 2003). Further, recent studies give insights in a much higher foraging flexibility than expected for some insectivorous phyllostomids, in which behavioral plasticity may lead to a better exploitation of their habitat (Schnitzler *et al.* 1995, Weinbeer & Kalko 2004).

In chapter IV, I therefore assessed the flexibility of foraging behavior, its association with echolocation behavior, and the performance in *M. macrophyllum* foraging close to and within clutter. In a first set of behavioral experiments with bats exposed to tethered prey above the water surface in the flight cage on BCI, Panamá, I tested whether M. *macrophyllum* is able to catch aerial prey. I then compared the echolocation behavior between experiments with prey suspended in the air and prey placed onto the water surface. In accordance with other trawling bats, I hypothesized that *M. macrophyllum* exhibits a highly flexible foraging behavior, including trawling and aerial hawking, which would grant it access to a wide variety of insects over water

surfaces. As similar perceptual tasks have to be performed when hunting floating or tethered prey, I expect that echolocation behavior is similar in both foraging modes.

When trawling or aerial hawking over clean and smooth water surfaces, *M. macrophyllum* is exposed to little or no clutter echoes. In contrast, wild *M. macrophyllum* were frequently observed to forage close to banks of a water plant, *Hydrilla verticillata* (Hydrocharitaceae), whose leaves slightly penetrate the water surface and thus produce clutter echoes, which may mask echoes of potential prey for bats foraging nearby. Increased amount of clutter may lead to reduced prey capture success, as has been shown in a study of a temperate trawling vespertilionid bat, where clutter was produced by duckweed floating on the water surface (Boonman *et al.* 1998). In a second set of behavioral experiments in the flight cage, where I offered prey at varying distances relative to clutter on and above the water surface, I assessed how clutter affects echolocation and foraging behavior of *M. macrophyllum*. I hypothesized that *M. macrophyllum* is able to find prey, as long as prey echoes only slightly overlap with clutter echoes. However, when prey echoes become increasingly masked by clutter echoes, I expected that prey perception would be progressively impeded and in turn, would reduce capture success.

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I

Home Range and Patterns of Space Use of the Long-legged Bat, *Macrophyllum macrophyllum*, Foraging over Water

Bat assemblages in the tropics are characterized by extraordinarily high species diversity; in Amazonian lowland forests, for instance, communities may be composed of more than 100 sympatric species that occur in geographically small areas (Kalko 1998, Voss & Emmons 1996). A central issue in community ecology hence is to get a better understanding of how these species-rich assemblages are organized and how the many morphologically or ecologically similar species may coexist. For many taxa, including tropical bats, it has been demonstrated that differential use of space can be an important factor structuring local communities (Begon *et al.* 1996, Findley 1993, Kalko *et al.* 1996). Yet, current knowledge about the size of home ranges, range use, and partitioning of space between co-occurring species of tropical bats is sill scant. The few results available point to differential use of space among feeding guilds and suggest that temporal and spatial segregation of foraging areas and foraging activity may separate species within guilds (Kalko 1998). Distinct differences in space-use appear to be tightly linked to the size of the animals and their foraging strategy as well as to the availability and distribution of resources (Fleming 1988, Handley *et al.* 1991, Kalko *et al.* 1999, Morrison 1978).

Fostered by recent advances in transmitter miniaturization, radio tracking has proven a particularly powerful technique to investigate many aspects of bat ecology, including home range requirements and patterns of space and habitat use. However, so far most radio tracking studies have concentrated on temperate-zone species (Catto *et al.* 1996, Entwistle *et al.* 1996, Leonard & Fenton 1983, Robinson & Stebbings 1997, Wai-Ping & Fenton 1989), while relatively few detailed studies have been conducted in the tropics (Charles-Dominique 1991, Fenton *et al.* 1993, Fleming 1988, Gannon & Willig 1997, Kalko *et al.* 1999, Morrison 1978, reviewed in Kalko 1998).

With about 150 species, New World leaf-nosed bats (Phyllostomidae) are dominant components of local bat faunas in Neotropical lowland forests. Phyllostomid bats are ecologically highly diverse and unparalleled in their feeding habits, exploiting a wide selection of foods, ranging from fruit, leaves, nectar, and pollen to insects and other arthropods, small vertebrates, and blood (Findley 1993, Kalko *et al.* 1996). While radio tracking studies have long focused on frugivorous members of this speciose family (Charles-Dominique 1991, Fleming 1988, Handley *et al.* 1991, Heithaus *et al.* 1975, Morrison 1978, Thies 1998), insectivorous species have just started to receive some attention (Kalko *et al.* 1999, Weinbeer & Kalko 2004).

In the present study, we investigate home range size and patterns of range use of the insectivorous phyllostomid long-legged bat, *Macrophyllum macrophyllum* Schinz, at a lowland forest site in central Panamá. This sole species of the genus occurs from southern México to Perú, northern Argentina, and southeastern Brazil (Harrison 1975). Besides some anecdotal reports in the literature on sporadic mist-net captures and brief descriptions of day roosts (Dickerman *et al.* 1981, Harrison & Pendleton 1974, Seymour & Dickerman 1982), there is very limited information on the species' ecology and behavior. *Macrophyllum macrophyllum* is a small,

slender bat, with adults having a mass of 6–9 g (Harrison 1975). Apart from the prominent, lanceolate noseleaf, which is reflected in the species' name, the peculiar anatomy of the posterior extremities including a broad interfemoral membrane (uropatagium), long legs and large feet with powerful claws (Harrison 1975), makes *M. macrophyllum* readily distinguishable from all other phyllostomid bats.

Previous field observations by several authors (Harrison & Pendleton 1974, Gardner 1977, Whitaker & Findley 1980) and our own findings (Chapter II) indicate that *Macrophyllum* forages primarily over water, where it gleans insects either directly from the water surface or hawks prey just above the water. Despite their high dietary diversity, phyllostomid bats typically forage in narrow-space habitats, close to or within obstacle-rich forests, where they glean food from the vegetation or the ground (Kalko 1998). In *M. macrophyllum*, hunting over water thus constitutes a unique foraging behavior in an unusual habitat within the Phyllostomidae. It has evolved only once in this speciose family and makes this species particularly interesting for study.

The specific objectives of our study were: (1) to assess space use of *M. macrophyllum* including individual variability and gender-specific differences in home range size and patterns of range and habitat use; (2) to provide an evaluation of the proposition that smaller bats should travel shorter distances and have smaller home ranges than larger species (*cf.* Fenton 1997); and (3) to increase our knowledge about the importance of space partitioning in promoting the high diversity of phyllostomid bats.

METHODS

Study site.— The study was conducted from April to July 2002 in the Barro Colorado Nature Monument (BCNM, 9°10'N, 79°51'W), Republic of Panamá (FIG 1). Barro Colorado Island (BCI), the largest of the approximately 200 islands in Gatún Lake, forms the heart of this 5600 ha biological reserve, which is covered with seasonal tropical lowland forest. BCI receives an average of 2600 mm of rainfall per year with a pronounced dry season from late December to late April, where only about 10% of the annual precipitation occurs. In the wet season, monthly rainfall averages 300 mm with a short, slightly drier period between August and September (Windsor 1990). Annual temperature averages 27°C, with a mean diurnal temperature range of about 9°C. More details on vegetation and climate can be found elsewhere (Croat 1978, Windsor 1990, Leigh 1999).

Capture and handling of bats.— The colony of *M. macrophyllum* studied on BCI was located in an old, half-sunken ship ("Barracuda") in the Laboratory Cove (FIG 2; names of locations mentioned throughout the text) and comprised approximately 60 individuals, mostly females. Bats were captured at an opening of the ship's hull with a net consisting of two poles with a

piece of mist-net suspended loosely between them. Individuals potentially suitable for tracking were held in soft cloth bags and taken to the nearby laboratory. For each individual, the following information was recorded: sex, age (juvenile, subadult, adult) based on the degree of closure of the phalangeal epiphyses (Anthony 1988, Handley *et al.* 1991), forearm length measured with a caliper to the nearest 0.5 millimeter, and body mass measured to the nearest 0.5 g using a 100 g Pesola spring scale. Reproductive condition of females was assessed by palpation: non-reproductive (nipples very small, no fetus palpable), pregnant (palpable fetus), lactating (enlarged nipples, hairless spot around nipples), and post-lactating (regrowth of hair around nipples, Handley *et al.* 1991). In males, length and width of the testes was measured. Only adult males and adult, non-reproductive females were selected for telemetry.

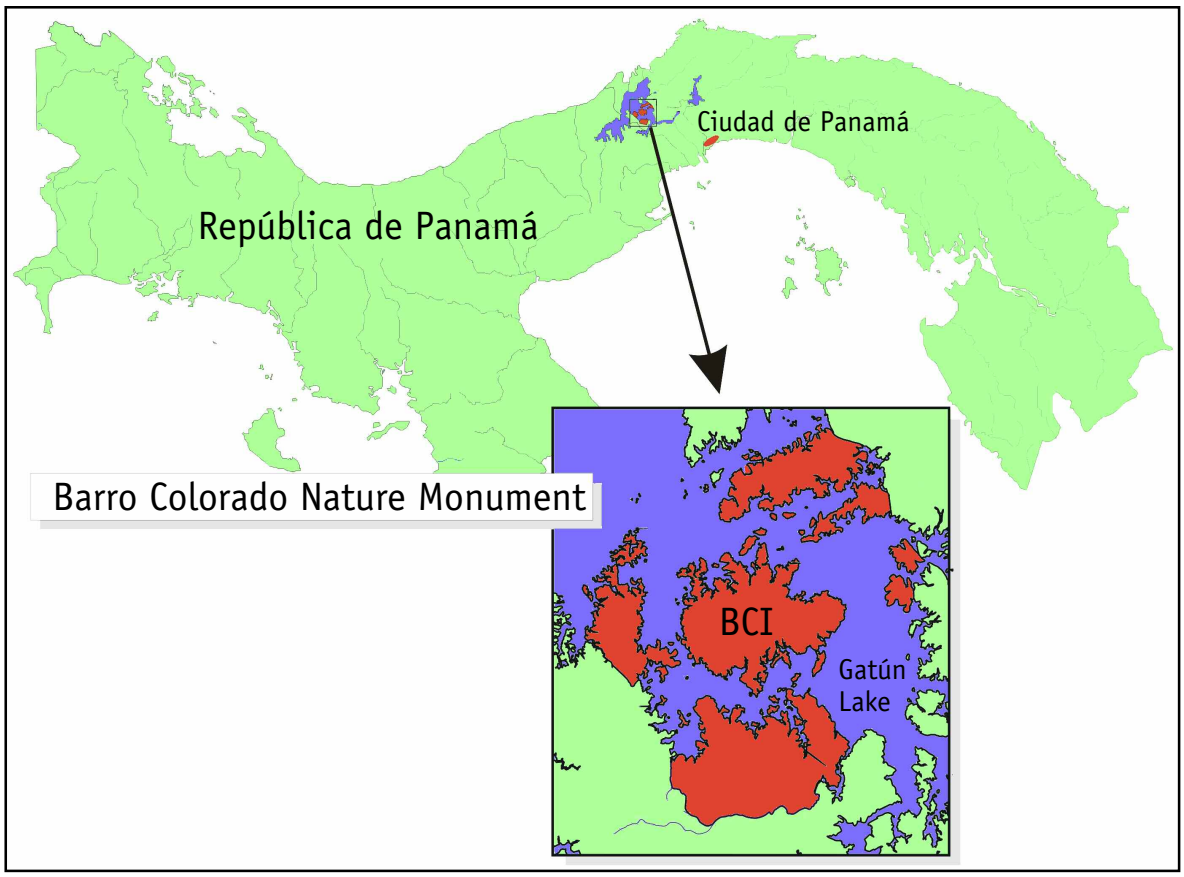


FIGURE 1. Map of the study area (Barro Colorado Nature Monument, red) and its location within the Gatún Lake in central Panamá. Barro Colorado Island (BCI) forms the heart of this 5600 ha biological reserve. Map: S. Paton, Smithsonian Tropical Research Institute, 1997 (modified).

Radio tracking.— We attached transmitters to the backs of the bats below the scapulae using histoacrylic glue. Recaptured individuals showed no signs of any injury that could have resulted from tagging. In an attempt to visually locate feeding bats at night, some transmitters were additionally marked with a small piece of red reflecting tape. We used position-sensitive radio-transmitters (150 MHz; model LB-2B, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitter mass was 0.84 ± 0.02 g, representing 9.5 ± 0.7% of the bats' body mass (mean body mass of the

tagged individuals 9.0 ± 0.7 g). This is under the 10% mass threshold above which transmitter mass is regarded to seriously affect an animal's foraging behavior (Brander & Cochran 1969). Based on numerous direct observations of tagged *M. macrophyllum* in the field and also considering that small bats can carry heavier loads relative to their body mass than larger species (Norberg & Rayner 1987), we conclude that transmitter mass did not negatively affect flight performance of tagged individuals. This is also indicated by a recaptured individual that did not loose any weight during the time it had been tracked. The radio-tagged animals were released at the day roost, mostly within 1.5 h after capture.

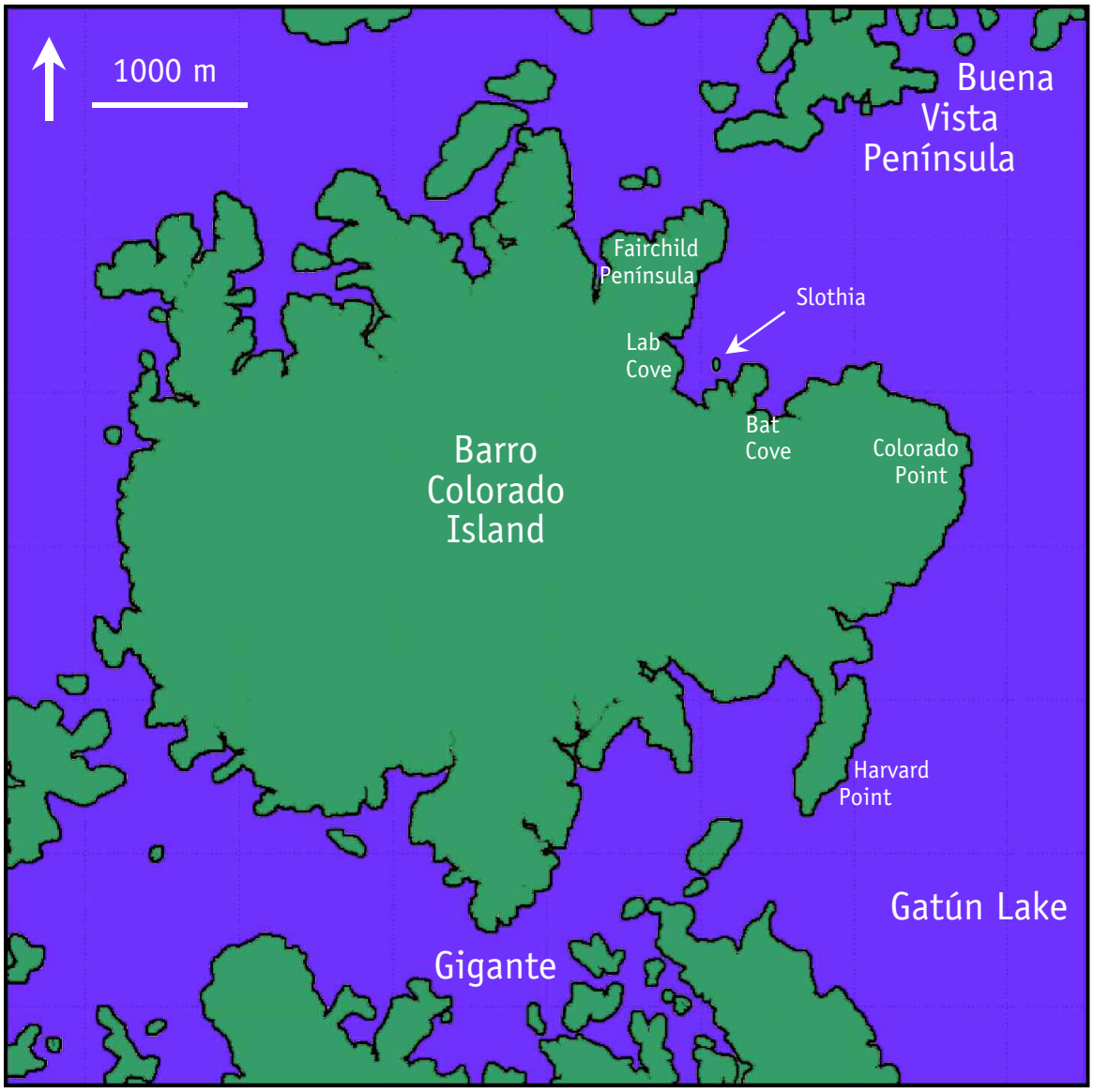


FIGURE 2. Detail of the study area (Barro Colorado Nature Monument) with Barro Colorado Island (BCI) in the center, surrounded by adjacent peninsulas. Map: Thies, Kinner, Clark, Rev. 6b (modified).

Starting the following night after tagging, individual bats were generally tracked for complete nights, from the time of emergence until they returned to their day roost the following morning. Two observers closely followed a bat by motorboat, monitoring the bat's location using modified YAESU VR-500 receivers (Yaesu Musen Co. Ltd., Japan) with hand-held H-aerial antennas

(adapted by Wagener Telemetrieanlagen, Cologne, Germany). We used FM-radios in the field to communicate and to take simultaneous bearings. We chose a constant time interval of 3 min between successive readings (de Solla *et al.* 1999). Only during rapid movements of the bats, readings were sometimes taken more frequently. We took bearings to the nearest degree with a compass attached to the antenna. When the bat was resting in a night-roost between foraging bouts, we recorded its position only once to avoid over-representation of these locations. Bearings were taken from fixed positions, using canal buoys, self-made buoys installed within a bat's home range, tree stumps, or branches to attach the boats. We geo-referenced the locations of the observers at these fixed positions with a Global Positioning System (GPS, Garmin Inc., Olathe, Kansas, USA, accuracy 3–7 m). Together with each bearing, time, observers' positions, signal pattern (fast, slow) and signal strength along with general observations such as information about the prevailing weather conditions were recorded on a dictaphone (SONY TCM-459V) and later entered into Microsoft Excel spreadsheets. A change in the pulse repetition rate depending on the position of the transmitter (higher pulse rate in the horizontal position versus lower pulse rate in the vertical position) allowed us to determine whether the bat was flying or roosting (Chapter II).

Database.— Between April and July 2002, we tagged five females and four males (hereafter referred to as F1–F5 and M1–M4, respectively) that were tracked each for an average of 5.3 ± 0.9 nights. This led to 519.5 hours of tracking with 422.5 hours (82%) of contact time during which a bat could be followed closely (TAB 1).

TABLE 1. Numbers of tracking nights, hours of tracking, and time of contact for five female and four male *M. macrophyllum* radio-tracked from April to July 2002 in the Barro Colorado Nature Monument, Panamá.

Bat	Tracking nights	Tracking [h]	Contact [h]	Contact [%]
F1	5	53.1	51.1	96.3 ± 2.9
F2	4	43.0	24.2	55.7 ± 31.1
F3	7	74.5	47.1	63.6 ± 32.2
F4	6	64.5	64.4	99.8 ± 0.3
F5	6	63.0	34.2	54.8 ± 37.8
M1	5	57.1	39.5	69.1 ± 16.7
M2	5	56.3	54.1	96.1 ± 3.7
M3	5	54.5	54.4	99.8 ± 0.5
M4	5	53.5	53.5	100.0 ± 0.0
Total	48	519.5	422.5	81.7 ± 20.3

Calculation of bat locations.— Radio-locations of the bats were calculated from bearings with the computer program Tracker™ (version 1.1, 1994, Camponotus AB, Solna, Sweden) and plotted on a custom-made map of the study area (compiled by Thies, Kinner, Clark, & Stallard, Rev. 6b, 2000). Since the bats typically returned to the same foraging areas on successive nights, we

pooled all bearings taken for one individual for analyses. Tracker uses a maximum likelihood method to calculate points from simultaneous bearings by triangulation. Whenever two observers could not take bearings simultaneously, e.g. if a bat moved too quickly, its position was determined from single bearings, along which the distance of the bat from the shore was estimated based on signal strength and gain setting. Since our telemetry data and numerous observations indicated that *M. macrophyllum* almost exclusively foraged in the immediate vicinity of the shoreline and did not use the forest as a hunting habitat, we considered the determination of a bat's position from single bearings in this way as reasonably accurate (*cf.* Bonaccorso *et al.* 2002, O'Donnell 2001, Winkelmann *et al.* 2000).

Estimation of home range size.— As a consequence of the hunting behavior of these bats, namely to restrict their foraging activity mostly close to the shore, it was not feasible to calculate home range size using minimum convex polygons (MCPs, Mohr 1947). This method is still the one most frequently employed in home range studies (Harris *et al.* 1990) although it suffers from several severe shortcomings (see Kenward *et al.* 2001 for a recent discussion). Using the MCP method, range size would be largely overestimated because large tracts of forest that were never visited by the bats would be incorporated in the estimate. In order to obtain a more realistic estimate of home range size for these bats, we chose to delineate areas based closely on the observed pattern of the obtained fixes and defined the lakeshore to constitute a range boundary line. Specifically, we estimated home range size with the computer program analySIS (version 3.1, Soft Imaging System Corp., Lakewood, Colorado, USA) as the area between the shoreline and an imaginary line at a distance of about 50 m from the shore. Choice of this value was an approximate average based on the tracking data and own observations of how far the bats occasionally ventured out onto the lake. We used 2812 fixes (312 ± 134 per bat) from four male and five female *M. macrophyllum* to calculate home ranges.

Analysis of range use.— We subsequently entered the point locations into a Geographical Information System (GIS, ArcView 3.2, Environmental Systems Research Group, Inc., California, USA) for analyses of range use, and plotted them on a GIS-based map of the study area (compiled by Mixon, Kinner, Wahl, & Stallard, V 1.1., 2002). We performed all calculations of range use with the ArcView extension Animal Movement (Hooge & Eichenlaub 2000). The program implements the bivariate normal density kernel as suggested by Worton (1989) and calculates a fixed kernel utilization distribution. Following the recommendation of Seaman & Powell (1996), we used least-squares cross validation to select the appropriate smoothing parameter. We calculated foraging areas (FA) using 95% kernel isopleths to facilitate comparison with other studies (White & Garrot 1990). In contrast to the home range, foraging areas do not include the day roost and areas traversed by a bat while commuting.

Animals commonly use space in a non-uniform manner within the boundaries of their home range and typically preferred areas where they spend most of their time (Harris *et al.* 1990,

Samuel *et al.* 1985). We determined the proportion of the range that could be defined as a core area (CA) in two ways. First, we used the 50% isopleth of the fixed kernel estimation to assess centers of activity, both because this allows for direct comparison of results obtained for different individuals and as it is widely employed in radio tracking studies. Second, we quantified range cores following the procedure outlined by Wray *et al.* (1992). Here, an array of kernel isopleths with a decreasing percentage of included fixes (from 95% down to 20%) is produced and the number of core areas generated for each isopleth subsequently counted. The isopleth with the largest number of core areas is then chosen for analysis. In those cases where no additional core area formed besides the 95% isopleth, an average of the results obtained for the other individuals (here, the 75% kernel isopleth) was used for calculations. Kernel estimations of foraging and core areas are based on 2352 position determinations (261 ± 116 per bat) because only fixes obtained at a regular time interval (3 min) were used for analysis (de Solla *et al.* 1999).

Finally, we identified the number and locations of foraging and core areas of each tracked individual and calculated the distances a bat traveled on a nightly basis within its range to describe patterns of range use. We calculated the minimum distance flown per night (based on the distance between successive fixes), the maximum distance between the day roost and the farthest point of a bat's home range, and the commuting distances from the day roost to the nearest foraging area.

Statistical analysis.— Statistical tests were performed using Statistica (V 6.0, StatSoft, Inc., Tulsa, OK, USA). We used Mann-Whitney U-tests to test for differences in home range size and patterns of range use between males and females. For all tests, $p < 0.05$ was chosen as level of significance. Because of the autocorrelated nature of the data, differences in size of foraging and core areas calculated with the kernel method were not subjected to statistical analysis. Since range sizes were generally not normally distributed, most results are reported as medians and interquartile ranges (IQR). All other numerical results are given as mean ± 1 SD.

RESULTS

Home range size.— Home range size varied considerably among individuals (7.3–150.7 ha; TAB 2, FIG 3 & 4). Median home range size for all individuals in this study was 23.9 ha (IQR = 13.5–61.5). Although there were no statistically significant differences in home range size based on gender (Mann-Whitney U test, $Z = -1.35$, $p = 0.178$), females on average had slightly larger home ranges (44.4 ha, IQR = 18.9–114.7, range = 16.3–150.7) than males (17.3 ha, IQR = 8.2–24.9, range = 7.3–24.9). In the case of two females (F3, F5), estimates of range size are minimum values since we were not able to stay in contact with the animals during their entire

tracking tenure. Thus, the difference in home range size between males and females would possibly be significant if we had been able to fully determine the home ranges of these two females.

TABLE 2. Median size of home ranges and size and number of foraging areas (FA; 95%-kernel) of five female and four male *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá. Errors are interquartile ranges (IQR) or ± 1 SD. Home ranges and foraging areas of some bats (*) should be treated as minimum values, as bats could not be followed over their whole range.

Bat	Home range size [ha] (IQR)	Size of FA [ha] (IQR)	Number of FAs (mean ± SD)
F1	16.3	2.7	1
F2	21.4	28.7	1
F3	44.4*	12.3*	3
F4	78.6	4.7	1
F5	150.7*	96.1*	3
Total	44.4 (18.9-114.7)	12.3 (3.7-62.4)	1.8 ± 1.1
M1	7.3	5.7	3
M2	24.9	41.5	4
M3	10.7	9.3	2
M4	23.9	15.3	3
Total	17.3 (8.2-24.7)	12.3 (6.6-34.9)	3.0 ± 0.8

Location of home ranges, foraging and core areas.— Our tracking data indicate that *M. macrophyllum* forages exclusively over water whereby all bats restricted their flight activity predominantly to the immediate shoreline of Gatún Lake (within approximately 50 m). This resulted in most cases in distinctly elongated home range shapes (FIG 3 & 4). We have no evidence that the bats also used the forest as a hunting habitat. With the exception of M2, which spent most of its foraging time around Colorado Point (FIG 5B), males in general and a harem male (M3) in particular, used small foraging and core areas close to their day roost that were located in the Laboratory Cove or Bat Cove (FIG 5A, C, & D). Females, in contrast, were much more variable, having FAs and CAs both close and very distant from the day roost.

In general, there was moderate spatial overlap between the FAs and CAs of individuals (FIG 5 & 6), which were distributed along the lakeshore in Bat Cove, at Fairchild and Harvard Peninsula and around Colorado Point. During some nights, one female (F3) crossed the Canal and spent part of the night foraging somewhere around the mainland peninsula Buena Vista. This individual thus had at least one other foraging area. However, we could not determine its exact location since we were unable to continuously follow this bat and obtain a sufficient number of radio-fixes within that area. Another female (F5) had by far the greatest home range, and its FAs were located far from one another. During some tracking nights, we lost contact with the bat as it moved quickly out of the range of the receivers. One night though, we managed to follow the bat

when it traveled about 7.5 km from the day roost along the BCI shoreline to another FA located around Gigante, a nearby mainland peninsula (FIG 6E).

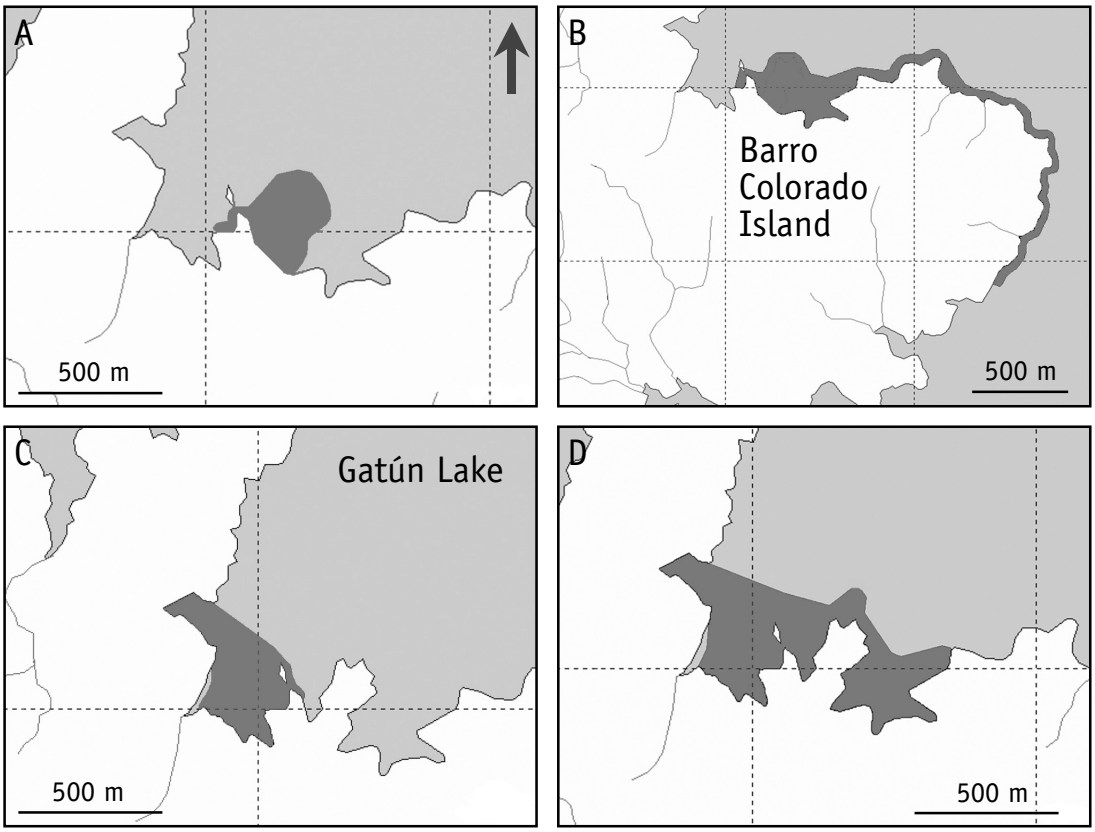


FIGURE 3. Home ranges (dark grey) of four radio-tracked male *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá. A: M1, B: M2, C: M3, D: M4.

Foraging areas.— Median foraging areas (95% kernel) of male *M. macrophyllum* were similar in size (12.3 ha, IQR = 6.6–34.9, range = 5.7–41.5) but showed less variation than those of females (12.3 ha, IQR = 3.7–62.4, range = 2.7–96.1). Most bats had several FAs; the number per individual ranged from one to four and was on average somewhat higher in males than in females (TAB 2, FIG 5 & 6). All individuals were highly consistent in their use of foraging areas, generally returning to them night after night.

Core areas.— Main foraging activity of all tracked *M. macrophyllum* was concentrated within distinct areas of their home range. As with FAs, nearly all individuals used several (up to five) core areas (TAB 3). On average, CAs corresponded to only 35.2 ± 13.8% of the total size of foraging areas, but they included most of the fixes (65–90%). Median core-area size was 5.3 ha for females (IQR = 1.1–30.8, range = 1.1–54.1) and somewhat smaller for males (3.5 ha, IQR = 2.7–7.4, range = 2.6–8.7). The large variation observed in females was mainly due to the high value for one individual (F5; TAB 3, FIG 5 & 6). These results pertain to core areas generated using kernel isopleths with decreasing percentage of inclusion of fixes. Comparative estimates of core areas based on 50% kernel isopleths are given in TAB 3.

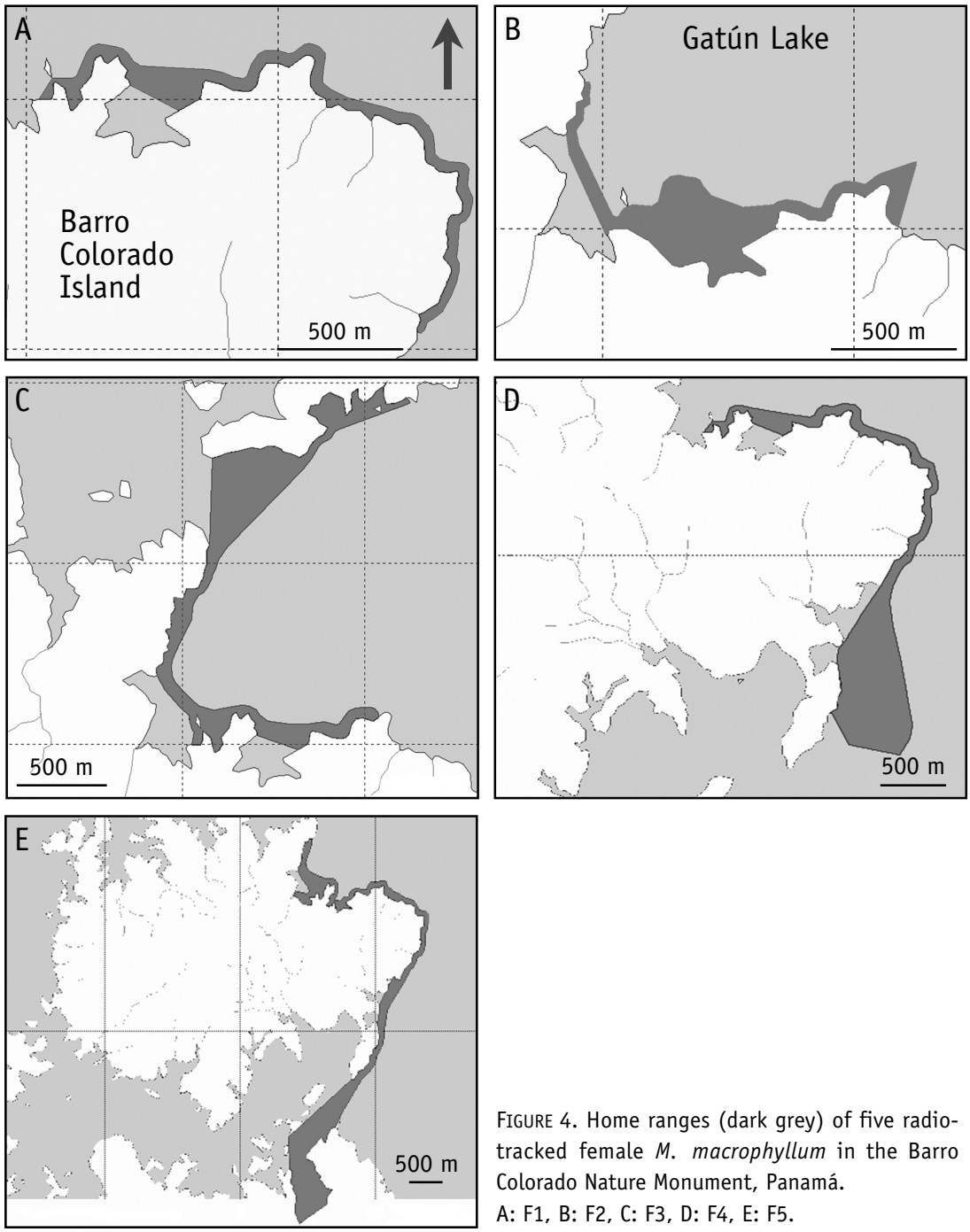


FIGURE 4. Home ranges (dark grey) of five radio-tracked female *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá.
A: F1, B: F2, C: F3, D: F4, E: F5.

Movement patterns.— Commuting distances between the day roost and the nearest FA, ranged from 0 to 4350 m, with no significant difference between sexes (TAB 4). With the exception of two females (F1, F4) whose single FAs were located more than 2 km and 4 km away from the day roost, the majority of individuals had their closest FA directly adjacent to their day roost. In commuting between the day roost and foraging areas or between the latter, the tagged individuals typically did not fly the direct route, which would have led them through the forest, but closely followed the shoreline or flew over open water instead. Some bats (M1, M2, F1) flew over or crossed only small, forested areas en route to their FAs such as the peninsula between Laboratory and Bat Cove (about 150 m in diameter). During commutes along the shoreline, the

bats attained a flight speed of approximately 8.3 ms^{-1} (30 km/h) as estimated based on the speed of our motorboats (determined by GPS) while closely tracking the bat.

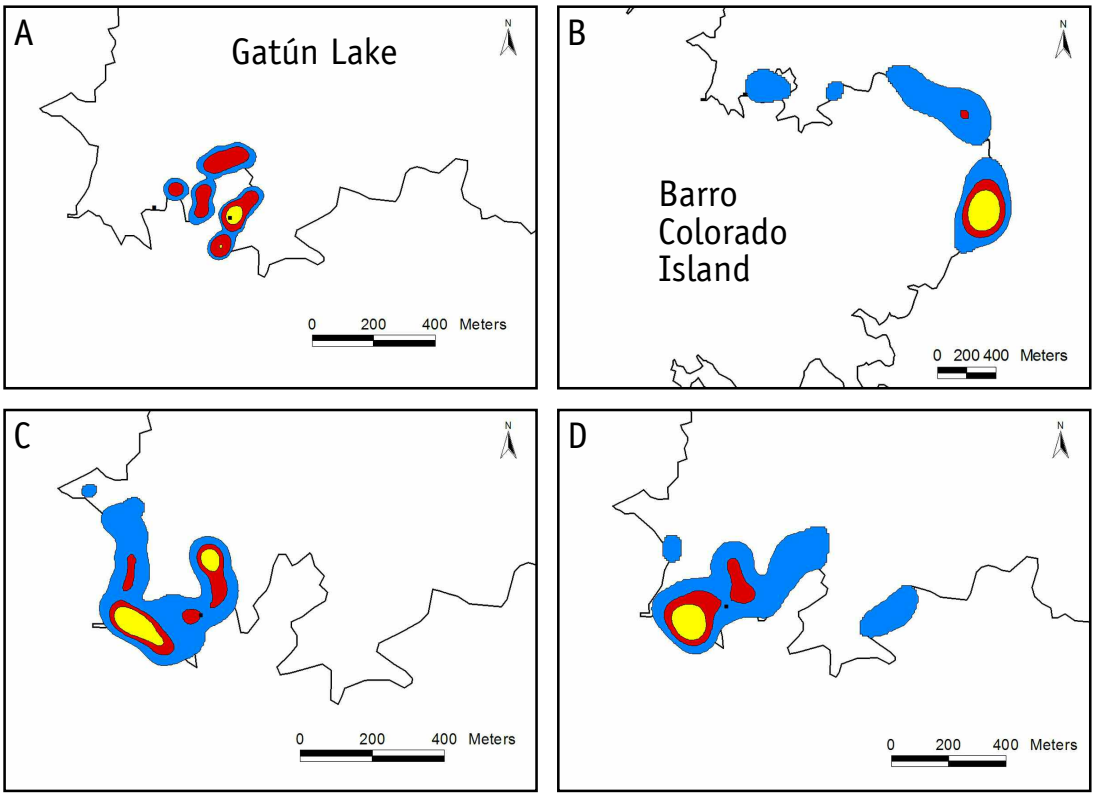


FIGURE 5. Foraging (blue) and core areas (yellow: 50% kernel; red: kernel of percentage including highest number of cores) of four radio-tracked male *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá. A: M1, B: M2, C: M3, D: M4.

We estimated nightly flight distances covered by the bats in two ways. Based on straight-line measurements between successive point locations, minimum flight distances per night ranged from 3 km to almost 18 km. On average, females traveled significantly longer distances than males (TAB 4). However, since in reality the bats were often turning and moving back and forth within their foraging areas, a more realistic estimate might be obtained based on average flight speed and the flight time per night. Thus, assuming an average flight speed of 3–4 ms^{-1} while foraging (about half of commuting speed) and a mean flight time per night of 195 min (Chapter II), these bats might travel distances on the order of 35 to 47 km on a nightly basis. A foraging flight speed of 3–4 ms^{-1} seems reasonable according to our observations and has been reported from other bats that hunt over water (Kalko & Schnitzler 1989).

Maximum distance between the day roost and the outermost point of the home range varied from 470 to 7470 m (measured along the shoreline) and was slightly higher in females than in males (TAB 4). This was probably again due to the fact that the range sizes for F3 and F5 could not be fully determined (see above).

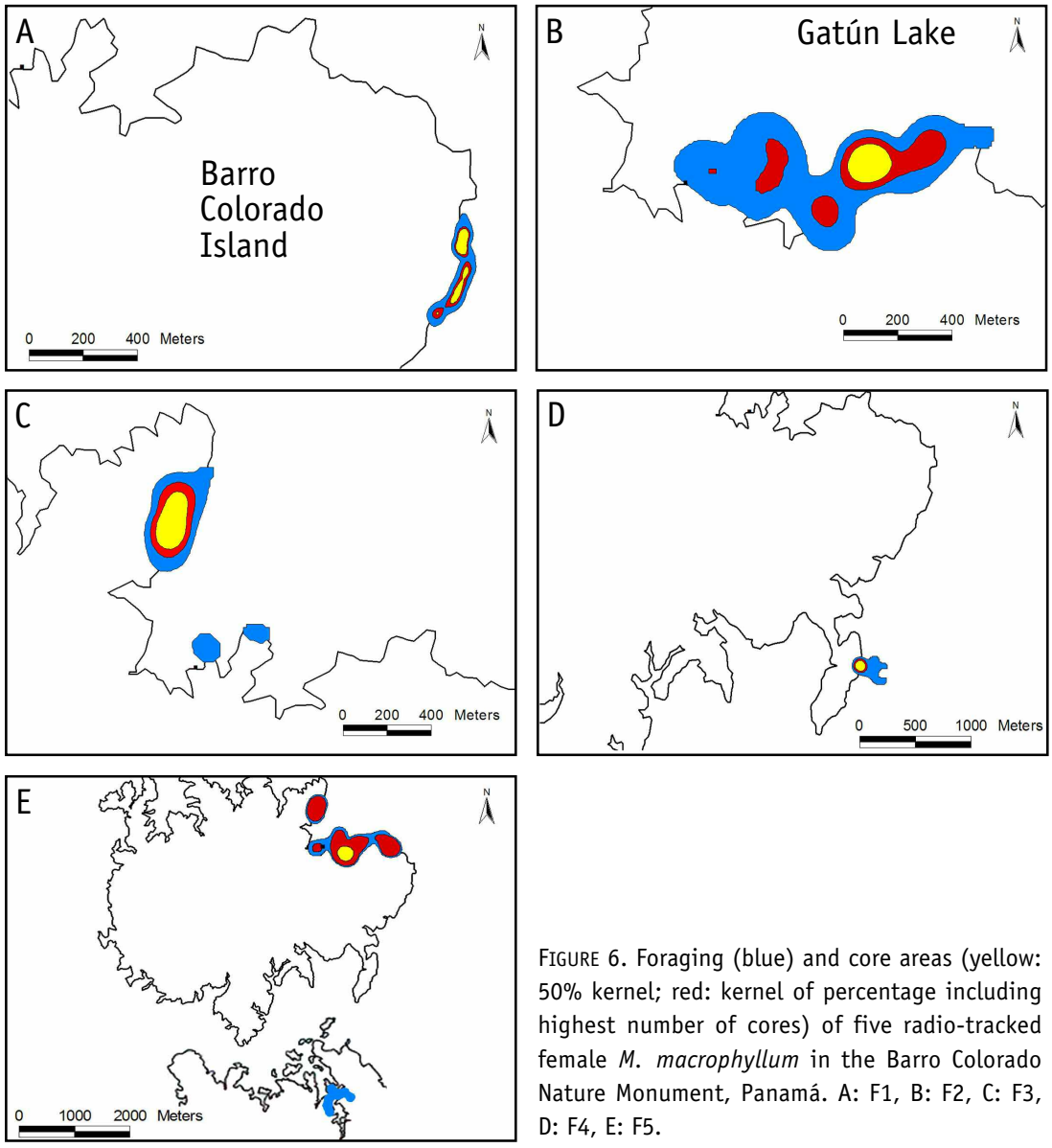


FIGURE 6. Foraging (blue) and core areas (yellow: 50% kernel; red: kernel of percentage including highest number of cores) of five radio-tracked female *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá. A: F1, B: F2, C: F3, D: F4, E: F5.

Roosting behavior.— All radio tracked bats were captured in the "Barracuda" and most individuals continued to use the ship as their day roost. The first male that we tracked (M1) did not return to the ship the next morning. It shifted its day roost, which also served as its main night roost, to Bat Cove where it hung under washed-out roots on the lakeshore (FIG 5A). One bat (M2) switched roosts during its tracking episode, as on some days it stayed in the ship while on others it roosted in a small abandoned shack on the nearby Slothia island.

Intermittent returns to the day roost during the night, sometimes even from distant foraging areas, were common in most individuals with the exception of F4. This female always spent the entire night in its single FA and did not fly back to the day roost until around 5:00 h in the morning. All other individuals tracked had multiple night roosts (6 ± 3, range = 1–10). Seven of the nine tagged bats used the "Barracuda" for night roosting during some point of their tracking period, three individuals (M3, M4, F3) occasionally also roosted in the small shack on Slothia. All

other night roosts characteristically consisted of earth holes under washed-out roots of trees along the shore of BCI. Often the bats revisited the same set of roosts each night although there was no consistency as to the order in which these visits were made.

TABLE 3. Range use of five female and four male *M. macrophyllum* in the Barro Colorado Nature Monument, Panamá. Size and number of core areas (CA) are given based on 50% contour lines of kernel estimation, and as determined by the percentage inclusion of fixes that generated the isopleth with most cores. Errors are interquartile ranges (IQR) or ± 1 SD.

Bat	Total CA [ha] (IQR) (50% kernel)	# of CAs (± SD) (50% kernel)	Total CA [ha] (IQR) (% inclusion)	# of CAs (± SD) (% inclusion)	% of fixes in core (± SD)
F1	0.58	3	1.13	3	65
F2	1.78	1	7.41	4	75
F3	2.87	1	5.26	1	75
F4	0.64	1	1.13	1	75
F5	6.02	1	54.13	4	90
Total	1.78 (0.6–4.5)	1.4 ± 0.9	5.26 (1.1–30.8)	2.6 ± 1.5	76.0 ± 8.9
M1	0.30	2	3.08	5	85
M2	4.53	1	8.72	2	75
M3	0.99	2	2.59	4	70
M4	1.15	1	3.53	2	75
Total	1.07 (0.5–3.7)	1.5 ± 0.6	3.31 (2.7–7.4)	3.3 ± 1.5	76.3 ± 6.3

TABLE 4. Comparison of male and female *M. macrophyllum* on BCI, Panamá in distance flown per night, maximum distance from day roost to outer-most point of foraging areas (range span), and commuting distance between day roost and foraging area. Interquartile range (IRQ) is given in parentheses; *p*-values given are based on Mann-Whitney U tests.

Parameter	Median distance traveled [m] (IQR)		*Z*	*p*
	Males	Females		
Distance flown per night	6420 (4880–9050)	10740 (9260–13330)	-3.40	< 0.001
Maximum range span	810 (550–2550)	2970 (2020–6090)	-1.59	0.111
Commuting distance	0 (0)	40 (0–3380)	-1.60	0.109

Field observations.— Occasionally we were able to follow a bat's flight path with a flash light by illuminating the reflecting tape attached to the transmitter. Characteristically, the bats foraged at low heights (< 50 cm) above the water surface, either flying under or close to the overhanging vegetation along the shore or venturing out onto the lake, in general, hunting within 50 m from shore. In this context, one female (F4) again was a notable exception as our tracking data indicate that this bat periodically foraged large distances, sometimes as far as 600 m, away from shore out on the lake.

DISCUSSION

Home range size.— Studies assessing home range size and patterns of range use in Neotropical bats are still few (Gannon & Willig 1997, Fleming & Heithaus 1986, Handley *et al*. 1991, Kalko *et al*. 1999, Morrison 1978, Thies 1998, Weinbeer & Kalko 2004). The available information indicates that there is large variation in home range size among species closely linked to the spatiotemporal distribution and abundance of food resources and the foraging strategies employed such as foraging in continuous flight versus perch hunting.

Radio-tagged long-legged bats in the BCNM occupied small to large home ranges of 7–151 ha with a median home range size for all tracked individuals of 24 ha. These values underestimate the true home range size because at least two females could not be followed continuously during all tracking nights. Especially when considering its small body size, it becomes apparent that *M. macrophyllum* has large home ranges compared to other insectivorous phyllostomid bats, a finding that contrasts the proposition that small bats should have comparatively small home ranges. For instance, *Lophostoma silvicolum*, a 34 g gleaning insectivorous bat (Kalko *et al*. 1999) is characterized by small home ranges (mean 17 ha, range 11–31 ha) even though it is much larger and heavier than *M. macrophyllum*. The small home ranges in this species mainly reflect the "hang-and-wait" strategy of the rather sedentary foraging behavior of these bats. The gleaning insectivorous-carnivorous bat *Trachops cirrhosus*, although it is approximately equal in body mass to *L. silvicolum*, has much larger home ranges similar in size to *M. macrophyllum* (mean 46 ha, range 8–100 ha, Kalko *et al*. 1999). Although *L. silvicolum* and *T. cirrhosus* both hunt prey from perches in short sally flights, the latter additionally forages for frogs in continuous flight and commutes longer distances, leading to the larger home ranges (Kalko *et al*. 1999). These examples show that differences in foraging strategy can have a profound influence on the range over which bats are active.

The point that home range size is strongly influenced by the availability and distribution of food in space and time is well illustrated by some Neotropical frugivores. Large canopy fruit-eating bats like *Artibeus jamaicensis* (*c*. 45 g) and *A. lituratus* (*c*. 75 g) are known to commute long distances of several kilometers and more between day-roosts and foraging areas in search of

ephemeral and patchily distributed food resources such as figs. This results in extremely large home ranges (Handley *et al*. 1991, Morrison 1978). In contrast, understory frugivores such as *Carollia castanea* whose main food source, fruits of *Piper*, constitutes a highly predictable resource in space and time, have much shorter commuting distances, make shorter foraging flights, and rarely undertake prolonged search flights. Consequently, this small (12 g) frugivore has rather small home ranges that average 29 ha (Thies 1998).

In contrast to patchy fruits, aerial insects are more widely distributed throughout the landscape. Thus, bats like *M. macrophyllum* exploiting this resource likely travel longer distances on a nightly basis and have large home ranges. For instance, the predominantly insectivorous bat *Lampronycteris brachyotis* (Phyllostomidae) was found to use large home ranges of *c*. 90 ha on BCI (Weinbeer & Kalko 2004). Similar to *M. macrophyllum* (Chapter II) this species was characterized by a high flight activity of more than 3 hours per night during which the bats traveled estimated distances of several dozen kilometers (*M. macrophyllum*: *c*. 35–50 km, *L. brachyotis*: *c*. 60 km).

Use of foraging and core areas.— Although overall ranges were large, tagged *M. macrophyllum* concentrated their activity in small core-use areas of typically less than 10 ha, representing roughly 35% of the size of foraging areas. There was moderate spatial overlap between the foraging and core areas of individual bats (FIG 5 & 6). However, since we were only able to track one bat at a time, we could not test whether there was also temporal overlap in the use of the same feeding sites.

Individual bats typically used the same foraging areas on successive tracking nights, a pattern in agreement with other studies of insectivorous bats (e.g. Entwistle *et al*. 1996, Wai-Ping & Fenton 1989). High night-to-night consistency in the use of the same general foraging areas by *M. macrophyllum* suggests that overall variability in insect abundance between successive nights was probably low. The fact that loyalty to a particular foraging site is often linked to constant availability of resources is illustrated by some frugivorous species. For instance, *A. jamaicensis* relies on food resources like figs that become rapidly depleted. It has to continuously explore its surroundings in search for new fruiting trees, and thus is often forced to shift its foraging areas to new locations (Handley *et al*. 1991, Morrison 1978).

On the other hand, many bat species appear to have knowledge of habitat patches in their range with high prey availability, and therefore may maximize food intake by preferentially feeding in such sites (Entwistle *et al*. 1996). This seems a likely explanation for the highly predictable foraging behavior and space-use shown by F4, which contrasted in many ways with the patterns observed in the other tracked individuals. After emergence from the day roost, this female commuted about 4.5 km each night to its single foraging area at Harvard Peninsula (FIG 6D) where it stayed until the next morning. Throughout the tracking period it used only one

night roost from where it made several foraging flights in the course of the night. However, it did not only forage close to the shore as was usually the case with the other individuals but often made forays of up to 600 m onto the lake. This idiosyncratic behavior might reflect a response to a particularly profitable resource patch, which seems plausible considering the presence of an exceptionally large number of mats of *Hydrilla verticillata* (Hydrocharitaceae), and thus large numbers of insects associated with these aquatic plants in that area.

Our results on spatial use obtained by kernel estimation also highlight the difficulty of adequately assessing home range utilization for species that show very distinctive patterns of habitat use like *M. macrophyllum*. That is because with conventional kernel smoothing (Worton 1989) it is not possible to take into account additional information ecologists may have about an animals' use of space that is external to the telemetry data (Matthiopoulos 2003). Such additional information may for instance comprise knowledge about the distribution of food resources or anecdotal behavioral observations, or as in our case, the finding that *M. macrophyllum* did not use the forest as a hunting habitat but foraged almost exclusively along the shoreline of Gatún Lake. Such supplementary information may in principal serve to aid and improve the estimation of range use from telemetry data alone. In a first attempt to integrate both types of information, Matthiopoulos (2003) recently advocated the use of a novel approach, model-supervised kernel smoothing, which combines both auxiliary independent information with the established method of kernel smoothing in order to improve the estimation of home range utilization. Further research in this respect is certainly worthwhile as the proposed method has the potential for increasing the overall accuracy of range use estimates in future radio tracking studies.

Commuting distances.— The high mobility gives bats access to a wide range of habitats and can often liberate them from their dependence on a particular location for foraging (Fenton 1997). Radio tracking studies reveal that bats commute distances from their roosts to foraging areas of less than one to more than 20 km (Fenton 1990, 1997); for some species even larger commuting distances have been reported (up to 50 km for *Leptonycteris curasoae*; Sahley *et al.* 1993). In this regard, evidence is mounting that distances that can be bridged by a variety of species are not consistent with the prediction that smaller bats should typically fly shorter distances than larger ones. Recent studies have shown that some small species fly remarkably long distances, which in turn results in very large home ranges. For instance, O'Donnell (2001) reported large distance commutes of up to 19 km for the 10 g temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand and home ranges that were among the largest known for microbats (median MCPs 660–1590 ha, max. 5630 ha). Similarly, 5 g lesser horseshoe bats *Rhinolophus hipposideros* foraged up to 4.2 km from their roosting site and were active over ranges of up to 368 ha (Bontadina *et al.* 2002). Our data for *M. macrophyllum* likewise do not support the idea that smaller body size in bats is tightly linked to shorter commuting distances or smaller home range sizes. Considering range size and movement distances, our results suggest

that *M. macrophyllum*, even though it employs a gleaning foraging mode, more closely resembles aerial insectivorous bats (*Eptesicus serotinus*, Catto *et al.* 1996, Robinson & Stebbings 1997, *C. tuberculatus*, O'Donnell 2001) than the "classical" gleaners that forage in and around vegetation (*L. silvicolum*, Kalko *et al.* 1999, *C. perspicillata*, Fleming & Heithaus 1986, Thies 1998).

In the present study, males and females differed considerably in their movement patterns. Females commuted up to 4.5–7.5 km from the day roost to their first foraging area. Long-distance movements can be expected to be frequent particularly in bats with high wing loading and high aspect ratio, morphological characteristics that generally confer great aerodynamic efficiency (Norberg & Rayner 1987). However, since wing loading (9.1 ± 0.9 N/m^2) and aspect ratio (5.5 ± 0.4, Chapter II) of *M. macrophyllum* were well within average values typical for bats foraging in edge and gap situations (Aldridge & Rautenbach 1987, Norberg & Rayner 1987), it does not necessarily appear to be very efficient for them to fly long distances. Nonetheless, distances flown were greater than those recorded for many bats with higher aspect ratio and wing loading (e.g. *Megaderma lyra*, Audet *et al.* 1991, *Eptesicus serotinus*, Catto *et al.* 1996, *Noctilio albiventris*, Fenton *et al.* 1993, *cf.* Fenton 1990, 1997).

Shorter foraging routes certainly help to conserve energy and can minimize exposure to predators, so there must be some benefit to female *M. macrophyllum* foraging far away from the day roost. Roosting in groups or colonies can have important implications for foraging movements and the spacing behavior of individuals. According to refuging theory (Hamilton & Watt 1970), individuals of colonial species should undertake long commuting flights to reach food resources not depleted or dominated by conspecifics in order to reduce intraspecific competition. For instance, southern long-nosed bats, *L. curasoae*, commute distances of 15 to 50 km to their foraging areas (Sahley *et al.* 1993). In contrast, solitary bats or species that live in small colonies usually incur minimal time and energy costs for commuting, although this often may be above all a consequence of their respective foraging strategy (e.g. Bonaccorso *et al.* 2002, Kalko *et al.* 1999, Winkelmann *et al.* 2000). Interestingly, in the present study, distances moved and home ranges were largest in the two post-lactating females (F4, F5). Range-expansion in post-lactating females has also been documented in other bats and interpreted as a mechanism to avoid competition with newly volant young (Clark *et al.* 1993, O'Donnell 2001). O'Donnell (2001) argued that while flight capabilities of juveniles are not yet fully developed, there will be considerable use of resources close to the day roost. It should therefore be advantageous for adults to move to more distant foraging areas, which would potentially reduce competition with juveniles at that particular time. Colony size in the day roost had roughly doubled after the birth peak in mid-May and consequently, tracking of these two females coincided with a large number (*c.* 50) of newly volant juveniles. The larger distances to foraging areas observed in females as opposed to males might, at least in part, also be explained by increased energy demands and nutritional requirements linked to female receptivity which might have forced them to forage over a wider range.

Influence of social status on range use.— Foraging movements of males appeared to be sensitive to their social status. The harem male (M3) we tracked restricted its foraging activity to a very small area around the day roost, most likely to be able to allocate more time to roost vigilance and female defense. The other males had foraging areas at various distances away from the day roost but in general, they also foraged closer to it than females. For these males, ranges closer to the day roost might be the best option if they want to increase their chances to gain access to females in the day roost and attempt sneak matings.

Night-roosting behavior.— Radio tracked long-legged bats commonly used several night roosts throughout their tracking period. Night roosts may serve as resting places between foraging bouts, a behavior, which is common among insectivorous bats (Entwistle *et al*. 1996, Weinbeer & Kalko 2004) and that we also observed in *M. macrophyllum*. Kunz (1982) postulated that night roosts should be located close to foraging sites in order to avoid costly commutes to day roosts and minimize predation risk. This is in part corroborated by our observations of *M. macrophyllum*. During the night, most individuals roosted in hollows under washed-out roots of trees along the lakeshore. These night roosts were always located on the periphery of foraging areas. However, flights back and forth between the day roost and foraging areas during the night were also common in most tracked individuals of *M. macrophyllum*.

It is well known that maternity roosts are commonly used as night roosts by lactating females, which reflects the need to suckle their young (e.g. Anthony & Kunz 1977, Kunz 1974, 1982). Conversely, it remains largely speculative why non-reproductive females should make long and costly flights back to the roost during the night, as was the case in this study. For some species, it has been proposed that these intermittent returns might be related to a lower risk of predation at the day roost (Fleming & Heithaus 1986, Thies 1998). This implies, however, that these flights are less costly in terms of energy expenditure and exposure to predators than the use of night roosts that are located close to a bat's foraging area. It can be assumed that the night roosts described above represent safe roosting sites for *M. macrophyllum* so it is not readily apparent why the bats undertake these flights to the day roost and back. Judging from their capability to travel these distances in moderately fast flight (about 30 km/h, which compares favorably with speeds reported for other species like *L. curasoae*, Sahley *et al*. 1993) such commutes may in fact not be as energetically costly as it might first appear. In addition, the long distances bats moved on a nightly basis were much greater (> 35 km) than these commutes between day roost and foraging sites. We do not know whether night roosts are shared by several individuals, and if so, to what extent social interactions in these roosts occur, but perhaps realization of mating opportunities might only be possible in the day roost. Therefore, these intermittent returns may be best explained by the increased social activity in the day roost associated with the onset of the reproductive phase.

Habitat use in relation to other species.— The air above water bodies was identified as the key habitat used by foraging *M. macrophyllum*. Aquatic habitats are generally rich in insects and therefore provide attractive feeding opportunities for a variety of bat species (Rydell *et al.* 1999, Siemers *et al.* 2001). In the study area occur five species that characteristically forage over water. Besides *M. macrophyllum*, this foraging habitat is also used by two species of bulldog bats, *Noctilio leporinus* and *N. albiventris* (Noctilionidae), the proboscis bat, *Rhynchonycteris naso* (Emballonuridae), and *Myotis albescens* (Vespertilionidae, Kalko *et al.* 1996). Except *N. leporinus*, which is well known for its fish-eating habits but also includes insects in its diet (Brooke 1994, Schnitzler *et al.* 1994), all of these species are insectivorous. *Rhynchonycteris naso* and *M. albescens* are both aerial insectivores, catching their prey above water on the wing. Similar to *M. macrophyllum*, the two *Noctilio* species catch their prey either in trawling mode from the water surface or hawk insects in the air (Brooke 1997, Hood & Pitocchelli 1983, Kalko *et al.* 1998, Schnitzler *et al.* 1994), exhibiting a high flexibility in foraging modes.

All five species, which regularly forage over water in the study area, differ considerably in body size and mass (*R. naso* 3.4 g, *M. albescens* 6.5 g, *M. macrophyllum* 8.4 g, *N. albiventris* 30.7 g, *N. leporinus* 55.3 g, Kalko *et al.* 1996). They can therefore also be assumed to select prey of different sizes. Generally, larger bats have access to larger and smaller prey, whereas smaller bats are limited to smaller prey items (Aldridge & Rautenbach 1987, Fenton 1990). Size-related spacing along the resource axis could hence be a mechanism of reducing potential competition for food. Besides the differences in foraging modes, comparative data are completely lacking to evaluate whether these species differ with respect to patterns of range use in space and time, which might further facilitate their coexistence. These hypotheses, however, imply that insects indeed constitute a limiting resource, an assumption that remains to be tested. Niche partitioning has been considered the basis of coexistence (Schoener 1974). However, Basset (1995) argued that coexistence between interspecific competitors should be possible even under complete niche overlap due to body size-related spatiotemporal constraints imposed on home range resource exploitation. He proposed that size-related inefficiency in home range exploitation should generate a size-structured guild and community organization, a scenario that could also be envisaged for the bat species that forage over water in our study area.

We conclude that factors such as foraging strategy, diet, and dispersion of food resources, rather than body size, are the chief determinants and best predictors of home range size for *M. macrophyllum* in particular but likely also for most bat species in general. Life history dynamics such as reproduction and intraspecific competition linked to colony size or social status further modified the spacing behavior and movement patterns of individuals to varying degrees, resulting in marked inter-individual and gender-specific differences and variability in the observed home range sizes. Further comparative studies on home range size and spatial use of the whole set of species that forage over water at our study site are ultimately essential if we

are to unveil mechanisms allowing their coexistence and for a better understanding of community organization.

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II

Patterns of Activity in the Long-legged Bat, *Macrophyllum macrophyllum*, Foraging over Water

Bats (Chiroptera) exhibit a wide variety of behavioral, morphological, and sensorial adaptations to foraging habitat and prey type, expressed by various foraging modes and activity patterns (*e.g.* Aldridge & Rautenbach 1987, Fenton 1990, Neuweiler 1989, Schnitzler & Kalko 1998). As an example, perch hunting bats with short and broad wings may spend most of their nocturnal time hanging in the vegetation (*e.g.* Kalko *et al.* 1999, Schnitzler *et al.* 1985, Tidemann *et al.* 1985) and catch few, mostly large prey items in quick sally flights distributed throughout the night. This leads to short flight times of only a few minutes per night. In contrast, open-space aerial insectivorous bats with longer and narrower wings spend up to several hours of flight time per night in pursuit of mostly small insects (*e.g.* Chruszcz & Barclay 2003). Despite this remarkable variation in activity patterns (Erkert 1982), some generalizations can be made. Size and spatio-temporal distribution of food as well as foraging mode and body size of bats are seen as main factors to determine activity patterns, which can be bimodal with two pronounced flight activity peaks, unimodal with one peak, or comparatively even without pronounced peaks.

A variety of activity patterns is found in the species-rich family of Neotropical leaf-nosed bats (Phyllostomidae), which mostly forage in narrow-space habitats, where they glean food from vegetation or ground (Kalko 1998). Some species, such as frugivores, usually reveal a more or less pronounced unimodal activity pattern with peak foraging activity early at night (Charles-Dominique 1991, Handley *et al.* 1991) in response to a high crepuscular abundance of fruits, which mostly had ripened during the preceding day. Supply of ripe fruit may often not be replenished later at night (Thies & Kalko 2004). In contrast to frugivores, some gleaning animal eating bats display a relatively even activity pattern throughout the night probably due to the more constant availability of a large variety of insects and small vertebrates. Perch hunting insectivores with small home ranges of only a few hectares, like *Lophostoma silvicolum*, display continuous, but very low activity and spent most of their time waiting for suitable prey, which they eventually catch in short, directed sally flights (Kalko *et al.* 1999). Other gleaners, such as *Trachops cirrhosus*, with larger home ranges, may use a combination of foraging strategies, including perch hunting and gleaning from flight, also likely an adaptation to food availability (Kalko *et al.* 1999). Finally, some gleaners with high flight activity, such as *Lampronycteris brachyotis*, presumably take mostly stationary prey from flight, and may occasionally catch insects in the air in continuous flight within large home ranges (Weinbeer & Kalko 2004).

In contrast to gleaning bats within Phyllostomidae and other families, such as *Plecotus auritus*, Vespertilionidae (Eklöf & Jones 2003) or *Megaderma lyra*, Megadermatidae (Rajan & Marimuthu 1999), aerial insectivores catch flying prey in the air on the wing in fast and continuous flight, covering large flight distances per night (Davis *et al.* 1962). Typically, they often display one or two pronounced activity flights (Brigham & Fenton 1991, Hayes 1997, Rautenbach *et al.* 1988), which usually correlate with maximum prey abundance (Rydell *et al.* 1996). Decrease in prey activity later at night likely reduces efficiency of continued foraging

(Meyer *et al*. 2004). Therefore, some bats, such as *Myotis evotis* (Vespertilionidae), adapt their foraging mode accordingly and continue foraging by switching between aerial hawking and gleaning (Chruszcz & Barclay 2003).

Macrophyllum macrophyllum Schinz (Phyllostomidae) differs from other leaf-nosed bats by several morphological characters, regarded as adaptations for foraging above water. Gaffing prey from water surfaces, as proposed for this species (Harrison 1975), is unique among phyllostomids (Kalko 1998), but is found in a small group of trawling bats of different families, including bulldog bats (Noctilionidae), the proboscis bat, *Rhynchonycteris naso* (Emballonuridae), and some evening bats (*Myotis* spp., Vespertilionidae). They catch prey (insects and small fish) directly from (trawling mode) or just above water surfaces in the air (aerial mode; Brooke 1997, Jones & Rayner 1991, Kalko & Schnitzler 1989, Rydell *et al*. 1999, Schnitzler *et al*. 1994, Siemers *et al*. 2001).

Although a widespread species, there are only anecdotal field observations on foraging *M. macrophyllum* (Harrison 1975 and references therein). In particular, very little is known about temporal aspects of its foraging behavior. In Panamá, *M. macrophyllum* has been observed to forage exclusively above water, hunting mostly within 50 m parallel to shore lines of a large freshwater lake (Chapter I). As other trawling bats, *M. macrophyllum* forages for similar prey with similar foraging modes, feeding predominantly on small nocturnal insects, such as Lepidoptera and Diptera, caught either in the air or taken from the water surface (Harrison 1975).

We radio-tracked nine individuals of *M. macrophyllum* during their nocturnal activity above Gatún Lake in the Barro Colorado Nature Monument, Panamá, in order to assess how habitat type and spatio-temporal distribution of prey influence foraging activity. Additionally, we documented flight behavior of *M. macrophyllum* in the field with infrared video, and simultaneously assessed bat flight activity and insect prey abundance. In contrast to many phyllostomids, trawling bats, such as the temperate *Myotis daubentonii* (Vespertilionidae; Dietz & Kalko, pers. com.) or Neotropical *Noctilio* spp. (Noctilionidae; Kalko *et al*. 1998, Schnitzler *et al*. 1994), exhibit high flight activity of many hours per night. According to the independent phylogenetic origin of trawling in *M. macrophyllum*, we hypothesize that it spends large parts of the night on the wing in search for small water insects in fast and continuous flight. This is supported by its relatively large home ranges (17–44 ha; Chapter I). We believe that prey availability is an important factor determining foraging activity.

METHODS

Study site.— We conducted our four-month field study (1 April to 31 July 2002) in the Barro Colorado Nature Monument (9°10' N, 79°51' W, area 56 km^2; Panamá), which consists of an array of islands and peninsulas surrounded by the freshwater Gatún Lake. Islands and mainland of the

nature reserve are covered with seasonal tropical lowland forest consisting of a mosaic of older (400–600 years) and younger patches (70–100 years; Windsor 1990). Climate is characterized by a distinct dry season from mid-December through April with 10% of total annual rainfall (2600 mm), and a wet season with a monthly precipitation of 300 mm. Mean temperature is 27°C with a diurnal range of about 9°C (Windsor 1990).

Study species.— The long-legged bat, *Macrophyllum macrophyllum* (Phyllostomidae), occurs in tropical lowlands from southern México to northern Argentina (Harrison 1975). All animals we tracked were caught with self-made hand-nets at their day roost, a half-sunken ship ("Barracuda"), close to the laboratories on Barro Colorado Island. The day roost has been continuously inhabited by a colony of more than 60 *M. macrophyllum*, mostly females, at least over the past four years since its discovery. Among 11 captured individuals, we found sexual dimorphism in body mass and size, where females were significantly larger (mass: 9.3 ± 0.6 g; $t = 3.51$; $p = 0.007$; forearm length: 35.0 ± 1.0 mm; $t = 2.30$; $p = 0.047$; $N = 6$) than males (8.4 ± 0.5 g, and 33.6 ± 0.5 mm, respectively; $N = 5$). Among phyllostomids, *M. macrophyllum* is distinguished by morphological characters, such as particularly large feet with powerful claws, necessary for prey removal, and a large interfemoral membrane with strong calcars (Harrison 1975). Its wing morphology largely conforms to the typical pattern of trawling bats (Norberg & Rayner 1987) with rather short and broad wings, a medium aspect ratio ($wingspan^2$/wing area) of 5.5 ± 0.4, and a low wing loading (body weight/wing area) of 9.1 ± 0.9 N/m^2 ($N = 8$).

Telemetry.— To study activity patterns of *M. macrophyllum*, we radio-tracked nine individuals (five adult, non-reproductive females: F1–F5, three adult non-reproductive males: M1, M2, M4, and one reproductive male: M3) fitted with lightest available transmitters providing satisfactory information about activity (LB2-BP, Holohil Systems Ltd., Carp, Ontario, Canada; mass 0.84 ± 0.02 g; frequency 150 MHz), which amounted to 9.5 ± 0.7% of the bats' body mass. This is around the 10% mass threshold above which transmitter mass may negatively affect the animals' foraging behavior (Brander & Cochran 1969). Transmitters lasted about a week on bats (5.3 ± 0.9 days) before they fell off. Using a hand-held H-aerial antenna and a Yaesu receiver (VR-500, both adapted by Wagener Telemetrieanlagen, Cologne, Germany), range of transmitters was up to 300 m, but could be as little as 50 m when bats flew close to the water surface or hung under washouts along the shore. Transmitters were glued onto bats' backs below the scapulae with histoacrylic glue. Recaptured individuals showed no signs of injury that could have resulted from tagging. In an attempt to visually locate feeding bats at night, transmitters were additionally marked with a piece of reflecting tape. Tagged bats were released at the day roost within 1 h after capture.

During telemetry, two observers were in continuous radio contact (Yaesu FT-26, Yaesu Musen Co. Ltd., Japan). Transmitters were equipped with a mercury position switch that provided information on a bat's activity (hanging versus flying) through changes in signal repetition rate

at a temporal resolution of 1 s (horizontal: 1 Hz; vertical: 0.5 Hz). Thus, it was possible to quantify activity in terms of time spent in flight versus time spent hanging in roosts. We assessed activity patterns of *M. macrophyllum* only during its nocturnal foraging behavior, where we defined the activity phase as time between first emergence of bats from their day roost in the evening until last entry in the morning. We tested the influence of daylight (measured as time between local sunset and sunrise) on exit and return times of tracked bats with linear regression. During the activity phase of a tagged *M. macrophyllum*, each change in its activity along with information about type and location of night roosts and prevailing weather conditions were recorded with a dictaphone (Sony TCM-459V).

Data base.— Bats were tracked for complete nights. We collected data from the first night after capture for one individual at a time. During 48 nights, we followed nine *M. macrophyllum* for 520 tracking h and achieved high contact times (average 81%). For final calculations, we used activity data of 421 h, where at least one of the two observers had received an unambiguous signal.

Prey availability and diet composition.— We assessed the composition of insects potentially available to bats to link observed flight activity of *M. macrophyllum* with prey abundance. We used a 15W UV-light trap (DC collecting light #2805, BioQuip Products, Inc., Gardena, California, USA) set up on a boat to sample aerial insects at a height about 50 cm above the water surface and approximately 20 m from the shore, where foraging *M. macrophyllum* were frequently observed. Sampling was conducted for one complete night each during the tracking period of four bats (F2, F4 & M2, M4) within each respective foraging area. Every 30 min, the light trap was operated for 10 min and all insects present on the sampling cloth (70 cm x 70 cm) were removed and stored in 70% ethanol for analysis. In addition, we took samples every 30 min from the water surface using a fine-meshed sweep net with a diameter of 50 cm. We slowly drove a short distance (about 25 m) with a motorboat, and continuously skimmed the water surface. Insects were identified to order or family. Finally, 20 fecal samples were arbitrarily picked from a spot within the "Barracuda", above which the colony usually clustered.

Statistical analysis.— All statistical tests were performed using Statistica (6.0, StatSoft, Inc., Tulsa, OK, USA), following Zar (1999). Before using parametric tests, data were tested for normality and homoscedasticity, applying standard transformations where necessary. Whenever these assumptions were not met, corresponding non-parametric tests were used. Numerical results are reported as mean ± 1 SE or SD, as indicated. Repeated measures Anova was used to test for significant within-night variation in activity levels (11 hour intervals as within-subjects factor) and differences in hourly flight activity throughout the night. Duration of flight and hanging phases were analyzed with a two-level nested Anova, where individuals were nested within gender. Differences between sexes in flight time per night, as well as in number of hanging and flight phases on a nightly basis were assessed with a Mann-Whitney U test. A *t*-test

was employed to evaluate differences in total flight time between nights with and without rain. Relationships between variables were assessed using linear regression analysis. For all tests, $p < 0.05$ was chosen as level of significance.

RESULTS

Activity pattern.— *Macrophyllum macrophyllum* exhibited significant within-night variation in flight activity ($F_{10,70} = 2.24$, $p = 0.03$; FIG 1). Activity was highest just after dusk (19:00–20:00 h), when total time spent on the wing averaged about 30 min and remained at a lower, relatively constant level, before slightly increasing again in the morning (4:00–5:00 h). This pattern was statistically significant (Fisher's LSD-test comparing hours of maximum activity with hours of lower levels of activity, $p < 0.05$; FIG 1).

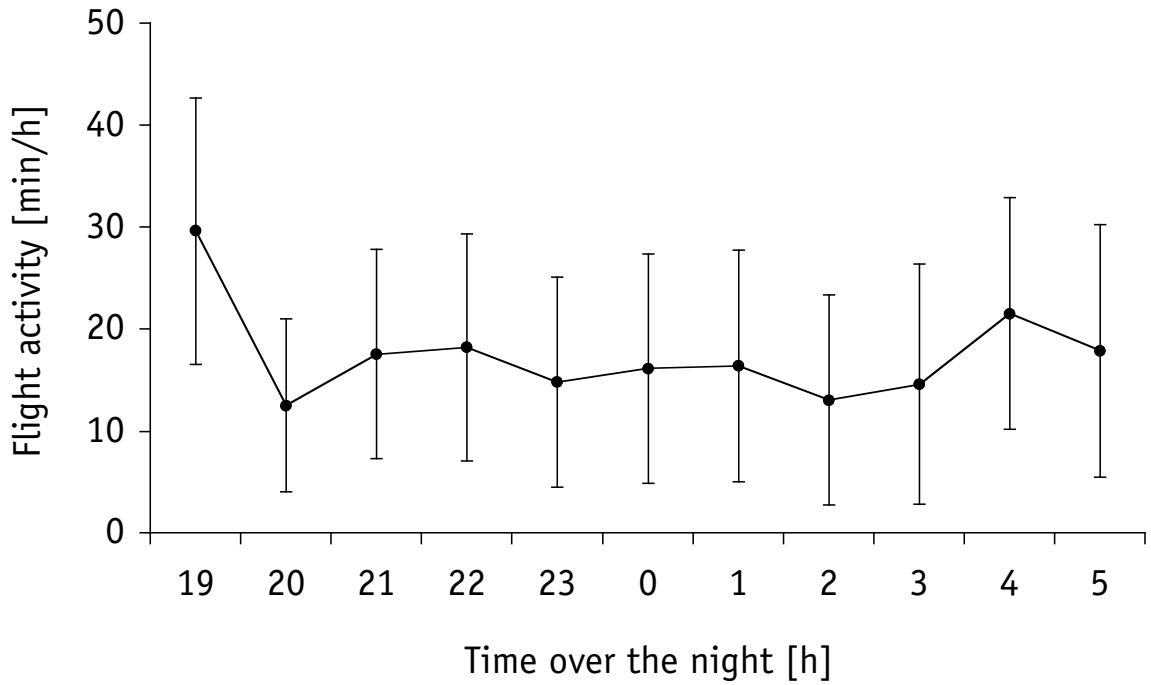


FIGURE 1. Flight activity (time [min] spent in flight per h; mean ± SD) of nine individuals of *M. macrophyllum* in Panamá varied significantly over the night ($F_{10,70} = 2.24$, $p = 0.03$).

Tracked individuals foraged in continuous flight of medium duration (mean ± SE: 6.6 ± 0.3 min; $N = 1128$). We found considerable variation, where foraging flights lasted up to one hour (61 min) or could be as short as a few seconds (TAB 1). Duration of foraging flights ($F_{1,7} = 0.81$, $p = 0.4$, TAB 1) and hourly flight activity throughout the night ($F_{1,7} = 0.14$, $p = 0.7$) were equal among both sexes. Flight time per night was slightly lower in males (median: 193.4 min, $N = 20$) than in females (207.0 min; $N = 26$, Mann-Whitney U test, $Z = -0.81$, $p = 0.4$; TAB 1). Periods of flight activity were interrupted by hanging phases in night roosts along the shore or in the day roost (median duration: 5.8 min [excluding M3]; maximum: 3 h; $N = 1059$, TAB 1). Duration of

hanging phases was equal among both sexes ($F_{1,7}$ = 3.59, p = 0.1, TAB 1); however, on a nightly basis, males were more restless as they flew and hung significantly more often than females (Z > 3.8, p < 0.001). Finally, duration of flights did not vary over the course of the night ($F_{10,70}$ = 1.17, p = 0.3). In contrast, we found significant nightly variation in duration of hanging phases ($F_{10,70}$ = 2.38, p = 0.02), that is, bats spent more time hanging in a night roost around and after midnight than they did around dusk or dawn (FIG 2).

TABLE 1. Time per night spent flying or hanging (mean ± SD), and durations of flight and hanging phases (mean ± SD and range) of five female and four male *M. macrophyllum*, in the Barro Colorado Nature Monument, Panamá. Sample sizes (*N*) are given in parentheses.

Bat	Time per night [min]		Duration [min]			
	Flying	Hanging	Flight phases	Range	Hanging phases	Range
F_1	234 ± 24.0 (5)	379 ± 21.5 (5)	11.1 ± 12.6 (111)	0.01–47	18.1 ± 21.5 (104)	0.20–144
F_2	86.2 ± 32.5 (4)	277 ± 188 (4)	6.8 ± 8.3 (52)	0.01–30	24.1 ± 26.1 (46)	0.10–92
F_3	139 ± 51.0 (7)	265 ± 153 (7)	8.2 ± 9.6 (119)	0.01–37	17.5 ± 25.9 (106)	0.10–152
F_4	220 ± 23.3 (6)	424 ± 22.5 (6)	7.3 ± 12.7 (182)	0.01–61	14.5 ± 15.6 (176)	0.10–79
F_5	111 ± 66.6 (4)	351 ± 215 (4)	5.5 ± 11.5 (100)	0.01–49	17.3 ± 25.7 (88)	0.10–110
M_1	175 ± 31.3 (5)	299 ± 91.7 (5)	4.4 ± 5.8 (199)	0.01–29	7.6 ± 11.1 (189)	0.01–56
M_2	237 ± 22.0 (5)	412 ± 24.4 (5)	13.2 ± 9.7 (91)	0.10–58	25.6 ± 24.3 (81)	0.10–180
M_3	144 ± 36.1 (5)	509 ± 28.9 (5)	0.6 ± 2.3 (1215)	0.01–26	2.3 ± 4.5 (1210)	0.01–53
M_4	183 ± 40.1 (5)	459 ± 40.3 (5)	3.1 ± 6.6 (274)	0.01–36	8.5 ± 15.6 (269)	0.01–118

Factors influencing activity.— Nocturnal flight activity of *M. macrophyllum* was affected by several extrinsic factors. Daylight was a significant determinant, which triggered onset and end of the activity phase. Usually, bats left the day roost shortly (mean ± SE: 20.6 ± 1.7 min, N = 50) after sunset, stayed in their respective foraging areas for most of the night and returned to the day roost half an hour (30.1 ± 2.5 min, N = 39) before sunrise. Exit and return times were significantly synchronized with daylight (exit / sunset: r^2 = 0.46, $F_{1,48}$ = 41.36, p < 0.001; return / sunrise: r^2 = 0.18, $F_{1,37}$ = 7.92, p = 0.008, FIG 3).

Another parameter influencing flight activity was moonlight. We estimated this influence by regressing two parameters of activity, hanging time per night and mean flight time per h, respectively, against duration of moonshine, which varied from less than 1 h (of very little light due to sickle-shaped moon) to almost 11 h (high light level, nearly full moon) per night during our study. While females did not respond to temporal variation in moonshine duration (p > 0.16, FIG 4), this had a significant influence on activity of males. In nights where the moon was up for a long time, males spent considerably more time roosting than in nights with only short periods of lunar illumination (r^2 = 0.39, $F_{1,12}$ = 7.71, p = 0.02, FIG 4). Likewise, on an hourly basis, males flew less during nights with long moonshine duration (r^2 = 0.56, $F_{1,12}$ = 15.45, p = 0.002), while females did not respond to moonshine with their flight activity (FIG 5). A similar pattern emerges

when comparing the bats' hourly flight activity in terms of hours when the moon was actually visible versus those when it was not up (females: $Z = -1.07$, $p = 0.3$; males: $Z = 4.49$, $p < 0.001$).

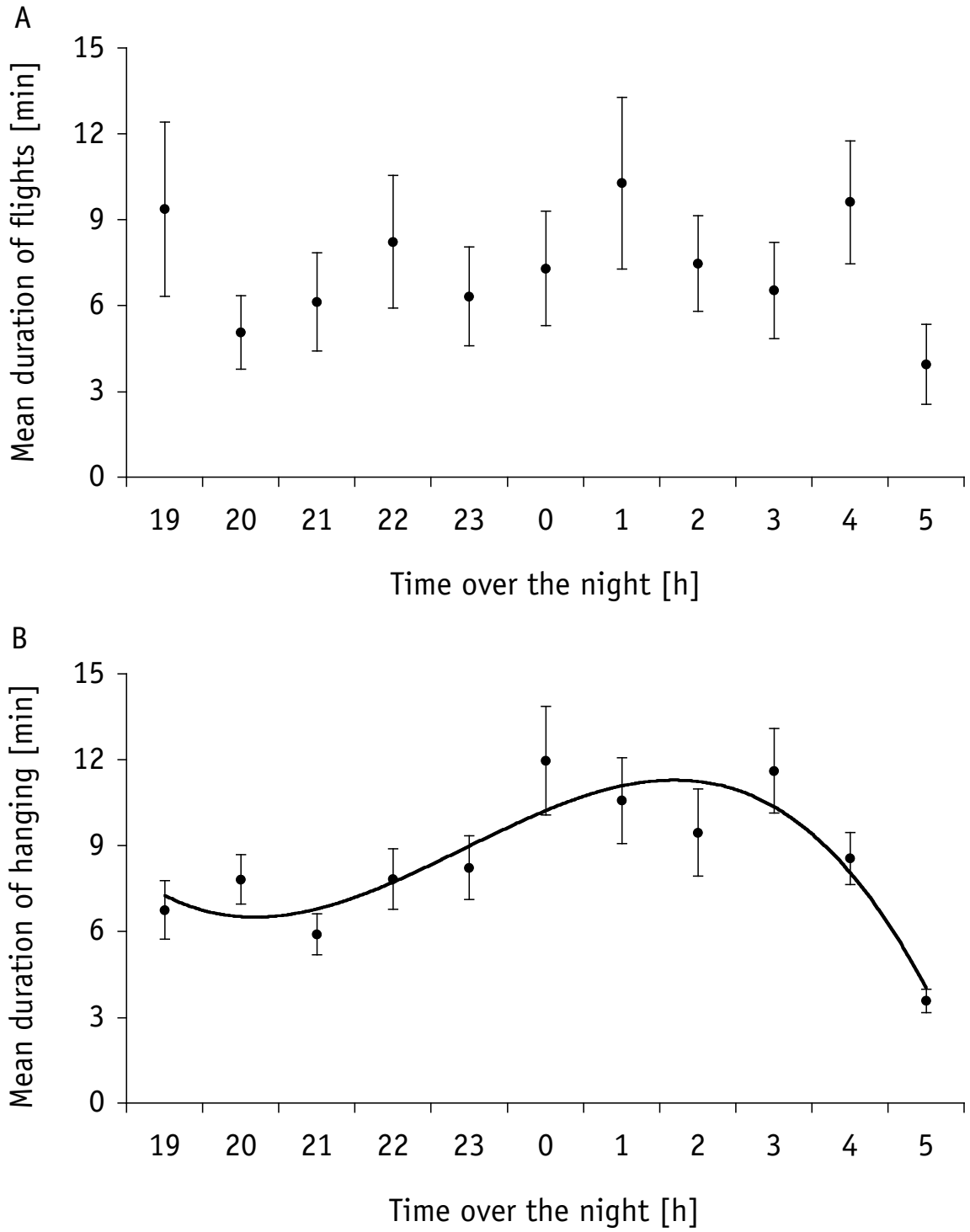


FIGURE 2. Duration of flight and hanging phases (mean ± SE): A) duration of flights did not change significantly in the course of the night; B) there was significant temporal variation in mean duration of hanging phases over the night ($F_{10,70} = 2.38$, $p = 0.02$).

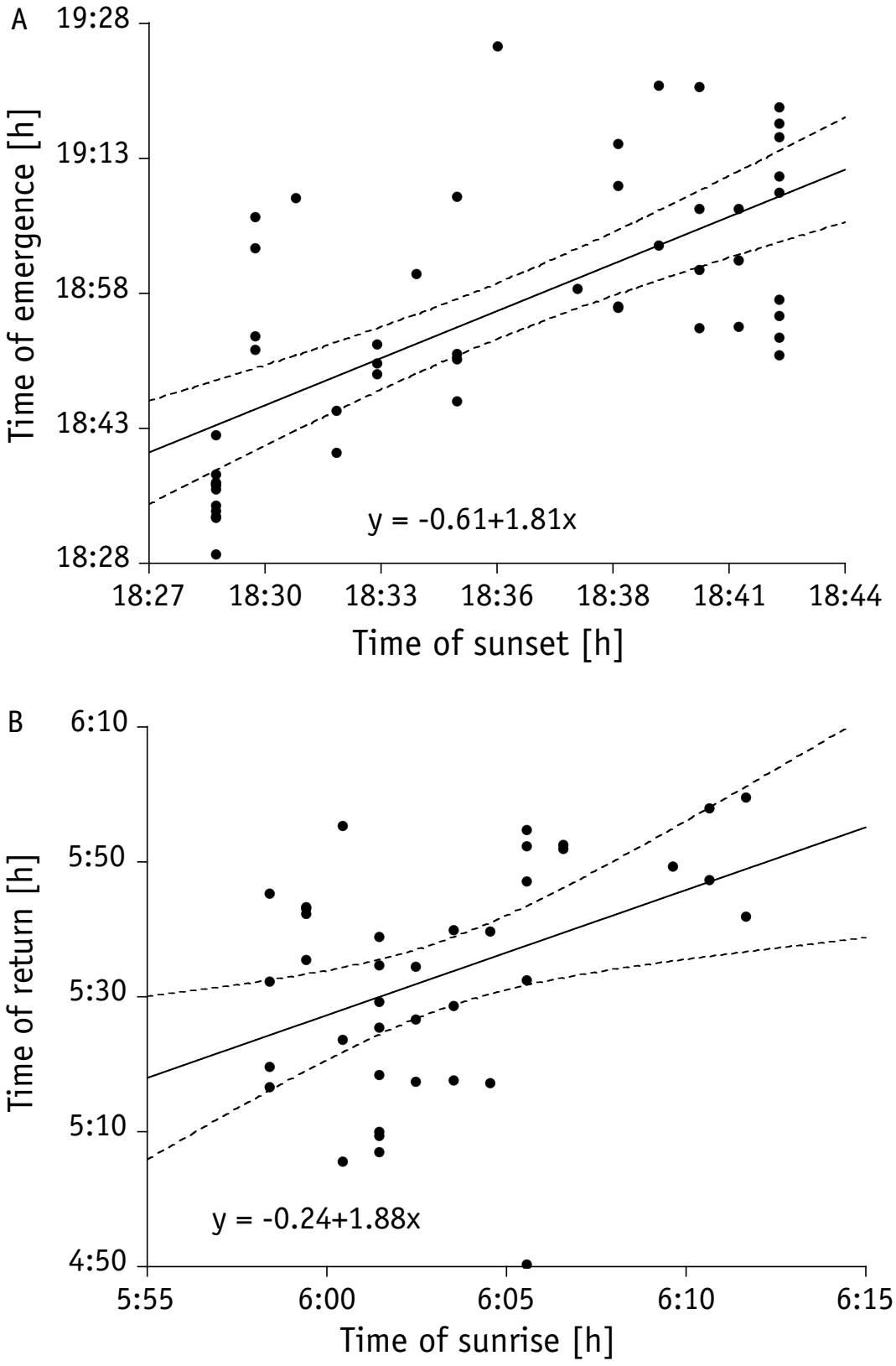


FIGURE 3. Relationship between A) time of emergence of *M. macrophyllum* and time of local sunset (r^2 = 0.46, $F_{1,48}$ = 41.4, p < 0.001), respectively, and B) time of return and time of local sunrise (r^2 = 0.18, $F_{1,37}$ = 7.9, p < 0.01). Dotted lines indicate 95% confidence intervals.

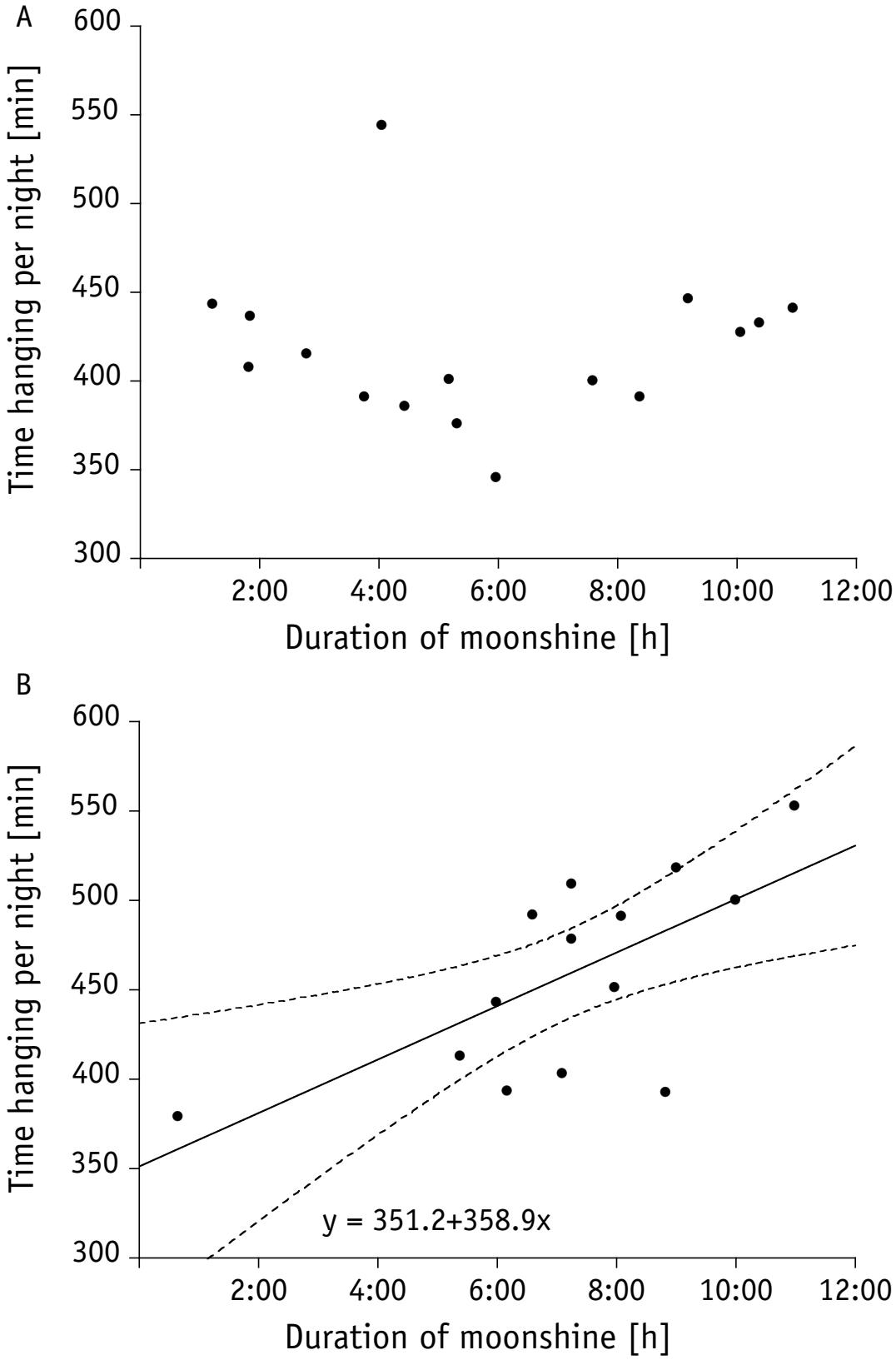


FIGURE 4. Influence of moon light on activity of *M. macrophyllum*, assessed by the relationship between the time bats spent roosting per night and moonshine duration. In contrast to females (A: $r^2 = 0.001$, $F_{1,14} = 0.01$, $p = 0.9$) males (B) showed a clear lunar-phobic response ($r^2 = 0.39$, $F_{1,12} = 7.71$, $p = 0.02$). Dotted lines indicate 95% confidence intervals.

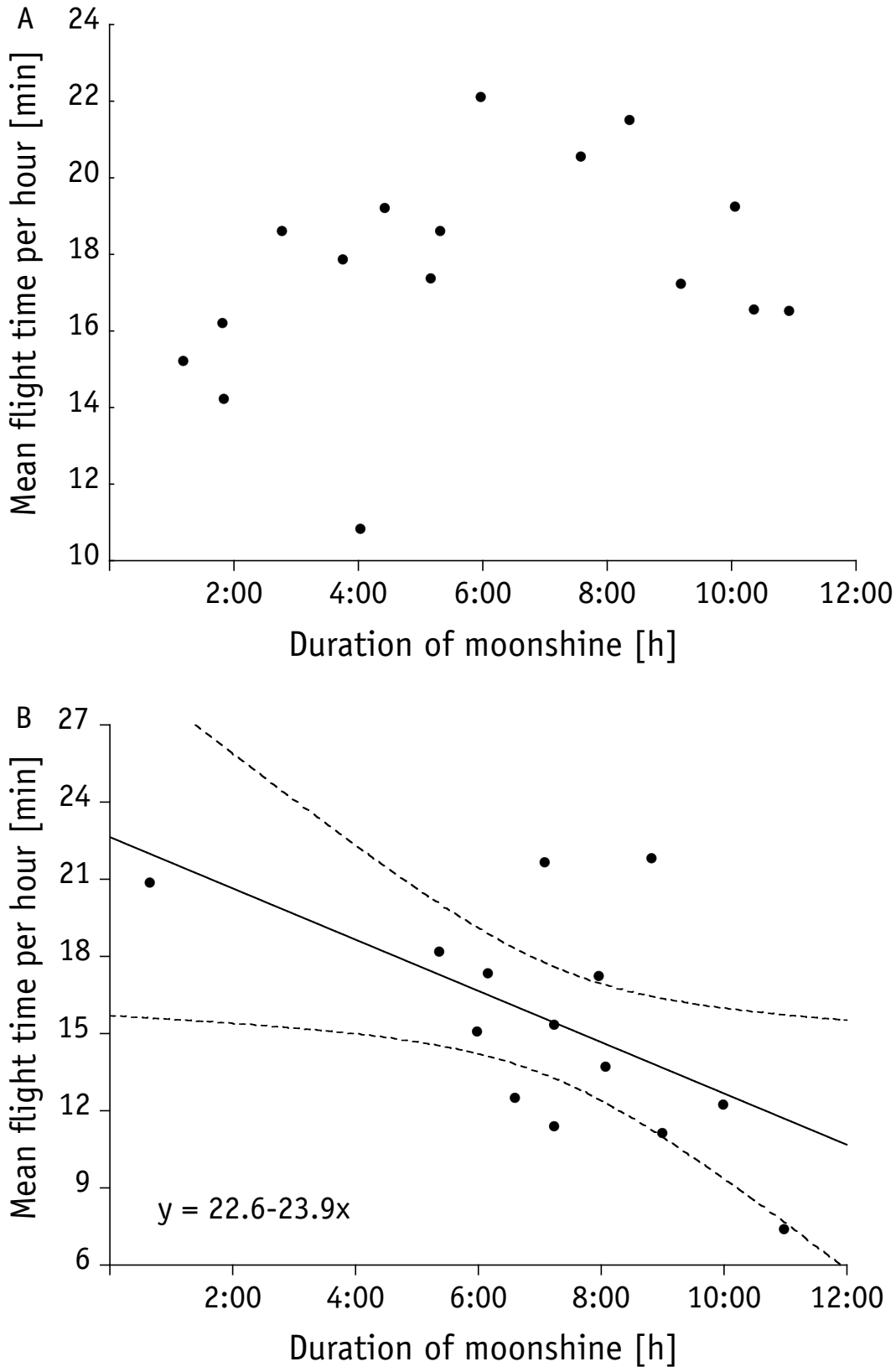


FIGURE 5. Influence of moon light on foraging activity of *M. macrophyllum* assessed by the relationship between average flight time/h and moonshine duration. No significant correlation was found in females (A: $r^2 = 0.14$, $F_{1,14} = 2.25$, $p = 0.2$), whereas males (B) flew less on an hourly basis during nights with long moonshine durations ($r^2 = 0.56$, $F_{1,12} = 15.45$, $p = 0.002$)

In addition to light, rain also affected flight activity of *M. macrophyllum*. During our study, it rained in 16 out of 48 tracking nights. Flight time per night was significantly reduced during rainy nights compared to nights without rain (t = 3.29, df = 29, p = 0.003), indicating that bats lost foraging time during periods of rain, which they could not make up for in the remaining night. Flight activity of *M. macrophyllum* was further influenced by rain intensity. While bats continued flying in drizzling or light rain, they usually interrupted foraging flights in heavy rain and immediately sought shelter in night roosts. Bats often resumed foraging before rain had completely stopped.

Finally, prey abundance had a significant influence on flight activity of bats. In one night each during the tracking episode of four bats (F2, F4 & M2, M4), in addition to flight activity of bats, we simultaneously assessed temporal variation in insect abundance within the respective foraging area. Flight activity of bats was positively correlated with number of aerial insects captured at the light trap (linear regression, r^2 = 0.44, $F_{1,9}$ = 7.16, p = 0.03, FIG 6) indicating that these bats tuned their foraging flights to the abundance of aerial prey.

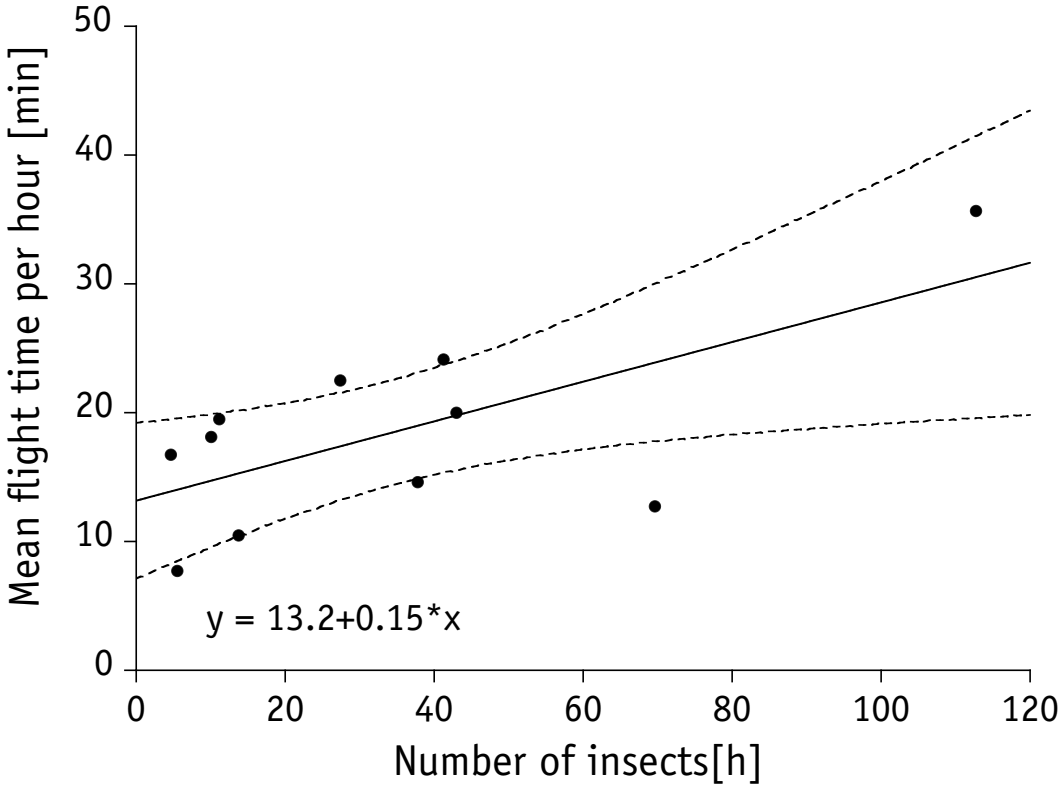


FIGURE 6. Relationship between activity of *M. macrophyllum* and availability of aerial insects assessed by light trapping in hourly intervals (r^2 = 0.44, $F_{1,9}$ = 7.16, p = 0.03).

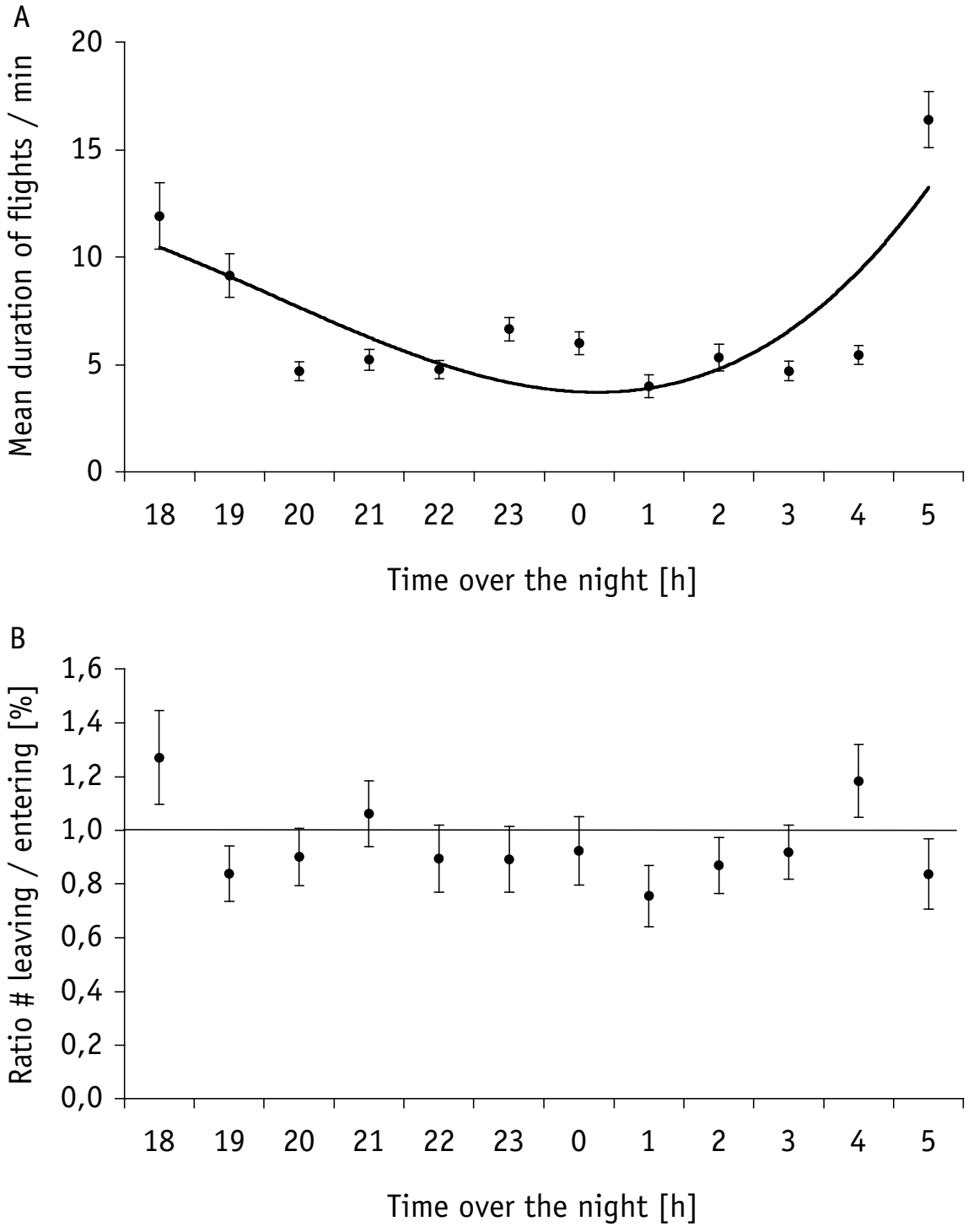


FIGURE 7. Flight activity of the colony of *M. macrophyllum* (mean ± SE) studied on BCI as determined by infrared video filming: A) mean number of flights/min inside the roost varied significantly over the night ($F_{11, 689} = 15.27$, $p < 0.01$). B) Ratio of number of bats leaving versus entering the day roost.

Activity pattern of the colony.— In order to determine how and to what extent activity patterns exhibited by tracked individuals are mirrored in the level of activity of the colony as a whole, the latter was video-filmed (Sanyo VC 1950; Sony GV-D900E; infrared-LED-panel) during one complete night (14/15 May 2002). Using mean number of flights inside the roost per min as a measure of bat activity, we observed a bimodal activity pattern (one-way Anova,

$F_{11, 689} = 15.27$, $p < 0.01$), while flight activity inside the ship was particularly high during morning hours (FIG 7A). Besides a considerable turnover of individuals regularly leaving and others entering the roost, most flights of bats leaving the ship occurred around dusk, while slightly more bats returned over the course of the night (FIG 7B). Although these results should be treated with caution because they are only based on one night of video filming, they corroborate our tracking data with respect to the general activity pattern and to the finding that individuals typically interrupted foraging and occasionally returned to the day roost, often several times over the course of the night (FIG 1 & 2).

Foraging mode.— Because of fast flight in *M. macrophyllum* (15–30 km/h; Chapter I), field observations of foraging bats were difficult. However, we succeeded in following the flight path of several tagged bats with a flashlight by illuminating the reflecting tape glued to transmitters. All bats observed in the field typically foraged at low heights (< 1 m) above water. They accomplished rapid pursuit maneuvers frequently down onto the water surface and occasionally soared into the air, likely catching prey on the water surface and from the air. We confirmed our assumptions on foraging behavior by infrared video filming (Sony DCR-TRV 125E, hand-held 70W directional IR-beam light), where we could clearly observe how *M. macrophyllum* skimmed the water surface and, on a few occasions, maneuvered into the air, likely to pursue flying insects (Chapter IV). Characteristically, *M. macrophyllum* did not forage alone. We usually observed groups of three to 10 individuals flying within small (approximately 50–150 m diameter) coves along the shore.

Prey availability and diet composition.— Four nights of insect sampling revealed a total of 4878 captures of aerial insects at the light trap, while insects captured directly from the water surface totaled 505. Most (> 97%) of these insects were small (< 0.75 cm body length). Lepidoptera (70%), Psocoptera (14%), Ephemeroptera (8%), and Diptera (3%) dominated light trap samples. Insects from the water surface included mainly three heteropteran families, Gerridae (62%), Notonectidae (16%), and Veliidae (10%), as well as a few lepidopterans (4%). Lepidopterans caught at the light trap consisted primarily (99%) of one species, *Parapoynx diminutalis* (Pyralidae), small moths that hatch from water plants (*Hydrilla verticillata*, Hydrocharitaceae). Even though in low abundance, scales of *P. diminutalis* were present in over 90% of 20 fecal samples picked from the "Barracuda". Nightly temporal variation in abundance of aerial insects at the light trap (*P. diminutalis* excluded) was significant (one-way Anova, $F_{10, 32} = 2.77$, $p = 0.01$), with one maximum shortly after dusk and another one before dawn (FIG 8A). In contrast, *P. diminutalis* revealed no significant temporal pattern of activity ($F_{10, 32} = 1.62$, $p = 0.1$), although abundance tended to be highest in the middle of the night as most imagoes hatched at that time (FIG 8B). This may lead to a relatively constant availability of flying insects over the course of the night, where emerging *P. diminutalis* substituted the decrease of other aerial insects.

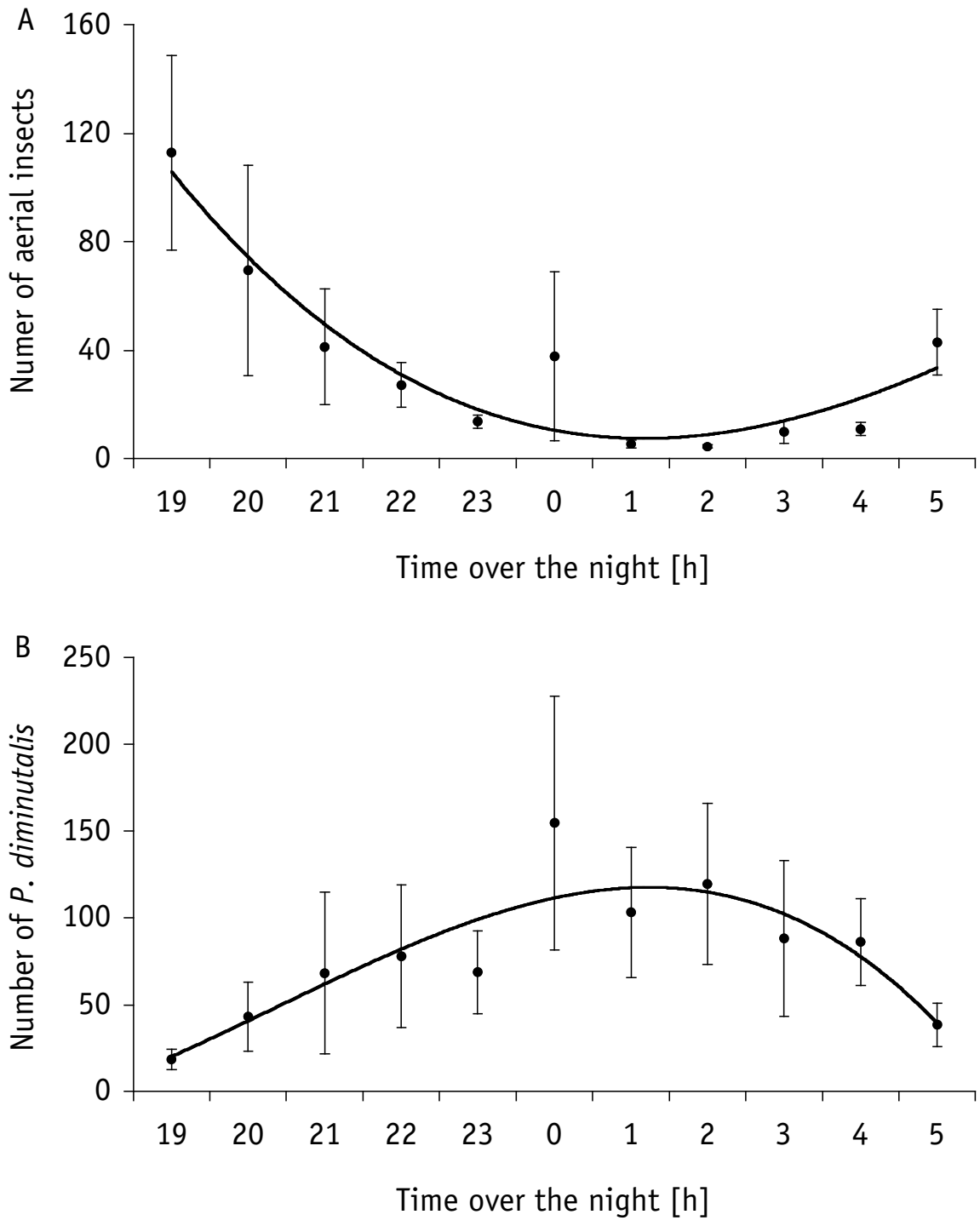


FIGURE 8. Temporal variation in prey abundance over the night assessed by light trapping (mean ± SE) within foraging areas of *M. macrophyllum*. A) Aerial insects, excluding *Parapoynx diminutalis* ($F_{10, 32}$ = 2.77, p = 0.014) B) only *P. diminutalis* ($F_{10, 32}$ = 1.62, p = 0.14).

DISCUSSION

Activity pattern and prey availability.— In our radio-tracking study in the Barro Colorado Nature Monument (Panamá), we showed that flight activity of *M. macrophyllum* varied over the course of the night with one maximum after sunset and a slight increase before dawn, interspersed with a constant, high level of activity. This pattern was independent of whether *M. macrophyllum* foraged near the day roost or in distant areas, and clearly distinguishes this bat from other phyllostomid species. Activity of most aerial insectivores follows a bimodal pattern, when they exploit twilight activity peaks of aerial insects (*e.g.* Hayes 1997, Kunz 1974, Meyer *et al.* 2004, Rydell *et al.* 1996, Speakman *et al.* 2000). As insect activity declines around the middle of the night, efficiency of continued foraging is reduced (Jones & Rydell 1994, Rautenbach *et al.* 1988). In contrast, many gleaning insectivores show low flight activity with several short foraging flights that are evenly spread over the night, where they characteristically feed on large insects, limiting food intake to a small number of prey items per night (Entwistle *et al.* 1996, Kalko *et al.* 1999, Schnitzler *et al.* 1985).

Our radio-tracking data combined with insect sampling show that flight activity of *M. macrophyllum* was positively correlated with abundance of diverse small flying insects. Even though this correlation is based on a rather small insect sample of only four nights and hence should be treated with caution, it is in accordance with findings of other studies (*e.g.* Hayes 1997, Meyer *et al.* 2004, Rautenbach *et al.* 1988, Speakman *et al.* 2000). Although seasonally highly abundant, *P. diminutalis*, by far the most common potential prey during our study, are most active when *M. macrophyllum* is least, we found some scales of *P. diminutalis* in almost all fecal samples obtained from bats. This shows that *M. macrophyllum* may prey primarily on a wide variety of insects, eventually including highly abundant moths, and indicates that *M. macrophyllum* combines two foraging modes, trawling insects from the water surface and hawking flying insects in the air. Unfortunately, tracking data do not allow any conclusion on the relative proportion of aerial hawking versus trawling.

Timing of nightly activity.— Besides spatio-temporal variation in prey availability other factors, such as light, precipitation, and reproductive status may influence levels of nightly activity in bats. Time of emergence and return of *M. macrophyllum* were synchronized with local sunset and sunrise times, respectively. In virtually all bat species studied to date, this pattern is evident to a certain extent. However, there is considerable variation among bat species as to when they start or when they end their flight activity (*e.g.* Catto *et al.* 1996, Entwistle *et al.* 1996, Erkert 1982, Kunz 1974, Shiel & Fairley 1999). While some species emerge very early, often before sunset, others initiate their foraging activity only when light intensities are already low (Duvergé *et al.* 2000, Lee & McCracken 2001, Weinbeer & Kalko 2004). Several factors, such as spatio-temporal variation in prey availability, predation pressure, and differences in foraging modes have been invoked to explain differential timing in emergence and return among bats

(Jones & Rydell 1994). Aerial insectivorous bats, for instance, are known to emerge earlier than gleaning insectivores or frugivores because they frequently exploit dusk peak of mass-emerging insects (Rautenbach *et al*. 1988, Speakman *et al*. 2000). However, due to an increased, light-dependent predation risk by visually orienting predatory birds (*e.g*. Fenton *et al*. 1994), actual emergence time of aerial insectivorous bats from their roosts is often viewed to constitute a trade-off between higher prey availability and lower predation risk (Jones & Rydell 1994, Rydell *et al*. 1996).

High flight activity of *M. macrophyllum* and a relatively early emergence after dusk place this bat close to activity patterns found in aerial insectivores and suggest that exploitation of small, mass-emerging insects at dusk plays an important role. Some individuals traveled into distant foraging areas (Chapter I). However, outward travel from the day roost was substantially used for foraging rather than direct commuting, as bats constantly flew within small coves along the shoreline, and travel towards foraging areas took considerably more time than return to the day roost. We observed that early emerging *M. macrophyllum* preferably foraged until complete darkness under overhanging waterside vegetation where some protection was provided against twilight predators. At dusk, we repeatedly observed bat falcons (*Falco rufigularis*, Falconidae) pursuing and successfully catching small bats flying close to the water surface. For gleaning insectivores, such as *Lophostoma silvicolum* (Phyllostomidae) or *Plecotus auritus* (Vespertilionidae), constraints imposed by increased predation risk at higher light intensities may not apply to the same extent since they can feed independently of aerial insect abundance peaks (*e.g*. Entwistle *et al*. 1996, Kalko *et al*. 1999, Rydell *et al*. 1996) and typically forage in more cluttered habitats, where dense vegetation offers more protection against potential predators. Intrinsic factors often further complicate timing of emergence in bats as energetic constraints resulting from differences in age, reproductive status, foraging efficiency, and overall physical condition might force some individuals, for example pregnant or lactating females as well as species with small body size, to emerge earlier, despite an increased predation risk in order to meet energetic demands (Duvergé *et al*. 2000).

Influence of rain on nightly activity.— While light rain did not inhibit flight activity of *M. macrophyllum*, heavy rain typically caused bats to temporarily cease foraging. They usually resumed flight after rain had tapered to a light shower but did not wait until it had completely stopped. In numerous bat species, light rainfall seems to exert little or no influence at all on foraging activity (*e.g*. Erkert 1982, Kunz 1974, Leonard & Fenton 1983), while it has been noted that many species are reluctant to fly in heavy rain (Erkert 1982). Heavy rainfall reportedly delays emergence or prevents flight activity in aerial insectivorous vespertilionids, such as *Eptesicus serotinus* (Catto *et al*. 1996), *P. auritus* (Entwistle *et al*. 1996), and *Myotis velifer* (Kunz 1974), or in the frugivorous phyllostomid, *Carollia castanea* (Thies, unpubl. data). Reduced flight activity during rain has been explained by thermoregulatory problems and by interference with echolocation due to atmospheric attenuation of high-frequency sound (Fenton & Kunz 1977).

Further, for physiological reasons, it seems advantageous for *M. macrophyllum* to temporarily stop foraging in heavy rain when increased heat loss across wet fur may be accelerated during flight. Finally, given that these bats rely to a great extent on echolocation for finding their prey (Chapter III), impaired echolocation during heavy rain is likely.

Influence of reproductive status on nightly activity.— While five females and three males of *M. macrophyllum* were non-reproductive during our study, the foraging activity of one reproductive male (M3), presumably a harem male (Chapter I), differed considerably from the pattern observed for the other individuals (TAB 1). This individual spent most of its active time at night in the roost and foraged only briefly. Our observations thus are consistent with results from other studies, where reproductively active, dominant males characteristically make relatively short foraging flights (Kunz *et al*. 1998, Williams 1986).

Foraging mode.—. In *M. macrophyllum* few long (up to 1 h) and mostly intermediate (mean: 7 min) foraging flights, interspersed with longer hanging phases (mean: 5 min; maximum 3 h), summed up to a relatively long flight time per night (about 3 h) and a flight distance of 35–47 km per night (Chapter I). Bats in general either search for prey in continuous flight, hunt from perches, or employ a combination of both strategies (reviewed in Fenton 1990). Perch hunting has been reported for a variety of tropical animal eating gleaners and is characterized by short sally flights and long interspersed resting phases leading to short flight times of only a few minutes per night (*e.g*. Audet *et al*. 1991, Kalko *et al*. 1999, Marimuthu *et al*. 1995, Vehrencamp *et al*. 1977). Long hanging periods and short foraging flights also characterize foraging behavior of many frugivorous phyllostomids, such as *Artibeus jamaicensis* (Handley *et al*. 1991). In contrast, aerial insectivores that capture prey in continuous flight show extended foraging flights (Fenton 1990), which in some species may last up to several hours (*Eptesicus serotinus*: Catto *et al*. 1996; *Euderma maculatum*: Wai-Ping & Fenton 1989). These species often travel considerable distances per night (*Leptonycteris curasoae* > 100 km: Horner *et al*. 1998; *Myotis daubentonii* up to 95 km: Dietz and Kalko, subm.; *Tadarida brasiliensis* > 100 km: Davis *et al*. 1962).

Unlike in many exclusively gleaning phyllostomid bats, such as frugivores, nectarivores, and many insectivores (Kalko 1997), a combination of gleaning and aerial hawking has been observed in several insectivorous species of other families (*e.g*. Johnston & Fenton 2001, Ratcliffe & Dawson 2003). With our direct observations of hunting individuals and video recordings in the field, we provide evidence that *M. macrophyllum* also forages over water both in trawling and aerial mode (see Chapter IV). Independent phylogenetic origin of this foraging behavior makes *M. macrophyllum* the only insectivorous phyllostomid known so far that deviates from the typical gleaning mode used by this family. Combination of two distinct foraging modes confers *M. macrophyllum* high flexibility to search for and acquire its insect prey from and at low heights above water surfaces (Chapter IV). In combination with morphological adaptations, this

behavioral flexibility has given *M. macrophyllum* the unique ability to conquer the open-space habitat above water, which is not used by any other phyllostomid.

Among gleaning insectivores, trawling species are to be considered a special group, because they hunt in open areas above water bodies and typically prey on much smaller insects than other gleaners. Trawling species comprise a number of ecological counterparts of *M. macrophyllum*, all of which likewise use a combination of trawling and aerial hawking (Brooke 1997, Jones & Rayner 1991, Kalko *et al*. 1998, Rydell *et al*. 1999, Schnitzler *et al*. 1994). This convergent evolution of a phyllostomid bat paralleling bats of other families in terms of foraging mode, activity, and habitat choice underscores the impressive morphological, behavioral, and sensorial plasticity that promotes high diversity within this speciose family of leaf-nosed bats.

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III

The Role of Echolocation in the Trawling Bat, *Macrophyllum macrophyllum*, when Foraging over Water

Echolocating bats (Chiroptera) use their sonar system to gather information about their environment (Griffin 1958). The development of this complex echolocation system in conjunction with specific morphological, sensorial, and behavioral adaptations is seen as one of the key factors that permit bats access to a wide range of resources at night (Arita & Fenton 1997, Fenton 1995, Schnitzler & Kalko 1998). Overall, bats have evolved a broad spectrum of echolocation call types that are often composed of several functional elements. Signal design and patterns of echolocation behavior reflect the sensorial tasks that have to be performed by bats, such as orientation in space, navigation, and in many species also perception of food, comprising detection, classification, and localization of prey (Fenton 1990, Neuweiler 1990, Schnitzler & Kalko 1998).

Aerial insectivores, which are present in many bat families, in particular, in the species-rich Vespertilionidae, Molossidae, and Emballonuridae, forage for insects in open and edge space habitats. These bats use primarily echolocation for prey perception. Typically, their echolocation sequences are composed of characteristic search, approach, and terminal group calls (Griffin *et al.* 1960). Search calls are emitted in a regular pattern, mostly one call per wing beat (Holderied & von Helversen 2003). Design of search calls is highly variable, including broadband frequency-modulated (FM) and narrowband shallow-modulated calls, or a combination of both. While shallow-modulated components facilitate detection of moving (fluttering) targets, short FM components are well suited for precise localization of prey (Neuweiler 1990, Roverud *et al.* 1991, Simmons & Stein 1980). After detection of potential prey, bats start pursuit, where pulse duration and pulse interval of approach calls are continuously reduced to gather detailed information about type and location of prey. Finally, in the terminal group, very short calls (< 1 ms) are produced at a very high repetition rate (up to 150–200 Hz) to achieve maximum localization accuracy for successful capture of moving prey.

In contrast to aerial insectivores, the endemic Neotropical leaf-nosed bats (Phyllostomidae) mostly take food from surfaces (gleaning) in obstacle-rich habitats within or around vegetation. Although they show the highest dietary diversity among bats, feeding on nectar, pollen, insects, vertebrates, and blood (Bonaccorso 1979, Findley 1993), they perform a relatively uniform echolocation behavior, using faint, multi-harmonic, steep FM calls. This is mostly due to the acoustic characteristics of their foraging habitat that hamper detection of food using echolocation, as background echoes from vegetation or ground (clutter) often mask prey echoes (Arlettaz *et al.* 2001, Schnitzler & Kalko 1998, 2001). Therefore, in addition, many leaf-nosed bats use visual, olfactory, or passive acoustic cues for finding food (Belwood & Morris 1987, Kalko & Condon 1998, Thies *et al.* 1998).

Echolocation calls of gleaning phyllostomid bats are well suited to measure distance and to orient in obstacle-rich space (Schnitzler & Kalko 1998). As in aerial insectivores, call design and pattern changes depending mainly on the behavioral situation. Phyllostomid bats emit search

calls in a regular pattern as well as groups of slightly shorter calls with a moderately higher repetition rate when approaching objects and flying in confined spaces (Kalko & Condon 1998, Thies *et al.* 1998). Yet, they do not produce a distinct terminal group, most likely because their food items are usually stationary and because echolocation is mainly used for orientation in space and not for prey perception (Schnitzler & Kalko 2001).

Within the Phyllostomidae, the long-legged bat, *Macrophyllum macrophyllum* Schinz (1821), is an exception as it hunts in unobstructed space over water, where it catches insects directly from (trawling) or in the air just above the water surface (aerial hawking; Chapter IV). In the Neotropics, up to five trawling species of four families may coexist, including the mouse-eared bat, *Myotis albescens* (Vespertilionidae), the proboscis bat, *Rhynchonycteris naso* (Emballonuridae; Kalko 1995a), two species of bulldog bats (*Noctilio albiventris*, *N. leporinus*, Noctilionidae; Kalko *et al.* 1998, Schnitzler *et al.* 1994), and the long-legged bat, *M. macrophyllum* (Harrison 1975).

The sensorial challenges bats foraging over water have to face, differ strikingly from the situation that phyllostomid bats encounter when gleaning in narrow space habitats (Kalko & Schnitzler 1989, Rydell *et al.* 1999). Acoustic properties of the space above water are rather similar to the edge space sensu Schnitzler *et al.* (2003a). Ensonification experiments showed that a smooth water surface reflects most of the signal energy of a low-flying bat away from the animal (Siemers *et al.* 2001a). Although trawling bats mainly take their prey from the water surface, they are exposed to little or even no clutter echoes in this situation (Boonman *et al.* 1998), similar to bats catching insects in mid-air. This is well reflected in call design, which differs strongly from call type and patterns of bats that glean food in clutter-rich situations. All trawling bats studied so far emit species-specific, loud echolocation calls with a distinct terminal group before prey capture. In addition, similar to aerial insectivores, *Noctilio* sp. and trawling *Myotis* sp. avoid pulse-echo overlap when closing in on prey by reducing pulse duration and pulse interval (Britton *et al.* 1997, Kalko *et al.* 1998, Kalko & Schnitzler 1989, Schnitzler *et al.* 1994). This indicates that in trawling bats, echolocation plays an important role for finding and acquiring food (Schnitzler & Kalko 2001).

In addition to ecological factors, in particular, the acoustic characteristics of foraging habitat, also evolutionary aspects, namely, phylogenetic relationships, may affect sensory ecology of bats (Schnitzler *et al.* 2003b). Due to its unique foraging habitat and foraging mode within the Phyllostomidae, *M. macrophyllum* offers an ideal opportunity to assess the relative contributions of habitat characteristics and phylogenetic constraints on the use of sensory cues for prey perception. If echolocation behavior were mainly determined by phylogeny, we would expect *M. macrophyllum* to produce faint calls of similar design as documented for other phyllostomid bats and to use primarily other sensory cues to find its prey. Conversely, if echolocation behavior is primarily shaped by the acoustic characteristics of the foraging habitat over water with little or no clutter echoes, we hypothesize that echolocation behavior of

M. macrophyllum should correspond to that of other trawling bats using echolocation as prime cue for prey perception. In this case, we expect that visual, olfactory, and passive acoustic cues play a minor or no role when foraging in fast flight for insects sitting on or flying just above the water surface. Finally, as *M. macrophyllum* also hawks potentially moving prey in the air (Chapter IV), we predict that the pattern of echolocation sequences of foraging individuals is similar to aerial insectivorous bats, consisting of search and approach calls and a distinct terminal group.

We assessed the role of echolocation and other sensory cues for finding prey in behavioral experiments with *M. macrophyllum* under controlled conditions in the flight cage on Barro Colorado Island, Panamá. We correlated changes in echolocation behavior with stages in foraging behavior and documented how *M. macrophyllum* takes prey from the water surface. Finally, we debate our results in the context of echolocation and foraging behavior of other trawling bats.

METHODS

Study site.— We conducted behavioral experiments from 6 January – 13 June 2004 on Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute in Panamá. We caught nine adult *M. macrophyllum* (four females, five males) one at a time in late afternoon from a colony of about 70 individuals near the lab buildings. The bats were released immediately after capture into a nearby flight cage (4.5 m x 4.5 m x 2 m), located inside the forest. Temperature, humidity, and noise level in the flight cage corresponded to ambient values. Bats were kept individually for four consecutive nights, after which we released them back into the colony. We did not conduct any experiments during the first night after capture to allow the animals to get accustomed with the cage. We offered mealworms (larvae of *Tenebrio molitor*, Coleoptera: Tenebrionidae) as prey, placed onto the water surface of a 2 m x 3 m water basin set up inside the cage, to initiate foraging. All bats started to forage within the first 2 h.

Behavioral experiments.— We designed an array of behavioral experiments to investigate the role of and possible interaction among visual, olfactory, passive acoustic, and echolocation cues for finding food in *M. macrophyllum*. In each experiment, one mealworm at a time was presented approximately 0.5 m away from the frame of the water basin. We conducted seven experiments: live mealworms were placed onto the water surface under well-lit conditions to offer all possible sensory cues simultaneously; live mealworms were presented on the water surface in total darkness to exclude vision; boiled mealworms were placed onto the water surface to further eliminate possible passive acoustic cues that might be caused by prey movements; deep-frozen prey was offered on the water surface to further exclude olfactory cues; live and dead mealworms were fixed on a thin wire about 1 mm below the water surface to finally also eliminate detection with echolocation. Rewarded experiments were interspersed with unrewarded controls where we offered rubber dummies (smooth electrical shrink-wrap tubing) with a diameter of 2 mm that

protruded 5 mm from the water surface in complete darkness. With this control, we wanted to minimize possible learning effects associated with rewarding each approach to an object on the water surface, and thus avoid habituation effects, like a possible decline in the use of echolocation.

Each type of experiment was conducted once and not repeated until all other experiments had been accomplished, following a different, arbitrary order each night. We performed twice as many unrewarded controls as rewarded experiments to keep the bats motivated in actively searching for prey. During the experiments, we counted capture success to assess the significance of different sensory cues for prey perception. A capture was defined as successful when the bats directed their flight towards prey, touched it with their tail membrane, and removed it from the water surface. We also counted the few trials as successful, where the bats lost prey after removal. Sequences were defined as unsuccessful when bats were searching for food, but passed prey three times or more without any obvious attempt to approach and remove it. We analyzed echolocation calls from each type of experiment to assess whether absence or presence of visual, passive acoustic, or olfactory cues would possibly influence echolocation behavior whilst closing in on prey.

Echolocation behavior.— For recording and analysis of echolocation behavior of foraging *M. macrophyllum*, calls were picked up by a custom-built condenser ultrasound microphone (frequency response ± 3 dB between 30 and 120 kHz; at frequencies down to 15 kHz or up to 200 kHz, sensitivity dropped by 0.2 dB/kHz), digitized (sampling rate: 312.5 kHz), and stored in a memory array (3.3 s real time). Signals were then read out at 1/15 of original speed, D/A converted with a custom-made time expansion system (department of animal physiology, University of Tübingen, Germany), and recorded (Sony Walkman professional WM-DC6; Maxell XL-II 90 audiotape). For analysis (Avisoft SAS-Lab Pro, Version 4.2), time-expanded signals were re-digitized at a sampling rate of 22.05 kHz, processed through a Fast Fourier Transformation (512 points, Hamming, 75% frame length, 93.75% time overlap), and displayed as color sonograms (dynamic range -72 dB). Calls were measured with a cursor on the screen at a time resolution of 0.097 ms and a frequency resolution of 645 Hz. For more details, see Siemers & Schnitzler (2000).

Selection of echolocation sequences.— We chose two sequences for each individual and experiment from a total of 56 to 83 echolocation sequences per bat to account for intra-individual variability. Selected sequences of an experiment were at least 6 h apart in time to minimize possible temporal autocorrelation. We only chose sequences with a good (> 40 dB) signal-to-noise ratio that were accompanied by high quality video sequences. The sequences included all calls and the corresponding foraging behavior starting at the point when bats searched for prey until they had captured or passed it.

Analysis of echolocation variables.— We limited our analysis of the multi-harmonic calls of *M. macrophyllum* to the second harmonic, since it consistently contained most of the signal energy. Based on sonograms, we measured pulse duration [ms], pulse interval [ms] (difference between starting time of two consecutive calls), bandwidth [kHz], and peak frequency [kHz] (frequency at maximum amplitude), and calculated repetition rate [calls/s], sweep rate [kHz/ms], and duty cycle [%] (percentage of time in which signals are emitted).

Analysis of echolocation sequences.— In correspondence with characteristic stages in foraging behavior of *M. macrophyllum*, we described the echolocation behavior of *M. macrophyllum* following the nomenclature of Schnitzler *et al.* (2003a). We discriminate between search calls, approach calls, and a distinct terminal group. We calculated means of call parameters over 1–21 search calls and 6–36 approach calls for each sequence, respectively. As call characteristics changed substantially throughout the terminal group, we separately analyzed call parameters for the first call, the numerically median call, the call with shortest pulse interval (usually, third to fifth last call of the terminal group), and the last call. For statistical analysis, we averaged values of variables of the two chosen sequences to avoid pseudoreplication (Hurlbert 1984). We compared echolocation call parameters between experiments with a two-factorial ANOVA design (experiment * individual; Statistica, StatSoft, Version 6.0) to assess whether presence or absence of visual, olfactory, and passive acoustic cues lead to differences in the structure and pattern of echolocation calls. All values are presented as mean ± SD.

Foraging behavior.— We filmed flying *M. macrophyllum* with two infrared-sensitive CCD video cameras (Sanyo, VC 1950; 50 half-frames/s) and recorded flight sequences onto Mini-DV (Sony GV-D900E) for 3-dimensional reconstruction of foraging behavior. An infrared strobe flash (duration: 10^{-4} s) froze each half-frame. A synchronization unit of the bat detector wrote a video time code onto both videos. For each flash, it also recorded a short (0.1 ms, 124 kHz) synchronization signal simultaneously onto the audio track to permit correlation of stages in foraging with phases in echolocation behavior (equipment custom-made, department of Animal Physiology, University of Tübingen, Germany).

Selection of video sequences.— Of the two sequences selected for echolocation analysis, we chose the one for 3-dimensional reconstruction of foraging behavior in which the bat was visible in more half-frames prior to prey capture. As we particularly focused in our analysis on the use of echolocation and its importance for capture behavior, we only analyzed videos of the experiment where all sensory cues other than echolocation were excluded (frozen prey on water surface in complete darkness).

Three-dimensional analysis of foraging behavior.— We analyzed the selected video sequences with the program Simi Motion (Version 6.0, 2002, 85705 Unterschleißheim, Germany) for 3-dimensional reconstruction of the flight paths of foraging bats. Position of bat (measurement

point at base of noseleaf), microphone, and prey were determined for both cameras and each half-frame (resolution 20 ms). A calibrated setup provided 3-dimensional coordinates for each point with an accuracy of ± 0.5% (approximately ± 1.5 cm at the largest distance), and allowed calculation of flight path, speed, and bat-prey distance. We also assessed the zone, where bat calls overlapped with echoes returning from prey, using a sound speed of 346 ms^{-1} in 25°C air. A pulse duration of 1 ms equals a distance of 17.3 cm from bat to prey, below which the emitted signal begins to overlap with the returning echo.

RESULTS

Sensory cues used for foraging.— In seven behavioral experiments we assessed the role of visual, olfactory, passive acoustic, and echolocation cues for finding food in long-legged bats, *M. macrophyllum*, in the flight cage. Our experiments revealed that echolocation was the key sensory cue crucial for finding prey. The bats always found food (capture success: 100%) whenever a mealworm was placed onto the water surface in experiments with live prey offered under well-lit conditions to provide the bat with all possible sensory cues (N = 76 trials); with prey offered in total darkness to exclude visual cues (N = 77); with boiled prey to exclude any prey-produced acoustic cues (N = 76 trials); and with deep-frozen prey to exclude olfactory cues (N = 79). Even in unrewarded control experiments in complete darkness, the rubber dummy protruding from the water surface was found in 98% of all trials (N = 141). Conversely, bats never found (capture success: 0%) live (N = 71) or dead prey (N = 72) submerged under water, where detection with echolocation was impossible.

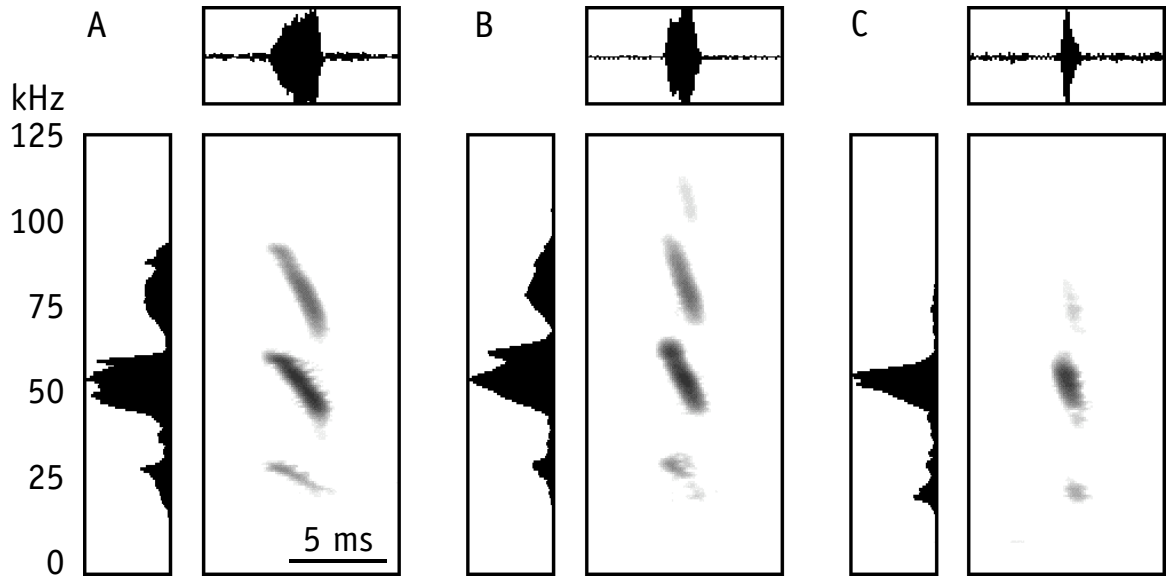


FIGURE 1. Representative echolocation calls of *M. macrophyllum* foraging in the flight cage on BCI, Panamá. Sonogram representation with relative time signal above and relative power spectrum to the left. A) Search call; B) approach call; C) terminal group calls, emitted prior to capture of prey.

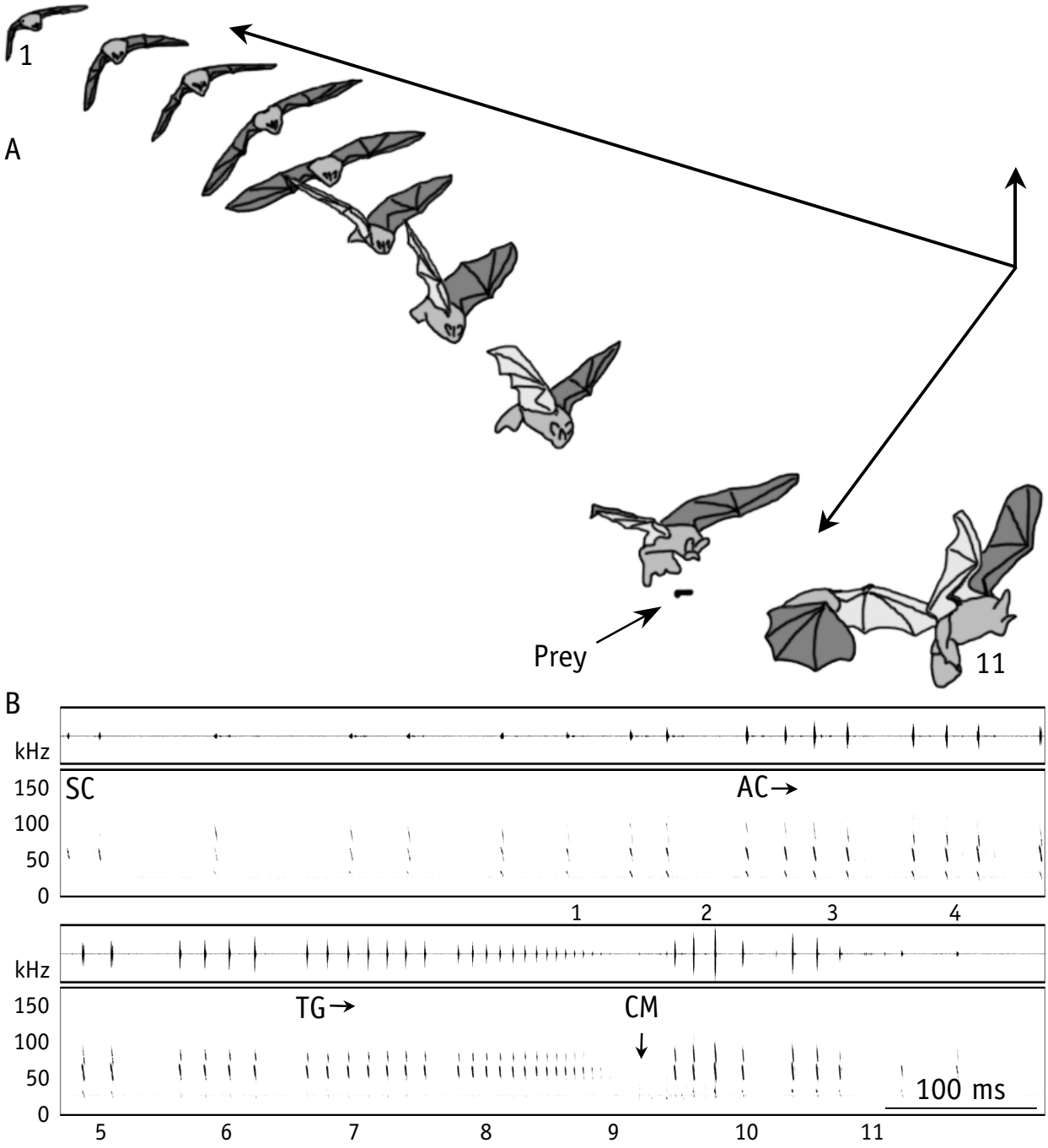


FIGURE 2. Foraging behavior in 3-dimensional space synchronized with the corresponding echolocation sequence of *M. macrophyllum* while closing in on and capturing a mealworm placed onto the water surface in the flight cage on BCI, Panamá. A) 11 images of the bat (temporal resolution: 80 ms). B) Sonogram of the echolocation calls with time signal above; numbers below correspond to images. Plots of call parameters of the same echolocation sequence including C) pulse duration, D) repetition rate, E) pulse interval, and F) duty cycle. Abbreviations: SC = search calls, AC = start of approach calls, TG = start of terminal group, CM = capture of mealworm.

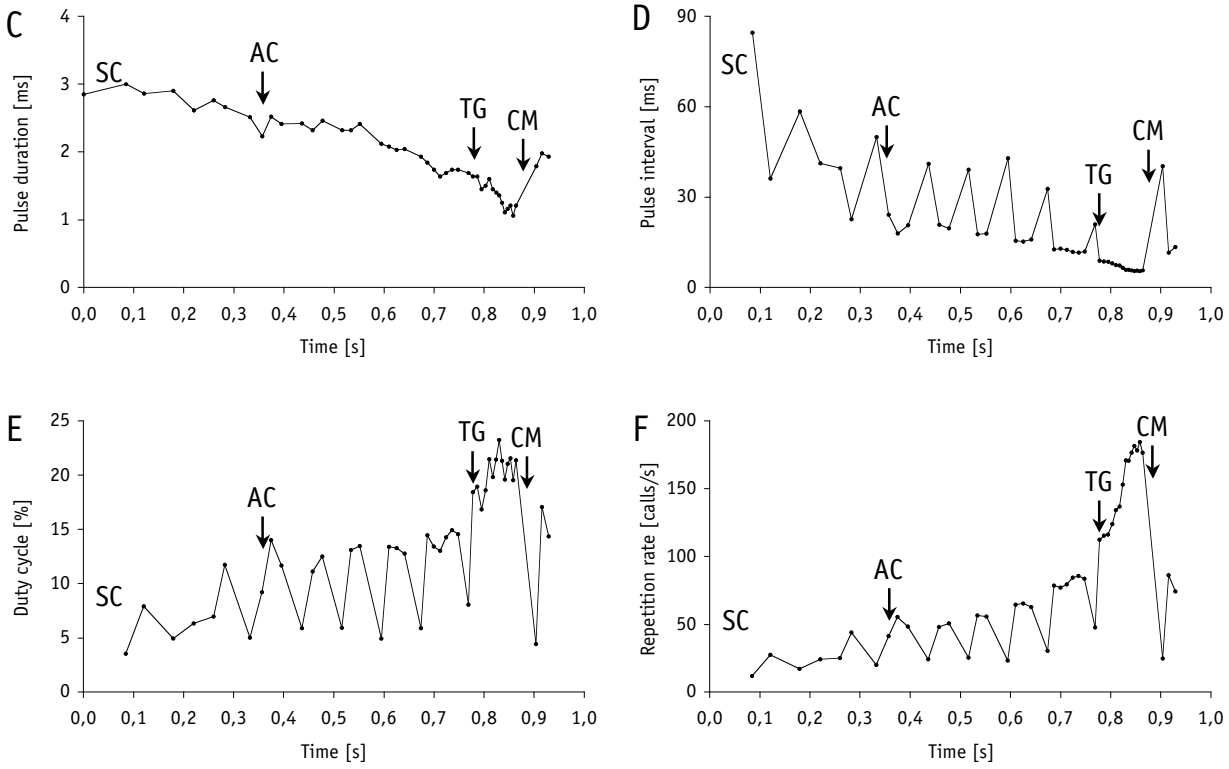


FIGURE 2. continued.

The crucial role of echolocation during prey capture was also supported by our finding that, whenever bats closed in on detected prey, stages in foraging behavior were accompanied by stereotypical, characteristic changes in the pattern of echolocation behavior that resembled patterns of aerial insectivorous bats including a pronounced terminal group (FIG 1 & 2B–F). In contrast, when prey was submerged under water, bats did not show any noticeable changes in echolocation and foraging behavior.

We compared four call parameters (pulse duration, pulse interval, bandwidth, peak frequency) throughout the characteristic parts of the echolocation sequences (search, approach, terminal group) to assess whether additional sensory cues (vision, olfaction, and audition) influenced echolocation behavior. We found no significant differences (two-factorial Anova; all $F_{(4,32)} < 2.75$, $0.045 < p < 0.96$) between the five experiments, where prey or the rubber dummy were placed onto the water surface. Hence, we pooled data of the five experiments for further calculations.

Correlation of foraging and echolocation behavior.— Bats ready to take prey in the flight cage circled low over the water surface of the water basin, actively searching for food at a flight speed of 2.95 ± 0.8 ms^{-1} ($N = 4$). They continuously emitted rather long search calls at varying pulse intervals and relatively large bandwidth (FIG 1A & 2B–F). In contrast, duty cycle, repetition rate, and sweep rate were relatively low. Peak frequency did not vary considerably over the whole sequence (TAB 1).

TABLE 1. Echolocation parameters (mean ± SD; minimum–maximum values) of nine foraging *M. macrophyllum* in five experiments with prey placed onto the surface of a water basin in the flight cage on BCI, Panamá. Values are based on measurements taken from 715 search calls, 1610 approach calls, and 360 terminal group calls. Abbreviations for terminal group: F = first call, M = numerically median call, S = call with shortest pulse interval, and L = last call.

Parameter	Search	Approach	Terminal group			
			F	M	S	L
Pulse duration [ms]	2.6 ± 0.3 1.9–3.6	2.3 ± 0.2 1.9–2.7	1.9 ± 0.2 1.5–2.4	1.5 ± 0.1 1.2–2.0	1.1 ± 0.1 0.9–1.6	1.0 ± 0.2 0.7–1.5
Pulse interval [ms]	43.0 ± 11 22–74	19.9 ± 2 16–23	12.5 ± 2 9.0–16	8.1 ± 1 6.1–11	6.0 ± 1 5.3–7.6	
Repetition rate [calls/s]	24.8 ± 6 14–46	50.7 ± 5 43–64	81.5 ± 12 61–112	126 ± 18 91–163	167 ± 14 132–190	
Bandwidth [kHz]	23.8 ± 2 21–28	25.9 ± 2 21–30	24.9 ± 3 18–30	21.7 ± 3 15–30	17.0 ± 3 12–24	15.0 ± 3 9.9–22
Peak frequency [kHz]	55.2 ± 2 50–59	54.9 ± 3 50–60	54.6 ± 3 50–63	54.4 ± 3 48–59	54.7 ± 3 48–58	53.6 ± 3 48–57
Sweep rate [kHz/ms]	9.4 ± 1 7.0–15	11.5 ± 1 9.5–13	12.9 ± 1 10–15	14.4 ± 1 11–17	14.9 ± 2 12–19	15.1 ± 2 11–24
Duty cycle [%]	7.0 ± 1 4.8–11	11.9 ± 1 9.8–15	15.8 ± 2 13–24	18.8 ± 2 13–27	19.1 ± 3 15–28	

After detection of prey, bats changed from search flight to target-oriented approach flight with slightly reduced flight speed of 2.48 ± 0.6 ms^{-1} (N = 9), where they directed their head, noseleaf, and ears towards prey (FIG 2A & 3). Simultaneously, *M. macrophyllum* switched from search calls to approach calls that were emitted in two to four groups of three to seven signals (FIG 1B & 2B–F). These call groups were interspersed by inter-group pulse intervals of intermediate (36.7 ± 3 ms, N = 45) duration. Approach calls were preceded by a relatively long pause of 46.3 ± 9 ms (N = 45). Taking the call before bats started with the formation of groups as the point where detection likely had occurred, we measured detection distances of 0.91–1.91 m (1.39 ± 0.3 m; N = 9) for *M. macrophyllum*. Approach calls had a lower pulse interval and shorter pulse duration than search calls, while repetition rate, duty cycle, sweep rate, and bandwidth were larger (TAB 1).

Finally, at a distance of 0.32–0.61 m (0.47 ± 0.1 m; N = 9) to prey, *M. macrophyllum* reduced flight speed to 2.22 ± 0.4 ms^{-1} (N = 9) and started to emit the terminal group (FIG 2B–F), where it produced 20.6 ± 2.2 (range: 14–27, N = 45) short calls (FIG 1C) at a very high repetition rate (TAB 1). The terminal group had a total duration of 179.6 ± 32.0 ms (range: 98–301 ms, N = 45) and was preceded by a short pulse interval of 28.3 ± 3 ms (N = 45). When *M. macrophyllum* was only 0.35–0.28 m (N = 9) from the prey and had already emitted the first two to eight terminal group calls, it entered the echo overlap zone, where the calls with a pulse duration of 1.6–2.1 ms

(*N* = 9) started to overlap with echoes returning from prey (FIG 4). Pulse duration was further shortened with decreasing distance to prey (TAB 1); however, it never dropped below 0.8–1.2 ms (*N* = 45; FIG 4). Throughout the terminal group, pulse interval and bandwidth were reduced continuously. In contrast, duty cycle and sweep rate slightly increased and repetition rate doubled (TAB 1).

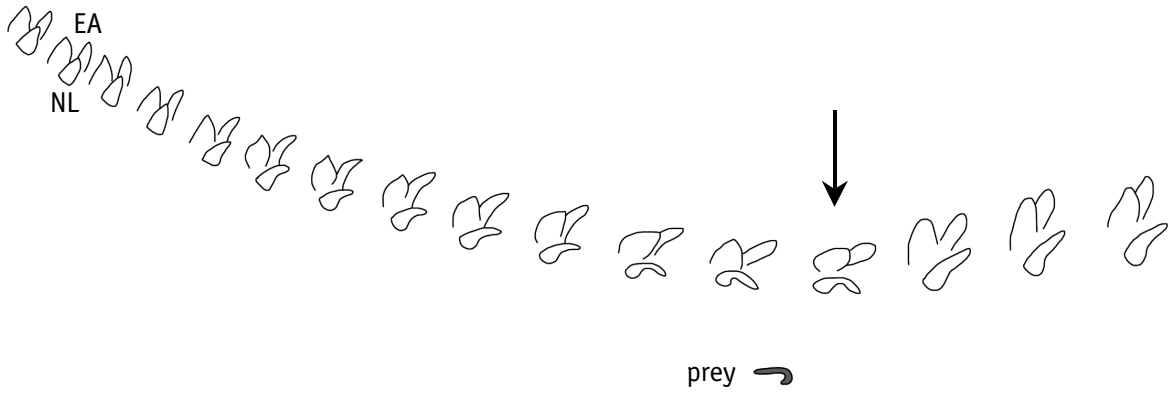


FIGURE 3. Detail of movement of noseleaf (NL) and ears (EA) of *M. macrophyllum* while approaching and capturing a mealworm floating on the surface of a water basin in the flight cage on BCI, Panamá. Note the immediate return of the head into the upright position after the prey was caught. Temporal resolution of the images: 20 ms. Arrow indicates the position of the head at the moment of prey capture.

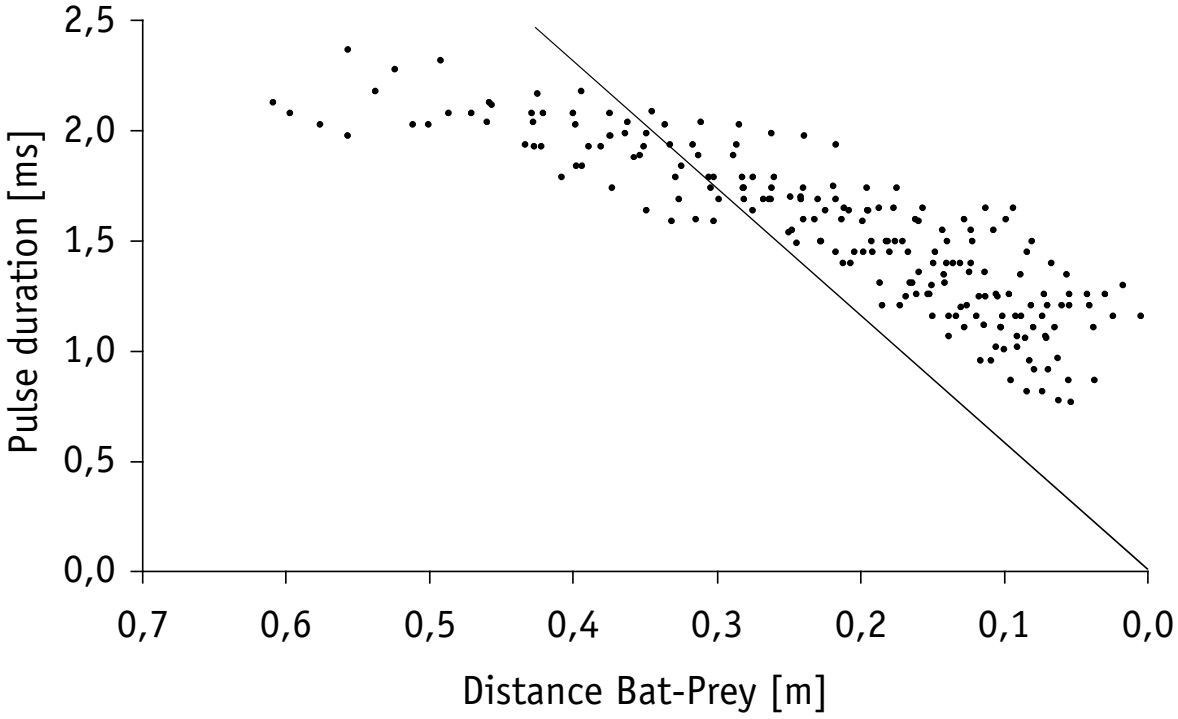


FIGURE 4. Decrease in pulse duration of terminal group calls from nine individuals of *M. macrophyllum* while closing in on mealworms placed onto the surface of a water basin in the flight cage on BCI, Panamá. The solid line indicates the limit beyond which calls overlap with returning echo from prey.

When *M. macrophyllum* had almost reached the prey, it lowered its tail membrane forming a pouch with the strong and long calcars stabilizing the distal edge of the membrane.

Simultaneously, the bat bent its head down towards the food and dipped both feet into the water parallel to its flight direction. Prior to capture, the bat dragged the tips of the calcars and approximately 1 cm of the distal part of the tail membrane over the water surface. When the bat was only a few cm from the prey, the terminal group ended. As soon as the bat touched the prey with its pouch, it moved its feet together. The prey was then caught with the pouch formed by the tail membrane and the calcars. The feet did not directly participate in removing the prey from the water surface. It is likely that the prominent dermal denticles on the ventral side of the tail membrane increase the friction of prey (FIG 5). At the same time, their alignment in rows may decrease the resistance of the tail membrane when sliding over the water surface prior to prey capture. Along with fine hairs they are probably also used for tactile reception of prey.



FIGURE 5. Ventral view of the large tail membrane of *M. macrophyllum* from BCI, Panamá. Note the long calcars, the rows of dermal denticles, and the fine hair on the membrane.

During capture, echolocation stopped for a brief period (43.3 ± 9 ms; N = 45; FIG 1). Immediately after capture, *M. macrophyllum* moved its head and ears back into the upright position (FIG 2). For a short moment, its body was aligned parallel to the water surface with its tail membrane approximately perpendicular to the body. At about the same time, the bat resumed echolocation. Subsequently, it quickly bent down its head to remove the prey with its mouth from the tail pouch, which had been moved forward. Finally, *M. macrophyllum* flew to a perch and usually processed the mealworm while hanging on the wall or ceiling of the flight cage. It started to search for the next mealworm as soon as it had finished its meal. Each bat consumed approximately 80–100 mealworms each night.

DISCUSSION

Sensorial cues used for prey perception.— We tested whether *M. macrophyllum* uses echolocation as the prime sensory cue for finding prey placed onto the water surface in edge space habitat. Based on the results of our behavioral experiments, where presence of echolocation cues alone were sufficient for the bats to find food (100% capture success), we conclude that echolocation plays the key role in *M. macrophyllum* for finding prey. This concurs with studies on other trawling bats, which also find food primarily with echolocation (Britton *et al.* 1997, Jones & Rayner 1988, Kalko 1995a, Kalko & Schnitzler 1989, Schnitzler *et al.* 1994, Siemers *et al.* 2001a). Perception of prey with echolocation is favored in bats foraging over water as the smooth surface reflects most of the signal energy away from low-flying bats, while prey on or above the water produces strong echoes and is likely to create distinct acoustic glints in the signal echoes (Boonman *et al.* 1998, Rydell *et al.* 1999, Siemers *et al.* 2001a).

The use of edge space above the water surface by *M. macrophyllum*, and its echolocation and foraging behavior are unique among phyllostomid bats, which mostly forage within or near vegetation. As these bats frequently face the problem of clutter echoes masking echoes from prey in this habitat, which impairs prey perception by echolocation alone (Arlettaz *et al.* 2001, Schnitzler & Kalko 1998, 2001), they often use additional olfactory, visual, and passive acoustic cues to find food (e.g. Heffner *et al.* 2001, Kalko & Condon 1998, Thies *et al.* 1998, Tuttle & Ryan 1981). In these bats, the use of echolocation is mostly limited to orientation in space and avoidance of obstacles.

However, there is increasing evidence that under certain, acoustically favorable conditions, some bats can use echolocation for perceiving prey even within narrow space habitats. For instance, phyllostomid bats may perform detection by echolocation when approaching flowers of *Mucuna holtonii* (Fabaceae; von Helversen & von Helversen 1999) and when preying on stationary dragonflies (Anisoptera; Kalko & Locher subm.). The raised petals of *M. holtonii* and the outstretched wings of dragonflies may create characteristic echo patterns that can be discriminated by nectar-drinking bats, *Glossophaga* sp., and the common big-eared bat, *Micronycteris microtis*, from the surrounding vegetation. Likewise, the exposition of food sufficiently far away from vegetation may permit the use of echolocation as prime cue for overlap-free perception like in the greater spear-nosed bat, *Phyllostomus hastatus*, feeding on fruits of *Gurania spinulosa* (Cucurbitaceae; Kalko & Condon 1998) dangling in semi-open space between canopy and subcanopy. Thus, acoustically favorable presentation of food may promote the use of echolocation for prey perception even in obstacle-rich surroundings.

Correlation of foraging and echolocation behavior.— Further support for the crucial role of echolocation for foraging in *M. macrophyllum* is given by the tight link between echolocation and foraging behavior, where stages of foraging behavior were accompanied by characteristic changes

in echolocation behavior, comprising search, approach, and terminal group calls. Most remarkably, the distinct terminal group present in foraging *M. macrophyllum* has not been observed in any other gleaning phyllostomid bat so far. This may largely be due to the fact that the food including fruit, nectar, pollen, or insects sitting on the vegetation or ground is mostly immobile and often close to uneven background producing scattered clutter echoes (Kalko & Condon 1998, Schnitzler & Kalko 2001, Thies *et al.* 1998). In contrast, prey hunted by *M. macrophyllum*, such as insects sitting on or flying just above the water surface (Chapter IV) requires an echolocation behavior similar to that of aerial and trawling insectivorous bats hunting mobile prey in open and edge space habitats. They all emit loud, mostly species-specific echolocation calls, and produce distinct terminal group calls before prey capture (Griffin *et al.* 1960).

We found that the echolocation behavior of *M. macrophyllum* searching for prey is more similar to that of trawling and aerial insectivorous bats hunting in open and edge space than to other phyllostomid bats. We argue that this resemblance is mainly due to similar perceptual tasks that have to be performed by the bats. Search calls of aerial insectivores are primarily adapted for detection of flying prey and orientation in space (Simmons *et al.* 1979, Schnitzler & Kalko 2001, Schnitzler *et al.* 2003a). As a function of clutter conditions of foraging habitat, signal design varies between species. Bats hunting in open space mostly use rather long search calls of narrow bandwidth (quasi-constant frequency: QCF) that are well suited for detection of fluttering prey (Schnitzler & Kalko 2001). Conversely, bats that forage in the edge space emit shorter search calls that are mostly composed of one or two broadband FM components and a shallow-modulated QCF component. The QCF component is seen as an adaptation for flutter detection, whereas the short and steep FM components are well suited for ranging and precise localization of objects including background clutter and potential food (Fenton *et al.* 1999, Schnitzler & Kalko 2001).

Mixed calls with short FM components and longer QCF components are characteristic for trawling bats including *Noctilio* sp. (Kalko *et al.* 1998, Schnitzler *et al.* 1994), *Myotis dasycneme* (Britton *et al.* 1997), and the proboscis bat, *R. naso* (Fenton *et al.* 1999, Kalko 1995a). Interestingly, we found a similar call structure in *M. macrophyllum* hunting in the field. Frequency-modulated search calls started with a distinct short (< 0.5 ms), shallow-modulated component with a sweep rate of only a few 100 Hz/ms (Chapter IV). We never observed this shallow-modulated component in search calls of *M. macrophyllum* emitted in the flight cage, which we regard as a possible adaptation to confined space.

Compared to trawling *Noctilio* sp. (Kalko *et al.* 1998, Schnitzler *et al.* 1994), search calls of *M. macrophyllum* were distinctly shorter. However, they showed, especially in bats recorded in the field (Chapter IV), similar or longer pulse durations at a much lower sweep rate than trawling *Myotis*. Further, main energy of search calls in trawling *Myotis* was concentrated almost

exclusively in the first harmonic comprising an overall bandwidth of about 44 kHz (*M. dasycneme*) to 57 kHz (*M. daubentonii*; Siemers *et al.* 2004). In contrast, the main energy of search calls in *M. macrophyllum* was found in the second harmonic (bandwidth: 24 kHz), while the first and third harmonic contained less energy (overall call bandwidth: approximately 70 kHz). In echolocation calls of *M. macrophyllum*, main energy remained in the second harmonic throughout the complete call, while in some phyllostomid bats, energy is typically shifted from one harmonic to another within a call (Kalko 2004, Thies *et al.* 1998). We conclude that in search calls, *M. macrophyllum* may increase chance for prey detection using a relatively low sweep-rate with an initial shallow-modulated component and, like other trawling bats, improves ranging and orientation capabilities with a high bandwidth.

In addition to search calls, also echolocation behavior of *M. macrophyllum* during approach of prey is similar to trawling bats, likely reflecting similar sensory tasks, such as classification and localization of prey. After detection of potential prey, trawling bats start pursuit typically using groups of approach calls for exact localization and tracking of prey (Britton *et al.* 1997, Kalko *et al.* 1998, Schnitzler *et al.* 1994). Comparable perceptual tasks between *M. macrophyllum* and other trawling bats is reflected in similar approach call design, in particular, a considerable reduction in pulse duration and pulse interval (Britton *et al.* 1997, Kalko & Schnitzler 1989, Kalko *et al.* 1998, Schnitzler *et al.* 1994). This also parallels the pattern of approach calls in some open and edge space vespertilionids, such as *Eptesicus*, *Myotis*, or *Pipistrellus* (Kalko 1995b, Kalko & Schnitzler 1993, Schnitzler *et al.* 1987, Siemers *et al.* 2001b, Surlykke & Moss 2000). Short calls emitted at a high repetition rate are particularly suited for localization of mobile prey (Schnitzler & Kalko 2001). Finally, detection distances found in *M. macrophyllum* in the flight cage (0.91–1.91 m) and in the field (0.85–2.33 m; Chapter IV) are comparable with detection distances of other trawling bats, such as *Myotis* sp. (1.3–2.0 m; Britton *et al.* 1997, Kalko & Schnitzler 1989) or *Noctilio* sp. (1.2–3.0 m; Kalko *et al.* 1998, Schnitzler *et al.* 1994).

We conclude from the high degree of convergence in echolocation behavior of *M. macrophylllum* with other trawling and also some aerial insectivorous bats that signal design is mainly determined by the acoustic properties of its foraging habitat and less by phylogeny. In particular, *M. macrophyllum* differs from all other phyllostomid bats in the presence of distinct terminal groups. They mainly serve to maximize localization accuracy for successful prey capture (Boonman & Jones 2002, Britton *et al.* 1997, Fenton & Bell 1979, Griffin *et al.* 1960, Schnitzler & Kalko 2001). Terminal groups are present in bats that hunt mobile prey in open or edge space, where they usually experience little or no clutter echoes. Trawling bats may benefit from a terminal group to successfully capture prey floating on the water surface, such as water striders, as well as insects flying over water that may perform rapid flight movements, including evasive maneuvers.

Access to food in 3-dimensional space is likely a reason why *M. macrophyllum* produces terminal groups in contrast to all other leaf-nosed bats that have been studied so far. Bats, which glean mostly stationary prey from surfaces, are probably not required to produce a terminal group, as their prey is unlikely to perform rapid maneuvers. In addition, these bats face the difficulty of prey echoes being masked by clutter echoes and thus, a terminal group would not provide them with additional information (Schnitzler & Kalko 2001). In accordance with perceptual tasks performed by other bats hunting mobile prey in open or edge space with little or no clutter echo, the repetition rate of terminal group calls in *M. macrophyllum* (130–190 Hz) is similar to trawling *Noctilio* sp. (130–180 Hz; Kalko *et al.* 1998, Schnitzler *et al.* 1994), and only slightly lower than in aerial and trawling vespertilionid bats (170–200 Hz; Britton *et al.* 1997, Jones & Rayner 1988, 1991, Kalko 1995a, Kalko & Schnitzler 1989, Siemers *et al.* 2001b, Surlykke & Moss 2000).

During terminal groups, some species of vespertilionid bats show a distinct decrease in peak frequency when pulse duration drops below 1 ms and pulse interval simultaneously reaches values around 4.5–5.0 ms ("buzz II"; Kalko 1995b, Kalko & Schnitzler 1989, Schnitzler *et al.* 1987, Surlykke *et al.* 2003), while others show only a slight decrease in frequency (Surlykke & Moss 2000). Although *M. macrophyllum* achieved similarly low values of pulse interval (5.3 ms) and pulse duration (0.7 ms), we did not observe a downward shift in frequency of the calls at the end of the terminal group. In a study on *M. daubentonii,* it had been proposed that the frequency shift might be due to a physiological limitation set by the high repetition rate (Kalko & Schnitzler 1989). With our observations on *M. macrophyllum,* we suggest that this shift in frequency may be an attribute of some Vespertilionidae rather than a physiological limitation. However, further research is necessary for a final conclusion.

Avoidance of masking.— Bats using FM calls generally reduce pulse duration when closing in on and capturing prey to prevent forward masking, where signals interfere with returning prey echoes and likely hamper accurate prey localization (Kalko 1995b, Schnitzler & Kalko 1998, 2001). In *N. albiventris*, pulse emission was even stopped 15–20 cm before reaching prey likely to avoid masking (Kalko *et al.* 1998). Conversely, as has been found in aerial hawking *Pipistrellus* sp. (Kalko 1995b) and trawling *M. dasycneme* (Britton *et al.* 1997), *M. macrophyllum* emitted calls with sound durations of > 0.7 ms until the bats were only a few cm from prey. Consequently, most signals of the terminal group overlapped with returning prey echoes.

However, the structure of downward FM calls may enable bats to reduce masking effects. It is likely that the echo of a broadband FM sweep is processed in the bat's hearing system by dividing it up into various frequency bands that can be analyzed separately by corresponding neuronal filters (Wiegrebe *et al.* 1996). When receiving an echo, each neuronal filter analyzing a respective frequency band would then be activated only for a much shorter time than the actual duration of the entire echo. In this scenario, the rather long (2 ms) terminal group calls of

Noctilio with low sweep rates of 13–16 kHz/ms (Kalko *et al.* 1998) may still overlap to some extent with returning echoes. *Noctilio* likely prevents further overlap by ceasing echolocation 15–20 cm prior to capture. In contrast, the broadband FM structure of the very short (0.6–0.8 ms) and steep terminal group calls of *Pipistrellus* (29–34 kHz/ms; Kalko 1995b), *M. dasycneme* (10 kHz/ms; Britton *et al.* 1997), and *M. macrophyllum* (15 kHz/ms), is likely to prevent an overlap in each neuronal filter and hence allow these bats to use echolocation until they nearly reached their prey.

To conclude, in our behavioral experiments with trawling long-legged bats, *M. macrophyllum*, we showed that echolocation is the prime cue for finding prey. Similar to other trawling bats and to bats foraging in edge and open space, pattern of echolocation behavior in *M. macrophyllum* consists of search and approach calls and a distinct terminal group. This is in contrast to all other leaf-nosed bats studied so far, which usually forage within vegetation, where clutter echoes hamper prey perception with echolocation alone. In particular, these bats do not produce a distinct terminal group, which is likely due to their immobile prey as well as clutter echoes interfering with echoes returning from prey. We propose that echolocation behavior in *M. macrophyllum* is primarily influenced by the acoustic characteristics of the foraging habitat over water, where little or no clutter echoes interfere with prey perception, while phylogenetic relationships play a minor role in shaping the echolocation behavior of *M. macrophyllum*. Our study of this species with a unique foraging niche within the phyllostomid family reveals the clear distinction between the roles of ecological and phylogenetic constraints and will contribute to a better understanding of mechanisms of coexistence and factors promoting radiations in the course of evolution.

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IV

Behavioral and Sensorial Flexibility in *Macrophyllum macrophyllum*, Catching Insects in the Air and Near Clutter

Species with flexible use of foraging modes may have access to more resources and exploit habitats better than species which are restricted to a certain foraging mode and hence a certain type of prey. For instance, it is well known that bats, which usually trawl insects or small fish from the water surface, such as *Noctilio* sp. (Noctilionidae) and some *Myotis* sp. (Vespertilionidae), also hawk aerial prey, thus taking advantage of the insect-rich space on and above water bodies (Britton *et al.* 1997, Jones & Rayner 1988, 1991, Kalko *et al.* 1998, Schnitzler *et al.* 1994). However, flexibility in foraging behavior requires specific behavioral and sensorial adaptations as the bats may face different perceptual challenges depending on foraging mode. In trawling bats, the smooth water surface reflects most call energy away from low flying bats and little or no background echoes (clutter) interfere with detection of prey (Boonman 1998, Siemers *et al.* 2001a). A similar situation exists for bats catching insects in the air away from obstacles. Therefore, in both modes, trawling and aerial hawking, these species find their prey primarily with echolocation. In addition to trawling *Myotis* sp., many evening bats (Vespertilionidae) regularly switch between gleaning and aerial hawking to exploit prey distributed over the night in space and time (Anderson & Racey 1991, Arlettaz *et al.* 2001, Chruszcz & Barclay 2003, Ratcliffe & Dawson 2003). During aerial hawking they use echolocation for prey perception and generally find their prey with visual or prey-generated acoustic cues during gleaning (e.g. Arlettaz *et al.* 2001).

Remarkable examples of flexibility in foraging behavior are also found within Neotropical leaf-nosed bats (Phyllostomidae), which typically classify as gleaners as they forage in narrow-space habitat close to or within dense vegetation where they take food from surfaces such as leaves, bark, or ground (Schnitzler & Kalko 1998). In this habitat, masking effects of clutter echoes, which overlap with echoes returning from prey, hamper perception of prey using echolocation alone. Therefore, phyllostomid bats generally find their prey by visual, olfactory, and passive acoustic cues, while echolocation is mostly used for orientation in space (Schnitzler & Kalko 2001, Schnitzler *et al.* 2003a). Recent studies have revealed that some insectivorous phyllostomids combine various foraging modes, in particular, gleaning and aerial hawking. For instance, *Lampronycteris brachyotis*, which was believed to be an understory gleaner, also forages in the upper canopy, where radio-tracking data suggest that it gleans insects from flight and likely performs aerial captures (Weinbeer & Kalko 2004). While the sensory ecology of this species remains largely unknown, other typical gleaning animal-eating phyllostomid bats, like *Micronycteris hirsuta*, *Tonatia saurophila*, and *Trachops cirrhosus* were observed hawking free flying or tethered katydids in a flight cage, where they detected the prey from a perch mainly by the noise of its beating wings, immediately took flight and caught it in mid-air (Spehn & Kalko subm., Schnitzler *et al.* 1995).

Ecological factors, in particular, the acoustic properties of habitat and food or the presentation of food at a distance far enough from background to allow overlap-free detection, affect how a bat finds food and determine the role of echolocation for foraging. Under certain

conditions, some phyllostomid bats are known to use echolocation for finding prey (Kalko & Condon 1998, Thies *et al.* 1998, von Helversen & von Helversen 1999). These species, as all other phyllostomid bats studied so far, emit largely uniform, faint, short, steep frequency-modulated (FM) echolocation calls and do not considerably change call parameters while approaching their food. In particular, they do not produce a distinct terminal group of very short calls emitted at a high repetition rate. This is probably the case because they are not required to perform skilful maneuvers to take their mostly stationary food, such as fruit or nectar. In contrast to all other phyllostomid bats, the long-legged bat, *Macrophyllum macrophyllum* Schinz (1821), hunts over water. In this clutter-poor habitat, it uses echolocation as prime cue for finding insects, which it trawls from the water surface (Chapter III). In contrast to other phyllostomid bats, the echolocation behavior of *M. macrophyllum* comprises characteristic search and approach calls, as well as a distinct terminal group (Chapter III), which maximizes localization accuracy of mobile prey (Schnitzler & Kalko 2001). The echolocation behavior of *M. macrophyllum* is similar to aerial insectivorous and other trawling bats of different families (Jones & Rayner 1988, 1991, Kalko *et al.* 1998, Schnitzler & Kalko 2001, Schnitzler *et al.* 1994, Siemers 2001a), which likely reflects similar perceptual tasks that have to be performed by the bats.

In the field, foraging *M. macrophyllum* fly low, usually within 50 cm, above the water surface (Chapter II), where they feed on prey sitting on the water surface. However, the use of a terminal group in *M. macrophyllum* indicates that this species may also catch insects flying in 3-dimensional space over water. In accordance with observations of other trawling bats, we hypothesize that *M. macrophyllum* may also exhibit a highly flexible foraging behavior, including aerial hawking of insects and trawling. To test their ability to catch insects in the air, we exposed individual bats to prey suspended in the air above the water surface in the flight cage. We subsequently compared our results with those of experiments with trawling *M. macrophyllum* (Chapter III) to assess the flexibility of echolocation and foraging behavior in this species.

While clutter echoes in dense vegetation usually hamper most phyllostomid bats from finding their food with echolocation alone (Schnitzler & Kalko 2001), trawling *M. macrophyllum* use echolocation as prime cue for prey perception, likely as a consequence of the clutter-poor environment over water (Chapter III). However, in the field, *M. macrophyllum* was also frequently observed foraging close to banks of a water plant, *Hydrilla verticillata* (Hydrocharitaceae). Although most of the plant is usually submersed, the upper-most leaves slightly protrude from the water surface (Chapter I) and produce clutter echoes for bats foraging nearby. This leads to a situation where *M. macrophyllum* would face strong clutter echoes, as is the case for most of the other phyllostomid bats.

When prey echoes are progressively masked by clutter (backward masking), unambiguous detection and localization of prey by echolocation alone become difficult or even impossible (Schnitzler & Kalko 2001). An experimental study on temperate trawling *Myotis daubentonii*

(Vespertilionidae) revealed that prey capture success declined with increasing amount of clutter produced by duckweed (Boonman *et al.* 1998). However, due to its steep FM calls, *M. macrophyllum* is likely to tolerate some overlap of prey echoes with its own echolocation calls (forward masking, Chapter III), as broadband calls are probably divided into many frequency bands. Corresponding neuronal filters separately analyze each band of a shorter duration than the complete call, thus reducing echo overlap (Wiegrebe *et al.* 1996). We therefore hypothesized that *M. macrophyllum* should be able to find prey near *H. verticillata* banks, as long as echoes only slightly overlap with clutter echoes, whereas perception of prey fully buried within clutter should be impeded. We assessed the influence of clutter on echolocation and foraging in behavioral experiments, where prey was presented under controlled conditions in a flight cage at varying distances relative to clutter on and above water surfaces and recorded echolocation and foraging behavior simultaneously.

METHODS

Study site.— We conducted behavioral experiments from 6 January – 13 June 2004 on Barro Colorado Island, Panamá, with nine adult *M. macrophyllum* (four females, five males) in a flight cage (4.5 m x 4.5 m x 2 m), located inside the forest. Temperature, humidity, and noise level in the cage were similar to ambient values. Bats were caught one at a time from a colony comprising approximately 60 individuals. We kept them individually for four consecutive nights each and subsequently released back into the colony. In addition, we studied bats in the field, foraging close (50 m) to their colony in a small cove at the shore of Gatún Lake.

Behavioral experiments.— We studied flexibility of foraging behavior of *M. macrophyllum*, described its echolocation behavior and flight performance while hawking prey suspended in the air, and compared our results with data obtained from bats foraging in the field. Finally, we assessed the influence of echo-producing background (clutter) on capture success. In each behavioral experiment, we presented one mealworm (larvae of *Tenebrio molitor*, Tenebrionidae) at a time. In the field, we observed foraging bats under natural conditions without offering prey.

We conducted two experiments in the flight cage to test for the ability of bats to hawk aerial insects. Frozen and live mealworms were suspended one at a time on a thin (0.1 mm) nylon thread 20 cm above the water surface to mimic aerial prey. In another set of experiments, we exposed the bats to various amounts of clutter. In the water basin, we installed a plot (about 0.5 m x 1 m) of *Hydrilla verticillata* (Hydrocharitaceae), a common water plant that floats in large, dense banks in the water within the foraging habitat of *M. macrophyllum* at our study site in Panamá. Leaf tips of the largely submersed plants slightly penetrate the water surface and therefore produce clutter echoes for bats foraging nearby. In six experiments, we placed prey onto the water surface at 20 cm, 10 cm, and 0 cm distance in front of the clutter plot, and

suspended prey 20 cm above the water surface 20 cm in front, at the edge of the *H. verticillata*, and 20 cm over the clutter plot (FIG 1).

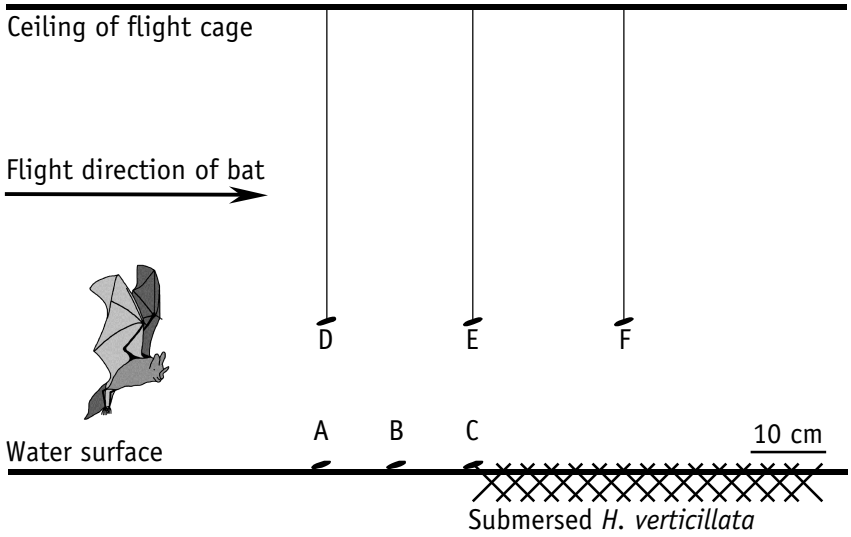


FIGURE 1. Array of clutter experiments in the flight cage on BCI, Panamá showing *M. macrophyllum* in search for floating mealworms on the water surface at A) 20 cm, B) 10 cm, and C) 0 cm distance to clutter, produced by leaves of *H. verticillata* water plants slightly penetrating the water surface, and prey tethered 20 cm above the water on a nylon thread D) 20 cm and E) 0 cm in front of clutter and F) 20 cm over the clutter plot.

Following an arbitrary order, each type of experiment was conducted once and not repeated until all other experiments had been accomplished. For each experiment with prey suspended in the air or at different distances to clutter, we counted capture success of the bats. We defined a capture as successful when the bats directed their flight towards prey, touched it, and subsequently removed it from the water surface or from the thread. Sequences were defined as unsuccessful when bats searched for food, but passed prey three or more times without any obvious attempt to approach and remove it. In addition, we analyzed echolocation calls from each type of experiment to assess whether presentation of prey (floating versus suspended) and presence of clutter would possibly influence echolocation behavior whilst closing in on prey. Finally, we compared results between captive and wild bats to assess the possible influence of confined space on echolocation behavior.

Echolocation behavior.— For analysis of echolocation behavior of foraging *M. macrophyllum* in the flight cage and in the wild, calls were picked up by an ultrasound microphone, processed through a time expansion system (Department of Animal Physiology, University of Tübingen), and recorded at 1/15 of original speed (Sony Walkman professional WM-DC6; Maxell XL-II 90 audiotape). For analysis, signals were displayed as color sonograms and calls were measured with a cursor on the screen (Avisoft SAS-Lab Pro, Version 4.2). We chose two of 14–21 echolocation sequences for each individual per experiment to assess echolocation behavior during aerial

hawking (frozen versus live mealworms) and one of 9–12 echolocation sequences for each individual per experiment to assess the influence of clutter on echolocation behavior. Finally, we selected 11 out of 65 echolocation sequences, recorded in 3 nights from wild bats in the field. See Chapter III for details on recording devices and on criteria for sequence selection.

Analysis of echolocation behavior.— We measured seven call parameters for the second harmonic, which consistently contained most of the signal energy of the multi-harmonic calls of *M. macrophyllum*. Based on the sonograms, we measured pulse duration [ms], pulse interval [ms] (difference between starting time of two consecutive calls), bandwidth [kHz], and peak frequency [kHz] (frequency at maximum amplitude), and calculated repetition rate [calls/s], sweep rate [kHz/ms], and duty cycle [%] (percentage of time in which signals are emitted).

Analysis of echolocation sequences.— Following Schnitzler *et al.* (2003a), we described changes in echolocation behavior and correlated them with characteristic stages in foraging behavior. We discriminated between search calls, approach calls, and a distinct terminal group emitted at a high repetition rate prior to capture (Chapter III).

We calculated means over search and approach call parameters, respectively. Because echolocation parameters changed considerably over the course of the terminal group, we separately analyzed the first call, the numerically median call, the call with shortest pulse interval (usually third to fifth last call), and the last call. We compared echolocation call parameters between experiments with a two-factorial Anova design (experiment * individual) to assess the influence of clutter on echolocation behavior. In experiments with prey suspended in air, we averaged parameter values of the two chosen sequences for statistical analysis to avoid pseudoreplication (Hurlbert 1984). We then compared these results in a two-factorial Anova design (experiment * individual) with those of another study (Chapter III) to evaluate whether echolocation behavior differs between aerial hawking of tethered prey and trawling from the water surface. We finally compared results of aerial hawking and trawling with results from bats in the field in a two-factorial Anova design (experiment * individual) to assess how similar our flight cage results are in relation to the field data. All values are presented as mean ± SD.

Foraging behavior.— We filmed flying *M. macrophyllum* with two video cameras for 3-dimensional reconstruction of foraging behavior under infra-red flash illumination. Videos were synchronized with echolocation recording to allow analysis of corresponding stages in foraging behavior and phases in echolocation (custom-made equipment, Department of Animal Physiology, University of Tübingen, Germany; for details see Chapter III). We analyzed nine video sequences of bats hawking aerial prey and eight sequences of wild bats in the field with the program Simi Motion (Version 6.0, 2002, 85705 Unterschleißheim, Germany) for 3-dimensional reconstruction of flight paths. Position of bat (measurement point at base of noseleaf), microphone, and prey were determined for both cameras and each half-frame (resolution 20 ms)

to assess 3-dimensional flight path, speed, and bat-prey distance. We also calculated the zones where bat calls overlapped with echoes returning from prey (forward masking), and where prey echoes overlapped with clutter echoes (backward masking), using a sound speed of 346 ms^{-1} at 25°C air temperature.

RESULTS

Flexibility of foraging behavior.— In two behavioral experiments we tested the ability of *M. macrophyllum* to hawk aerial prey. All nine individuals readily caught prey suspended in the air just (20 cm) above the water surface in the flight cage. One bat did not take any further tethered mealworms for unknown reasons after it had caught the first one, and thus was excluded for subsequent analyses of aerial hawking experiments. In the remaining eight bats, we found that, like in trawling mode, echolocation was the prime sensory cue used by *M. macrophyllum* for finding prey suspended in the air. The bats removed tethered mealworms equally well with a capture success of 100% in experiments with live prey (N = 68) that provided the bat with a range of prey-generated cues (smell, movements) in addition to echolocation, and dead prey (N = 65), where all sensory cues but echolocation were excluded. The important role of echolocation for finding aerial prey was further emphasized by the stereotypical echolocation behavior of *M. macrophyllum*. When closing in on tethered prey, stages in foraging behavior were tightly linked with characteristic changes in the design of echolocation sequences. Equally, we observed this behavior in our study on trawling behavior of *M. macrophyllum* (Chapter III).

We compared four call parameters (pulse duration, pulse interval, bandwidth, peak frequency) for each characteristic part of the echolocation behavior (search, approach, terminal group) to assess whether presentation of dead or live prey may have influenced echolocation behavior. We found no significant differences in call parameters (two-factorial Anova; all $F_{(1,7)} < 3.4$, $0.1 < p < 0.96$) between the two experiments with tethered prey, except for peak frequency of search calls, which was slightly higher (55.9 kHz) in experiments with dead prey than with live prey (55.1 kHz; $F_{(1,7)} = 7.5$, $p = 0.03$). However, as this slight difference in frequency was within the range of the frequency resolution (645 Hz) of the analysis, we pooled all data of the two experiments for further calculations (TAB 1).

Correlation of foraging and echolocation behavior.— Experiments with prey suspended in air were arbitrarily interspersed by experiments with prey floating on the water surface (Chapter III) to impede accustoming of the bats to a particular situation. Echolocation and flight behavior prior to detection of prey was similar, whether prey was tethered in the air or placed onto the water surface (TAB 1, FIG 2). For detailed description of trawling behavior, see Chapter III.

TABLE 1. Seven echolocation parameters of *M. macrophyllum* foraging in the flight cage and in the field at BCI, Panamá. Presented data (mean ± SD; min–max) are based on measurements taken from 715 search calls, 1610 approach calls, and 360 terminal group calls of nine bats trawling prey floating on the water surface in the flight cage (see Chapter III); 278 search calls, 579 approach calls, and 128 terminal group calls of eight bats hawking tethered prey in the flight cage; and 100 search calls, 137 approach calls, and 44 terminal group calls of 11 sequences of bats trawling floating prey in the field. Significant differences between captive bats and bats in the field are given as $*p<0.5$ and $**p<0.001$. Abbreviations for terminal group: F = first call, M = numerically median call, S = call with shortest pulse interval, and L = last call.

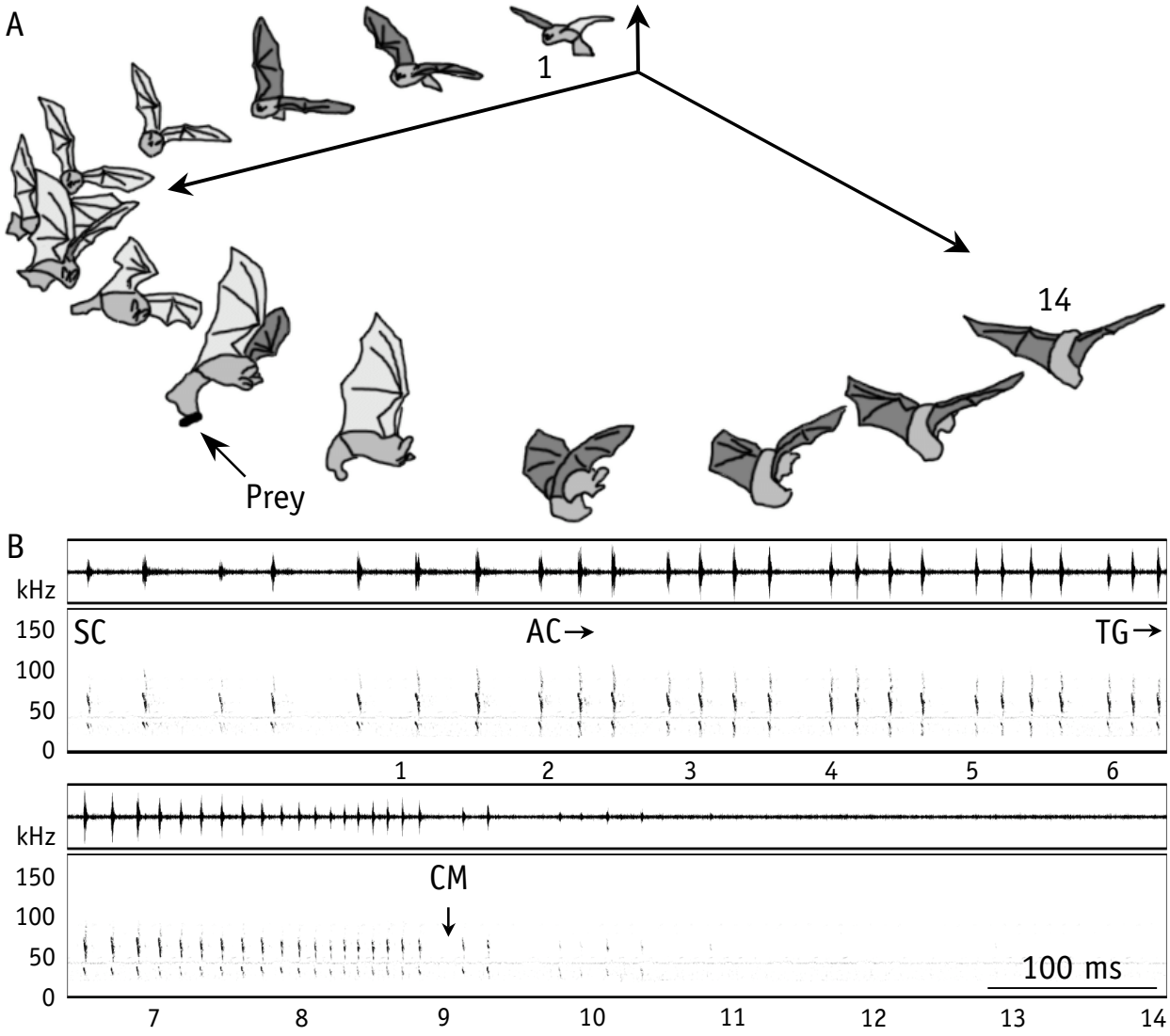
Parameter	Habitat	Search	Approach	Terminal group			
				F	M	S	L
Pulse duration [ms]	Water	2.6 ± 0.3 1.9–3.6	2.3 ± 0.2 1.9–2.7	1.9 ± 0.2 1.5–2.4	1.5 ± 0.1 1.2–2.0	1.1 ± 0.1 0.9–1.6	1.0 ± 0.2 0.7–1.5
	Air	2.5 ± 0.2 2.1–2.8	2.3 ± 0.1 2.1–2.5	2.0 ± 0.1 1.7–2.2	1.5 ± 0.2 1.3–1.7	1.2 ± 0.2 1.0–1.6	1.1 ± 0.2 0.9–1.6
	Field	3.2 ± 0.7** 2.2–4.7	2.6 ± 0.2** 2.4–2.8	2.1 ± 0.3* 1.6–2.5	1.4 ± 0.3 0.8–1.9	1.0 ± 0.2* 0.6–1.4	0.9 ± 0.2* 0.7–1.4
Pulse interval [ms]	Water	43.0 ± 11.5 22–74	19.9 ± 2.0 16–23	12.5 ± 1.7 9.0–16	8.1 ± 1.2 6.1–11	6.0 ± 0.5 5.3–7.6	
	Air	44.9 ± 14.9 29–81	19.1 ± 1.4 17–22	12.6 ± 1.2 10–14	8.0 ± 1.5 6.3–11	6.1 ± 0.6 5.4–7.6	
	Field	54.5 ± 11.9 30–66	17.9 ± 3.3 15–22	10.7 ± 1.8* 9.3–14	7.5 ± 1.8 5.7–12	5.8 ± 0.8 5.2–7.8	
Repetition rate [calls/s]	Water	24.8 ± 6.4 14–46	50.7 ± 5.3 43–64	81.5 ± 11.7 61–112	125.7 ± 17.6 91–163	166.7 ± 13.9 132–190	
	Air	24.2 ± 6.7 12–35	52.5 ± 3.7 46–58	80.3 ± 8.3 70–97	128.4 ± 21.8 90–158	166.6 ± 15.8 131–185	
	Field	19.4 ± 5.5 15–33	57.8 ± 11.4 45–68	96.2 ± 17.2 70–108	139.5 ± 27.6 83–177	174.6 ± 19.6 128–193	
Band-width [kHz]	Water	23.8 ± 1.8 21–28	25.9 ± 2.0 21–30	24.9 ± 2.6 18–30	21.7 ± 3.1 15–30	17.0 ± 2.7 12–24	15.0 ± 2.7 9.9–22
	Air	23.7 ± 2.0 22–28	26.5 ± 1.6 24–30	25.8 ± 2.9 21–31	22.6 ± 2.7 19–28	18.9 ± 3.5 14–25	16.3 ± 3.5 11–22
	Field	25.0 ± 2.4 20–30	26.9 ± 2.5 23–30	25.1 ± 3.1 20–31	21.0 ± 4.2 11–26	17.5 ± 2.2 14–20	16.4 ± 2.2 13–20
Peak frequency [kHz]	Water	55.2 ± 2.4 50–59	54.9 ± 2.5 50–60	54.6 ± 2.8 50–63	54.4 ± 2.5 48–59	54.7 ± 2.5 48–58	53.6 ± 2.6 48–57
	Air	55.3 ± 2.2 51–58	54.8 ± 2.2 51–58	55.0 ± 2.6 49–59	53.9 ± 2.0 50–56	54.5 ± 1.7 51–58	54.3 ± 2.6 48–57
	Field	54.4 ± 1.7 51–56	51.9 ± 3.1* 47–57	51.9 ± 3.7* 47–59	51.7 ± 2.6* 48–56	53.3 ± 3.1 47–57	50.8 ± 5.3* 43–56

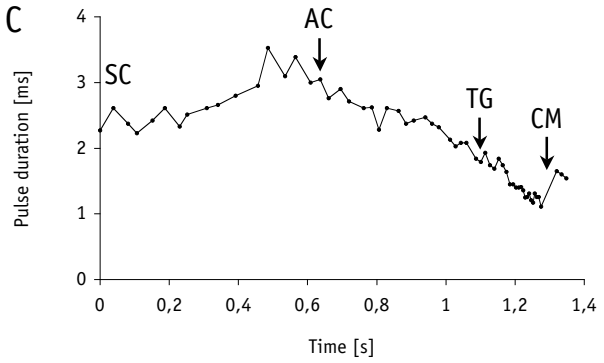
TABLE 1 continued.

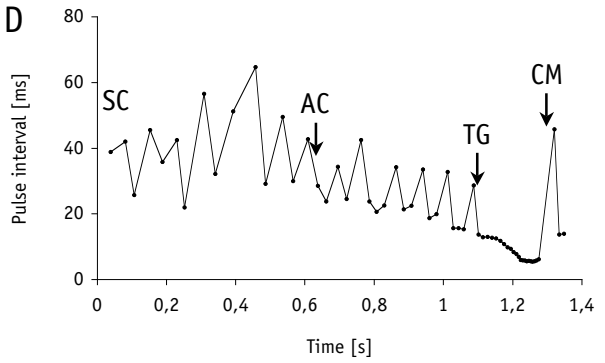
Parameter	Habitat	Search	Approach	Terminal group			
				F	M	S	L
Sweep rate [kHz/ms]	Water	9.4 ± 1.4 7.0–15	11.5 ± 0.8 9.5–13	12.9 ± 1.1 10–15	14.4 ± 1.2 11–17	14.9 ± 1.9 12–19	15.1 ± 2.2 11–24
	Air	9.6 ± 1.3 8.0–13	11.6 ± 0.8 11–13	13.0 ± 1.1 11–15	15.2 ± 1.1 13–17	15.4 ± 1.6 13–19	14.5 ± 1.5 12–17
	Field	8.0 ± 1.3 5.9–11	10.5 ± 0.9 9.2–12	11.9 ± 1.1 10–14	14.8 ± 1.6 12–18	17.3 ± 3.2 12–22	18.6 ± 4.1 12–24
Duty cycle [%]	Water	7.0 ± 1.2 4.8–11	11.9 ± 1.2 9.8–15	15.8 ± 2.2 13–24	18.8 ± 2.5 13–27	19.1 ± 3.0 15–28	
	Air	6.9 ± 1.2 5.2–9.7	12.3 ± 0.8 11–13	15.9 ± 1.5 13–19	19.1 ± 3.4 15–27	20.5 ± 3.8 16–28	
	Field	7.0 ± 1.8 5.3–11	15.3 ± 2.3 12–18	20.1 ± 2.8 16–23	19.5 ± 4.3 12–27	18.0 ± 3.2 12–23	

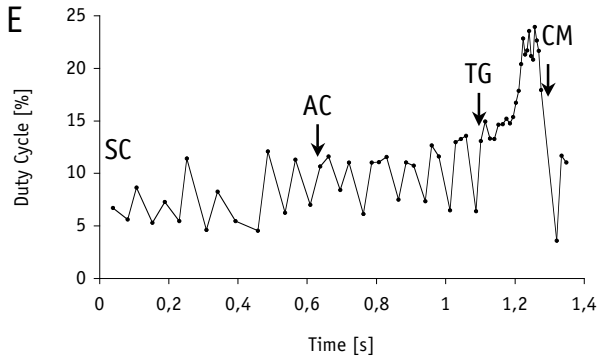
The moment of detection of tethered prey was only observed in two video sequences. In the remaining six video sequences, it occurred a few half-frames before the bat was visible. To calculate the detection distance in these cases, we used the characteristic changes in the echolocation sequences indicating a reaction to and therefore detection of prey (Chapter III), combined with the flight speed at which bats appeared in the video. Bats thus detected prey at distances of 0.99–1.96 m (1.48 ± 0.3 m, N = 8). During target-oriented approach flight at a speed of 2.38 ± 0.3 ms^{-1} (N = 8), bats clearly focused on the tethered prey with their head, nose leaf, and ears aimed at it. Similar to approach behavior towards floating prey, they emitted groups of three to seven approach calls with an inter-group interval of 36.1 ± 2.7 ms (N = 16). In comparison to search calls, approach calls were characterized by lower pulse intervals, slightly shorter pulse duration, approximately doubled repetition rate and duty cycle, and somewhat increased bandwidth and sweep rate (TAB 1, FIG 2).

When *M. macrophyllum* was 0.35–0.54 m (mean: 0.46 ± 0.07 m, N = 8) away from prey, it started to emit a terminal group of 23.3. ± 2.6 calls (16–33, N = 16) of a total duration of 203.6 ± 33.3 ms (range: 127–307 ms, N = 16). Flight speed was slightly reduced to 2.22 ± 0.3 ms^{-1} (N = 8). It emitted terminal group calls at a high repetition rate and characterized by short pulse duration, decreasing bandwidth, increasing duty cycle, and a relatively high sweep rate (TAB 1). After the first up to 10 terminal group calls, *M. macrophyllum* entered the echo-overlap zone 0.25–0.40 m (N = 8) in front of the prey, where calls began to overlap with echoes returning from prey (FIG 2).


A
1
14
Prey
B
kHz
150
100
50
0
SC
AC→
TG→
1
2
3
4
5
6
kHz
150
100
50
0
CM
100 ms
7
8
9
10
11
12
13
14


C
Pulse duration [ms]
SC
AC
TG
CM
Time [s]


D
Pulse interval [ms]
SC
AC
TG
CM
Time [s]


E
Duty Cycle [%]
SC
AC
TG
CM
Time [s]

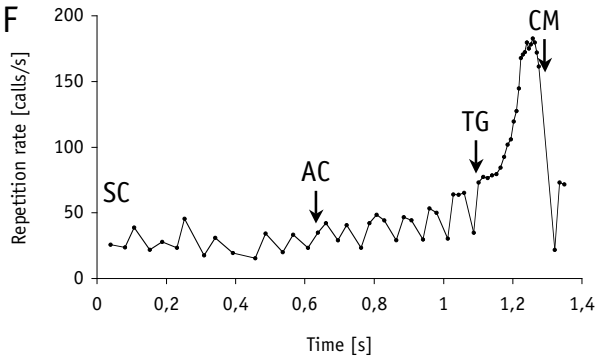

F
Repetition rate [calls/s]
SC
AC
TG
CM
Time [s]

FIGURE 2 (opposite side). Foraging behavior in 3-dimensional space synchronized with the corresponding echolocation sequence of *M. macrophyllum* while closing in on and capturing a mealworm suspended in the air above the water surface in the flight cage on BCI, Panamá. A) 14 images of the bat (temporal resolution: 80 ms). B) Sonogram of the echolocation calls with time signal above; numbers below correspond to images. Plots of call parameters of the same echolocation sequence including C) pulse duration, D) repetition rate, E) pulse interval, and F) duty cycle. Abbreviations: SC = search calls, AC = start of approach calls, TG = start of terminal group, CM = capture of mealworm.

Prior to capture, *M. macrophyllum* lowered its tail membrane, approximately perpendicular to its flight direction. It formed a pouch with its large tail membrane stabilized by its large feet, tail, and strong calcars. Head, nose leaf, and ears, were directed throughout the approach towards the prey. Echolocation stopped a few cm in front of the prey. As soon as the distal part of the tail membrane touched the suspended mealworm, the pouch was subsequently closed with the help of feet and calcars. Similar to removal of food from the water surface (Chapter III), feet and claws were not directly involved in the capture of suspended prey. The bat then wrapped the mealworm into its tail membrane and pressed it against its belly. At that time, head, ears, and nose leaf were moved back into the upright position and the bat resumed echolocation. After the bat had taken the food with its mouth by bending its head briefly towards the pouch, *M. macrophyllum* flew to a perch and ate it. Usually, as soon as the bat had finished its meal, it started for the next search flight. Grooming occurred only occasionally between foraging bouts and usually took place after the bats had successively consumed several (10–20) mealworms and rested for longer periods before they resumed foraging.

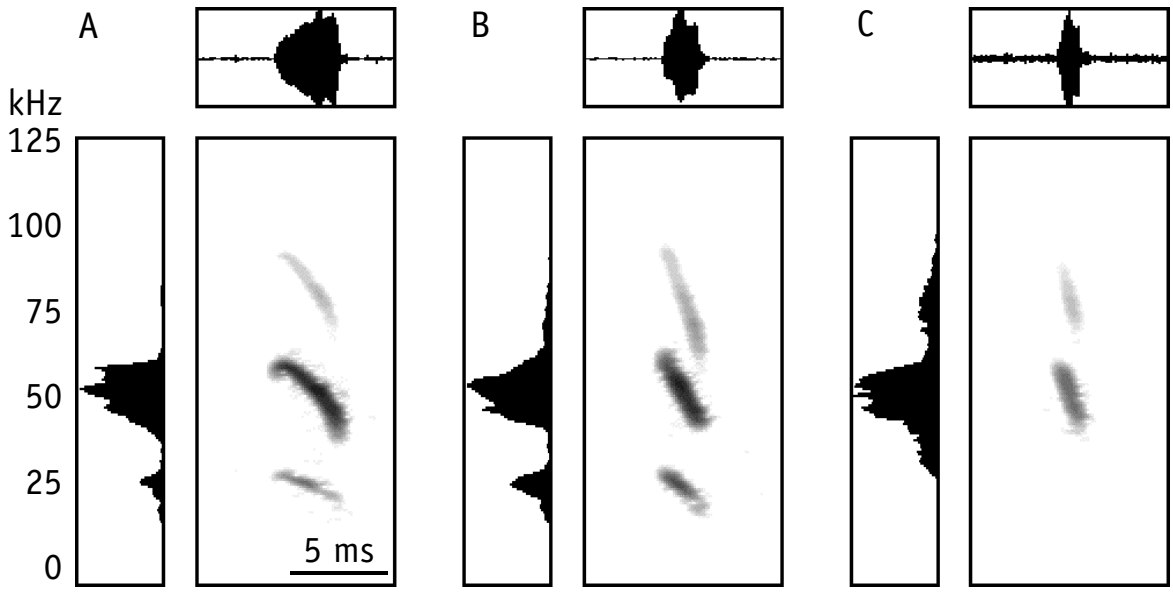


FIGURE 3.. Representative echolocation calls of *M. macrophyllum* foraging in the field above the water surface near the colony on BCI, Panamá. Sonogram representation with relative time signal above and relative power spectrum to the left. A) Search call; note the short shallow-modulated onset of the call; B) approach call; C) terminal group calls, emitted prior to capture of prey.

We compared echolocation parameters of experiments with suspended prey with those of our study with floating prey (Chapter III) and with data obtained from bats in the field. Call parameters did not vary significantly between flight cage experiments with prey suspended in the air and with prey placed onto the water surface (two-factorial Anova; Tukey post-hoc comparison: all $p > 0.06$; $df = 69$). However, we found several significant differences in call parameters between bats in the flight cage and in the field (two-factorial Anova; all $F_{(2,69)} < 15.5$; Tukey post-hoc comparison: all $p > 0.0001$; TAB 1). As a general pattern, pulse duration of search and approach calls was longer in the field than in the flight cage, while terminal group calls were shorter. Similarly, in the field, search calls had longer and approach and terminal group calls had shorter pulse intervals than in the flight cage. Peak frequency was always lower in calls of bats recorded in the field than of bats recorded in the flight cage, while bandwidth did not vary significantly (TAB 1). Finally, most search calls started with a short shallow-modulated component (FIG 3).

Foraging and echolocation behavior in the field.— Bats flew faster in the field (3.17 ± 0.3 ms^{-1}, $N = 6$) while searching for food than in the flight cage, whereas the distances of 0.85–2.33 m (1.37 ± 0.5 m, $N = 8$), at which they detected prey, was similar to captive bats capturing floating or tethered prey. After a pause of 46.32 ± 18.0 ms ($N = 8$), bats in the field began to emit groups of approach calls (FIG 3) with an inter-pulse interval of 34.95 ± 4.6 ms ($N = 7$) similar to bats in the flight cage. Flight speed remained at 3.09 ± 0.5 ms^{-1} ($N = 8$). At a distance of 0.32–0.61 cm ($N = 8$), similar to captive bats, *M. macrophyllum* in the field started to produce a distinct terminal group (FIG 3) with 19.2 ± 3.8 (range: 15–26, $N = 11$) calls and a duration of 153.6 ± 43.1 ms (99–245 ms, $N = 11$) after a short pause of 27.66 ± 3.8 ms ($N = 8$). Flight speed remained high (3.03 ± 0.5 ms^{-1}, $N = 8$). After up to 12 terminal group calls, *M. macrophyllum* entered the overlap zone at a distance of 21–37 cm to the mealworm with a pulse duration of 1.78 ± 0.3 ms ($N = 8$), where echoes returning from prey started to be masked by echolocation calls (forward masking; FIG 4). A few cm before bats reached the prey, echolocation stopped for a period of 41.41 ± 13.3 ms ($N = 8$), during which *M. macrophyllum* took the prey from the water surface. Subsequently, the bats resumed echolocation.

Effect of clutter on foraging and echolocation behavior.— We offered prey in the flight cage at different distances close to and above clutter-producing background composed of floating *H. verticillata* to assess the influence of backward masking on capture success (FIG 1). We found a distinct decrease in capture success the closer the prey was to the background. Live prey in the dark was equally well detected and removed by *M. macrophyllum* when placed at 20 cm (removal rate: 100%, $N = 28$) and 10 cm (97%, $N = 29$) in front of the water plants. However, capture success considerably dropped (23%, $N = 31$) when prey was offered at no distance (0 cm) to the clutter plot (FIG 1). Even when we offered prey under well-lit conditions with vision as an additional cue to the bats, capture success did not improve; in contrast, it was even lower (7%, 0 cm distance to clutter, $N = 28$) than in the dark. Similarly, *M. macrophyllum* detected prey

dummies made out of electrical shrink-wrap at no distance (0 cm) to clutter in the dark in only 11% of all cases (N = 28), while capture success increased with larger distances (10 cm: 82%, N = 28, 20 cm: 89%, N = 27). Finally, when prey was suspended 20 cm above the water surface in the air, bats had no difficulties in detecting it in front of (20 cm: 100%, N = 25; 0 cm: 100%, N = 24) or 20 cm over the *H. verticillata* plot (93%, N = 28).

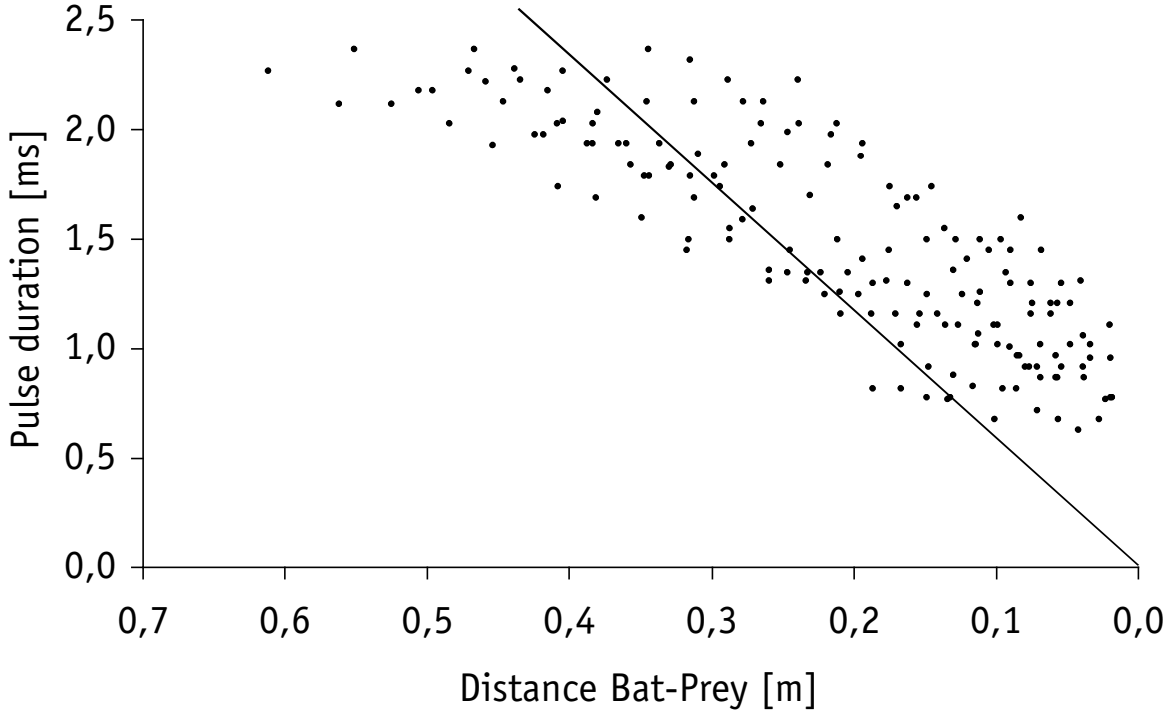


FIGURE 4. Decrease in pulse duration of terminal group calls from nine individuals of M. macrophyllum while closing in on potential food floating on the water surface of Gatún Lake near the shore of BCI, Panamá. The solid line indicates the limit beyond which calls overlap with returning echo from prey.

We then compared sound parameters of experiments where prey was placed onto the water surface at two distances to clutter-background (10 cm and 20 cm, respectively) to test for possible differences in echolocation behavior. We omitted the data from the experiment with prey offered at 0 cm distance to clutter for further comparison, as the bats generally emitted search calls only. Most call parameters did not vary significantly between the experiments where prey had been placed at different distances to clutter (two-factorial Anova; $F_{(1,8)} < 6.2$; $0.04 < p < 0.95$; TAB 2). Only bandwidth of terminal group calls with shortest pulse interval was slightly narrower (14.4 kHz versus 15.8 kHz) in experiments with prey closer to clutter ($F_{(1,8)} = 9.4$; $p = 0.02$), and pulse distance of search calls was longer (44.1 ms versus 39.0 ms) in experiments with prey at larger distance to clutter ($F_{(1,8)} = 10.1$; $p = 0.01$). However, as these differences are small and likely to be mainly an effect of small sample size (N = 9 bats), we pooled all data for further calculations (TAB 2).

TABLE 2. Seven echolocation parameters of nine *M. macrophyllum* foraging in the flight cage on BCI, Panamá. Presented data (mean ± SD; min–max) are based on measurements taken from 85 search calls, 234 approach calls, and 72 terminal group calls of bats trawling prey floating on the water surface near the clutter plot in two experiments. Abbreviations for terminal group: F = first call, M = numerically median call, S = call with shortest pulse interval, and L = last call.

Parameter	Search	Approach	Terminal group			
			F	M	S	L
Pulse duration [ms]	2.4 ± 0.3 1.9–2.8	2.1 ± 0.1 1.9–2.2	1.7 ± 0.1 1.6–1.9	1.4 ± 0.2 1.1–1.7	1.0 ± 0.1 0.8–1.3	0.9 ± 0.1 0.8–1.2
Pulse interval [ms]	41.6 ± 10.5 24–62	17.9 ± 1.5 15–21	11.0 ± 1.2 8.9–14	7.9 ± 1.6 6.2–11	5.9 ± 0.7 5.1–7.8	
Repetition rate [calls/s]	25.6 ± 6.8 16–42	56.3 ± 4.9 48–66	91.9 ± 9.6 74–113	130.7 ± 22.8 87–161	172.3 ± 18.0 129–195	
Bandwidth [kHz]	22.9 ± 3.1 17–29	25.4 ± 1.9 23–29	23.5 ± 2.8 18–28	19.6 ± 2.6 16–24	15.1 ± 2.2 11–20	13.6 ± 1.7 11–16
Peak frequency [kHz]	56.4 ± 2.2 53–60	55.4 ± 2.1 50–58	55.9 ± 2.7 52–62	54.8 ± 3.2 47–59	54.2 ± 2.8 49–59	53.2 ± 3.6 47–58
Sweep rate [kHz/ms]	9.7 ± 0.9 7.9–11	12.3 ± 1.1 10–14	13.5 ± 1.5 11–16	14.5 ± 1.7 12–18	15.3 ± 2.4 10–19	15.2 ± 2.0 12–19
Duty cycle [%]	6.4 ± 1.3 4.2–8.9	12.2 ± 1.2 9.8–14	16.0 ± 1.9 13–20	17.6 ± 3.0 13–24	17.2 ± 2.7 13–23	

Finally, we also calculated the overlap zone, where echoes returning from background masked prey echoes (backward masking). Taking a sound speed of 346.5 ms^{-1}, echoes of prey and clutter overlapped in all trials, in which prey was presented 10 cm or closer to the background. This was also the case in trials, where prey was 20 cm away from the water plants, as long as calls had a minimum pulse duration of 1.15 ms. Hence, when bats emitted search and approach calls echoes of prey and clutter overlapped, while at the end of terminal groups calls were short enough to avoid backward masking effects.

DISCUSSION

Flexibility of foraging behavior.— Our behavioral experiments revealed that foraging behavior of *M. macrophyllum* is highly flexible, comprising two modes, trawling prey from the water surface (Chapter III) and hawking tethered prey in the air above water. This behavioral flexibility parallels observations of a variety of trawling bats. The larger of two *Noctilio* species, which occur in the same habitat as *M. macrophyllum*, trawls prey from the water surface and occasionally performs aerial captures (*N. leporinus*: Kalko, pers. obs.), while the smaller *N. albiventris* frequently forages in trawling and aerial hawking mode (Kalko *et al.* 1998). With its large feet

and laterally compressed claws, *N. leporinus* is specialized to scoop fish and large insects from the water surface. In contrast, *N. albiventris* feeds on much smaller insects and may hence benefit more from behavioral flexibility than the larger species, which is probably constrained in its maneuverability due to its size. Another sympatric bat, the small proboscis bat, *Rhynchonycteris naso* (Emballonuridae), mainly feeds on aerial prey, but was also observed taking insects from the water surface (Kalko 1995; unpubl. data). Finally, various temperate *Myotis* species are known to trawl and to hawk insects in the air (e.g. Britton *et al.* 1997, Jones & Rayner 1988, 1991).

Considering the perceptual tasks, which have to be performed by bats for finding prey, foraging above water is rather similar to aerial hawking in edge-space, since the smooth water surface reflects most of the call energy away from a low-flying bat. Hence, in both habitats, bats forage in an environment with little or no clutter echoes (Boonman *et al.* 1998, Rydell *et al.* 1999, Siemers *et al.* 2001a). Consequently, similar constraints should lead to a similar echolocation behavior in both habitats, which we have shown for *M. macrophyllum* in accordance with studies on other trawling bats (e.g. Jones & Rayner 1988, 1991, Kalko *et al.* 1998, Kalko & Schnitzler 1989, Schnitzler *et al.* 1994). In contrast to trawling bats, species that glean prey from surfaces such as vegetation or ground and hawk flying insects have to perform different perceptual tasks. Consequently, they should modify their echolocation behavior according to acoustical constraints imposed by the respective foraging situation. In fact, several mouse-eared bats, *Myotis* sp. (Vespertilionidae), emit shorter steep FM search calls at a higher repetition rate and increased bandwidth mainly to avoid echo masking and increase fine-grained resolution of prey objects close to clutter when gleaning compared to aerial hawking (Faure & Barclay 1994, Ratcliffe & Dawson 2003, Siemers *et al.* 2001b). Other vespertilionids approaching prey supposedly cease echolocation during gleaning and rely on different sensory cues than during aerial hawking, although in this case, technical problems in the recording situation such as reduced sensitivity of the microphone to pick up the faint, high-frequency calls of bats approaching food cannot be ruled out as an explanation (Anderson & Racey 1991, 1993).

With regard to optimization of habitat exploitation, flexibility in foraging behavior is likely to grant *M. macrophyllum* access to a potentially wider range of prey, including insects sitting on the water surface or flying just above water. This applies in particular to an abundant moth, *Parapoynx diminutalis* (Pyralidae), introduced to the Gatún Lake, where its larvae develop in *H. verticillata* plants and imagoes emerge in large numbers within the foraging areas of *M. macrophyllum*. Scales of this moth were frequently found in the feces of *M. macrophyllum* (Chapter I, II) indicating that it forms an important prey item. Similarly, in addition to prey sitting on the water surface and trawled by *M. macrophyllum*, aerial insects, such as Lepidoptera and Diptera, form important components of its diet (Harrison 1975). This efficient exploitation of particular resources in combination with flexibility in foraging behavior is in accordance with studies on other insectivorous bat species (e.g. Arlettaz 1996, Chruszcz & Barclay 2003).

Capture behavior.— In all experiments, *M. macrophyllum* exclusively used the distal part of its tail membrane to remove prey from the water surface (Chapter III) or to hawk it in mid-air, while feet and claws were not directly involved in prey capture. It was further proposed that the dermal denticles on the ventral side of the tail membrane might facilitate lifting the prey from the water surface (Chapter III). This intricate morphological and behavioral mechanism differs from all other trawling bats studied so far. Trawling *Noctilio* sp. and the temperate *M. daubentonii* scoop prey from the water surface with their feet and claws, while during aerial hawking, *N. albiventris* and *M. daubentonii* use their tail membrane and occasionally their wings to funnel prey into the tail pouch (Kalko & Schnitzler 1989, Kalko *et al.* 1998, Schnitzler *et al.* 1994). Similar to *M. macrophyllum*, *M. daubentonii* may occasionally involve the tail membrane in scooping prey from the water surface (Jones & Rayner 1988). This behavioral variety likely reflects the multiple independent evolution of trawling in bats of several families.

Effect of clutter on echolocation and foraging behavior.— With decreasing distance of prey in relation to clutter, and hence increasing backward masking effects, detection performance of *M. macrophyllum* declined. As long as prey echoes were only slightly masked by clutter echoes, bats were able to find mealworms, while prey, which was completely buried within clutter, could not be perceived. This perceptual difficulty was reflected in the echolocation behavior of *M. macrophyllum*, which did not switch to approach and terminal group calls, when prey was located at no distance to the clutter plot. Our findings are in accordance with results of *M. daubentonii* that continued foraging when the amount of duckweed covering the surface of a pond was rather low. However, when the covering of the water surface reached higher levels, the bats ceased foraging in low flight and foraged higher (Boonman *et al.* 1998). This flexible foraging behavior allows them to avoid unfavorable conditions, such as duckweed cover, and instead exploit the space above water surfaces.

Besides changes in foraging behavior to avoid masking, effects of clutter on prey detection may also be reduced by changes in echolocation design. For instance, pipistrelle bats change from longer and shallow-modulated search calls emitted when flying in open-space to shorter calls with a pronounced steep initial FM component in narrow-space to increase resolution of prey objects close to clutter, and thus to enhance their ability to detect prey, which would otherwise be buried within clutter (Kalko & Schnitzler 1993). This tight link between bandwidth and clutter tolerance has been studied in five species of *Myotis* (Siemers & Schnitzler 2004). Species, such as *M. nattereri*, with steep FM search calls and a high bandwidth of 120 kHz, had no difficulty (capture rate: 100%) in finding prey presented at a distance of 5 cm relative to clutter. In contrast, *M. dasycneme* or *M. daubentonii*, which emit calls of lower bandwidth (44 kHz and 57 kHz, respectively), caught 100% of the offered prey only at 25 cm distance to clutter (Siemers & Schnitzler 2004). Our results show that *M. macrophyllum* fits well into this scenario, as it was able to find most (capture rate: 97%) prey at a distance of 10 cm relative to clutter, emitting search calls with an intermediate bandwidth of approximately 70 kHz (Chapter

III). However, while the *Myotis* sp. reach very high bandwidths by locating call energy mainly in the first harmonic, *M. macrophyllum* emits calls of three and occasionally up to four harmonics (Chapter III). Whereas the highest call energy is always located in the second harmonic in *M. macrophyllum*, the high bandwidth over three harmonics may increase its ability to detect prey close to clutter.

Foraging flexibility in *M. macrophyllum* may also be seen in an evolutionary context. In a postulated evolutionary scenario, extant bats are descended from an echolocating aerial hawking insectivore. However, some groups, like phyllostomid bats, may have returned to gleaning mode within vegetation (Schnitzler *et al.* 2003b, Simmons & Geisler 1998). In this transition, they had readapted the presumably phylogenetically older passive prey detection mode using visual and passive acoustic cues and in some species also olfaction (Schnitzler *et al.* 2003b). Consequently, most extant leaf-nosed bats use echolocation primarily for spatial orientation and not for finding food. In general, narrow-space habitats hamper the use of echolocation for finding prey close to surfaces, as clutter echoes from the vegetation mask faint echoes of potential prey (e.g. Arlettaz *et al.* 2001a, Jones *et al.* 2003, Rydell *et al.* 1999, Schnitzler & Kalko 1998, 2001). Only under certain circumstances and depending on the presentation of food, some phyllostomid bats are known to use echolocation for finding prey (e.g. Kalko & Condon 1998, Thies *et al.* 1998, von Helversen & von Helversen 1999). However, *M. macrophyllum* differs from all phyllostomid bats studied so far by its high intensity calls and the use of a terminal group and thus, its echolocation behavior is more similar to that of aerial and other trawling bats, likely as an adaptation to the acoustic properties of edge space habitat above water. Based on new molecular data, *M. macrophyllum* is placed near highly derived phyllostomid genera (*Lonchorhina*, *Macrotus*, *Mimon*, *Trachops*; Freeman 2000, Lee *et al.* 2002, Wetterer *et al.* 2000) that all show the typical echolocation behavior of phyllostomids gleaning food within cluttered habitats without distinct terminal groups, primarily using senses other than echolocation. This supports the assumption that the use of echolocation in *M. macrophyllum* for finding prey has evolved in response to the ecological conditions rather than representing a primitive form of the Phyllostomidae.

To conclude, in behavioral experiments, we showed that long-legged bats, *M. macrophyllum*, are able to hawk prey suspended in the air in addition to trawling insects from the water surface (Chapter III). In accordance with other trawling bats, this foraging flexibility enables them to exploit the insect-rich habitat on and above water surfaces. The steep multi-harmonic FM calls of *M. macrophyllum* further allow this species to detect prey at close distances to clutter, which permits this species to exploit abundant insects, such as *P. diminutalis*, sitting on or flying close to clutter-producing *H. verticillata* (Chapter II).

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Appendix
Color Plates





Top: Portrait of *M. macrophyllum* at BCI, Panamá, showing the large noseleaf
Bottom: Dorsal view of tail memebrane of *M. macrophyllum* with long calcars, large feet and powerful claws





Top: Individual *M. macrophyllum* carrying a small radio transmitter with reflecting tape
Bottom: Dayroost of the colony inside the half-sunken ship "Barracuda"; the second individual to the left carries a transmitter with reflecting tape



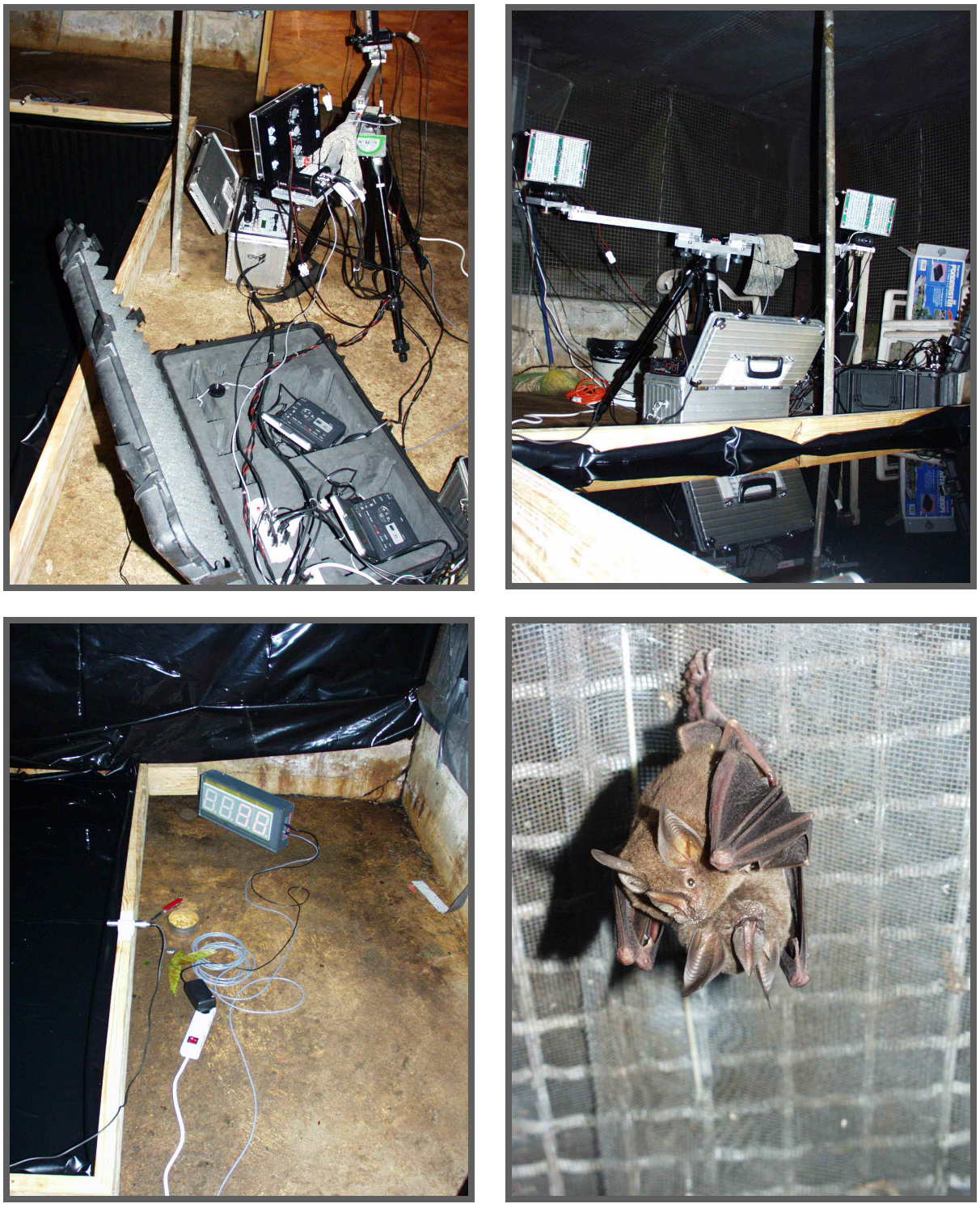


Top: Stranded, half-sunken ship on the shore of BCI in which the colony of *M. macrophyllum* lives
Bottom: Detail of the ship's bow





Top: Typical foraging habitat of *M. macrophyllum* at BCI with small coves along the shoreline
Bottom: Washed-out cave at the shore of BCI with overhanging vegetation where *M. macrophyllum* usually roost during their nocturnal foraging flights



Top left: Set-up in the flight cage on BCI with 3-dimensional video and synchronized audio recording system. In the forground the two video recorders; fixed on the tripod: the two cameras with IR-flash units on top, and to the left the synchronized audio recording device (Delayline) inside the aluminum case
Top right: Front-view of the set-up in the flight cage on BCI, with the Delayline case in the foreground; fixed on the tripod is the 3-dimensional video recording system with cameras and IR-flash units on top
Bottom left: Digital counter synchronized with video and audio recording system, used in all experiments to identify video sequences
Bottom right: Two individual *M. macrophyllum* hanging on the ceiling of the flight cage during pre-study

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ERKLÄRUNG

Hiermit erkläre ich, die vorliegende Dissertationsarbeit selbständig angefertigt und keine anderen als die in der Arbeit aufgeführten Hilfsmittel verwandt zu haben. Wörtlich oder inhaltlich übernommene Stellen wurden als solche gekennzeichnet.

Ulm, den 17. März 2005