Geophagy of tropical fruit-eating bats – mineral licks as a link between ecology and conservation

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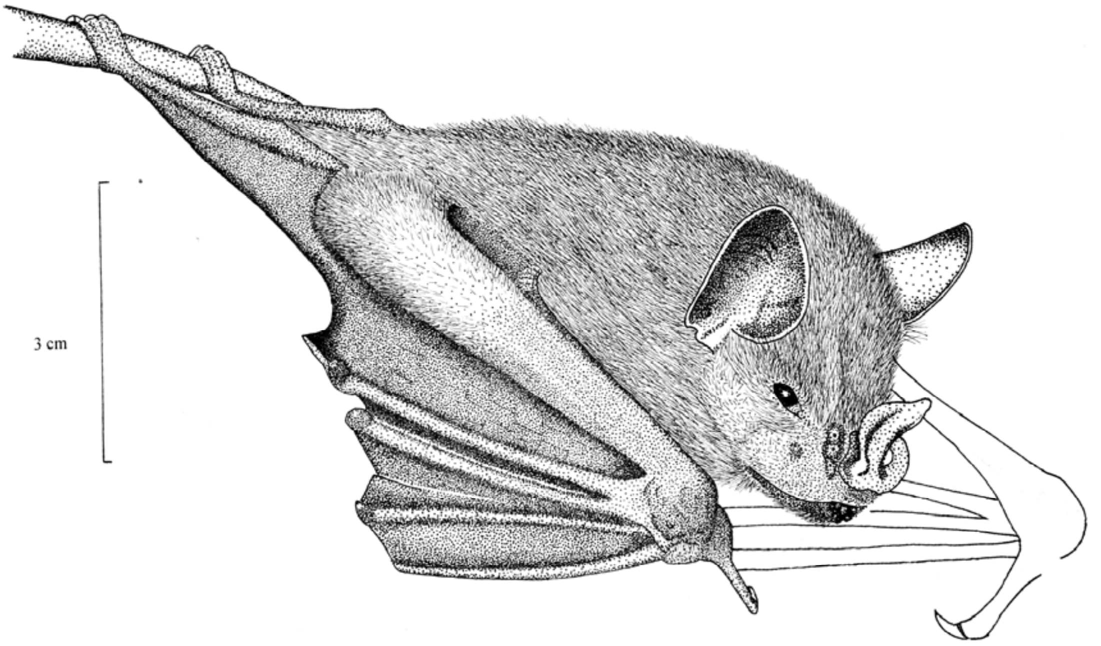

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1. Ghanem[a,d], S.J., Ruppert[b], H., Kunz[c], T.H., and C.C. Voigt[a,d]. (in revision). **Frugivorous bats drink nutrient and clay-enriched water in the Amazon rainforest: Support for a dual function of mineral lick visitations.**

2. Ghanem[a,d], S.J., and C.C. Voigt[a,d]. (in revision). **Defaunation of tropical forests reduces habitat quality for seed-dispersing bats in Western Amazonia: an unexpected connection via mineral licks.**

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Zusammenfassung

Geophagie (die Aufnahme von Bodenmaterial oder bodenhaltigem Wasser) ist ein bei Vögeln und Säugetieren häufig auftretendes Phänomen. Dennoch sind die zugrunde liegenden Beweggründe für dieses Verhalten oft nicht ausreichend geklärt. In den Neotropen fungieren Minerallleckstellen, an denen Geophagie vorkommt, als ökologische Schlüsselressource für viele frugi- und omnivore Tiere, wie zum Beispiel die Fledermäuse. Ziel dieser Dissertation war es, einen Einblick in die Geophagie fruchtfressender Fledermäuse und in die Verbindung zwischen Minerallleckstellen und Ökosystemfunktionen zu gewinnen. Die Rolle von Fledermäusen für Ökosystemfunktionen wird für gewöhnlich, sehr wahrscheinlich aufgrund ihrer nächtlichen und kryptischen Lebensweise, weit unterschätzt.

In **Kapitel II** wurde Geophagie bei Fledermäusen auf ihre Funktion hin untersucht. Die Ergebnisse dieser Arbeit zeigen, dass in der Yasuni Biosphäre in Ecuador vor allem fruchtfressende Fledermausweiblichen während der Laktation oder Trächtigkeit bodenhaltiges Wasser an Minerallleckstellen aus zumindest zwei Gründen trinken. Einerseits ergänzen fruchtfressende Fledermäuse ihre nährstoffarme Fruchtnahrung durch das Trinken von mineralreichem Wasser, andererseits können durch die Aufnahme suspendierter Bodenpartikel schädliche Sekundärmetabolite in der Fruchtnahrung abgepuffert werden. Durch ICP-MS und ICP-OES Analysen wurde aufzeigt, dass Fledermäuse Nährstoffe durch das Trinken von Wasser an den Minerallleckstellen aufnehmen. Blutproben solcher Minerallleckstellen besuchender Fledermäuse zeigten gegenüber Blutproben von Fledermäusen, die an anderen Orten gefangen wurden, eine veränderte Nährstoffzusammensetzung (Na, K, Mg, Fe). Zusätzlich wurden anhand von Kotuntersuchungen bei fruchtfressenden Fledermäusen höhere Konzentrationen von nicht-pflanzenverfügbaren Bodenelementen (Al, Ti, Y, Ce, La, Nd) nachgewiesen, als sie im Kot von nicht Lecken besuchenden insektivoren Fledermäusen vorhanden waren. So liefern diese Ergebnisse deutliche Hinweise darauf, dass Fledermäuse sowohl Nährstoffe, als auch Bodenmaterial, durch das Trinken von angereichertem Wasser an den Minerallleckstellen aufnehmen.

Minerallleckstellen nehmen eine wichtige ökologische Funktion für fruchtfressende Fledermäuse im westlichen Amazonasgebiet ein. Daher widmet sich diese Arbeit auch der Bedeutung von Minerallleckstellen für die Aufrechterhaltung von funktionierenden Ökosystemen und Habitaten. Im östlichen Ecuador haben sowohl

Ölabbaufirmen als auch indigene Gemeinden einen substanziellen negativen Einfluss auf größere Säugetiere, die wiederum eine wichtige Rolle für die Erhaltung der Mineralleckstellen spielen. Diese bilden sich im Laufe der Zeit zurück, wenn sie nicht mehr von größeren Säugetieren besucht werden.

In **Kapitel III** wurde aufzeigt, dass sich die Jagd im Amazonasgebiet nicht nur direkt auf die gejagten größeren Tiere auswirkt, sondern auch indirekt auf Fledermausgemeinschaften und ihre reproduktiven Tiere, die durch fehlende Großsäuger schlechteren Zugang zu nährstoffangereichertem Mineralleckenwasser haben. Daher werden Ökosystemdienstleistungen von Säugetieren durch das Jagen zweifach aufs Spiel gesetzt: Zum einen durch das Ausmerzen von samenausbreitenden größeren Säugetieren und darüber hinaus durch die Verschlechterung der Habitatqualität für samenausbreitende Fledermauspopulationen.

Obwohl Fledermäuse das zweitgrößte Säugetiertaxon bilden, wird ihr ökonomischer Wert und ihre Bedeutung für funktionierende Ökosysteme weit unterschätzt (**Kapitel IV**). Der Grund hierfür liegt auch an der kryptischen Lebensweise von Fledermäusen und ihr meist schlechter Ruf als potentieller Krankheits-vektor. Dieses Kapitel diskutiert die aus der bestehenden Literatur zusammengefassten Belege für die ökologische Schlüsselrolle von Fledermäusen, die sie durch das Ausbreiten von Samen, das Bestäuben von Blüten und das Fressen von Insekten einnehmen. Durch dieses Verhalten fördern Fledermäuse weltweit die Regeneration des Waldes, das Initiieren des Fruchtansatzes und die Kontrolle von Schadinsekten. Aktuelle Bedrohungen, wie die Ausbreitungen des Weißnasensyndroms in Nordamerika, oder der Verlust von nutzbaren Habitaten, bedrohen Fledermäuse und ihre Ökosystemdienstleistungen.

Mineralleckstellen sind eine Schlüsselressource für viele fruchtfressende Ökosystemdienstleister, insbesondere für Fledermäuse. Daher spielt der Schutz von Mineralleckstellen eine herausragende Rolle für die Regeneration und Erhaltung von Wäldern im westlichen Amazonasgebiet. Der zumeist negative Einfluss des Menschen auf Biodiversität und auf Ökosysteme im Generellen, verleiht der ökologischen Grundlagenforschung eine wichtige Bedeutung. Laufende sowie zukünftige Naturschutz-programme können durch das Identifizieren von Schlüsselakteuren in Ökosystemen profitieren, indem sie durch fundierte wissenschaftliche Informationen besser geplant und koordiniert werden. Die Bereitstellung dieser Information ist für das Bekräftigen der Bedeutsamkeit von Biodiversität und den Dienstleistungen der Natur für das globale Ökosystem essentiell.

Summary

Geophagy is a common phenomenon among many birds and mammals but the underlying causes for the uptake of clay or clay-enriched water is not yet fully understood. However, mineral licks in the Neotropics, where geophagy takes place, function as a key ecological resource for many frugivorous and omnivorous animals, such as bats. The aim of this thesis was to gain insight on geophagy by fruit-eating bats and the link between mineral licks and ecosystem functioning. The role of bats for functioning ecosystems is oftentimes undervalued, most likely due to their nocturnal and cryptic lifestyle.

I investigated the function of geophagy for bats in **Chapter II**. The results of this thesis show that pregnant and lactating fruit-eating bats in the Yasuni Biosphere of Ecuador frequently visit mineral licks for at least two reasons. Frugivorous bats supplement their mineral-depleted fruit diet by drinking nutrient-rich water, and they possibly buffer dietary secondary plant compounds by the consumption of soil. With the use of ICP-MS and ICP-OES analyses, I was able to demonstrate that bats ingest minerals by drinking nutrient-rich water at mineral licks by showing that blood sampled from bats captured at mineral licks differed in mineral composition (Na, K, Mg, Fe) from those captured at other sites. Moreover, I examined elemental tracers for soil consumption (Al, Ti, Y, Ce, La, Nd) in faeces that are insoluble in water and thus not part of their fruit diet. The concentration of soil tracers were higher in droppings of bats captured at mineral licks than in droppings of bat species never recorded at mineral licks. These findings provide evidence that frugivorous bats ingest both nutrients and clay by drinking clay-enriched water at mineral licks, thus supporting the hypothesis that the visitation of mineral licks by frugivorous bats has a dual function in the Amazon rainforest.

Since mineral licks are ecologically relevant for frugivorous bats in Western Amazonia, this study draws attention to the important role of mineral licks in habitat conservation and ecosystem functioning. In eastern Ecuador, both oil extraction companies and indigenous communities have a substantial negative impact on larger mammals that are essential for mineral lick maintenance. Mineral licks deteriorate over time if not kept open by visitations by larger herbivorous mammals. In **Chapter III,** I could demonstrate that defaunation of Amazonian forests affects not only large mammals directly, but also most likely affects frugivorous bat assemblages indirectly because reproductive female bats have less access to the nutrient-enriched water of mineral licks. Thus, hunting puts the ecosystem services of mammals at risk in two ways: by

eliminating seed-dispersing large mammals, and by reducing habitat quality for populations of seed-dispersing bats.

Even though bats comprise the second largest mammal taxon, their economic value and their relevance for ecosystem functioning have been largely underestimated (**Chapter IV**). This is probably due to the cryptic lifestyle of bats and their negative reputation as potential vectors for diseases. Here, I reviewed the available literature for evidence of how bats are ecological key players. By dispersing seeds, pollinating flowers and feeding on insects, bats promote forest regeneration, initiate fruit set, and control pest insects worldwide. Recent threats, such the spread of white nose syndrome in North America or habitat loss, have put bats together with their ecosystem services at risk.

Since mineral licks and their visiting, frugivorous ecosystem service providers are central for forest regeneration and maintenance, their conservation should be considered a major goal for Western Amazonia. Human activity negatively affects biodiversity and ecosystems in various ways. Thus, fundamental research in ecology, as carried out in this thesis, will help to plan and to coordinate on-going and future conservation efforts by identifying keystone ecosystem players. Because bats provide ecosystem services worldwide, and not only in Western Amazonia, the provisioning of scientifically sound information is crucial to maintain and increase awareness of the importance of biodiversity and the services nature can provide for the global ecosystem.

Chapter I

General Introduction

Biodiversity and the value of nature

Today, the human need for growth and development is shaped by patterns of production and consumption. These patterns lead to the depletion of resources, which ultimately results in the devastation of environments with a massive loss of species (The Earth Charter). Commencing with the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992, many efforts have been undertaken in the recent decades to link economic development with environmental sustainability. Since then, researchers and lobbyists are increasingly working on guidelines for policy and decision-makers to highlight the value of nature and biodiversity for mankind. The overall aims are to use biological resources sustainably and to prevent a long-term decline of the variety of life on earth. In 2005, the Millennium Ecosystem Assessment made a first attempt to link the economy to the value of the environment by introducing the concept of ecosystem services, or benefits to people resulting from resources and processes supplied by natural ecosystems (Millennium Ecosystem Assessment 2005). The use of monetary values for ecosystem services may now help to express financial damage created as a result of unsustainable development. In order to underline the importance of functioning ecosystems and biodiversity for the human well-being, the United Nations declared the year 2010 to be the International Year of Biodiversity. In the same year, Margot Bass and her colleagues (2010) reported Ecuador’s Yasuni National Park (YNP) to be located in one of the world’s last high-biodiversity areas and highlighted its global conservation significance.

A study site with conflicts - a hotspot for biodiversity and resource extraction

The Yasuni Biosphere Reserve (YBR) is covered by tropical lowland rainforest and located in the Ecuadorian Amazon. This area in the east of the Andes is globally exceptional for its outstanding biological richness on landscape and local scale, across taxonomic groups (Finer *et al.* 2008, Bass *et al.* 2010). It is ranked as one of the most biodiverse spots globally, showing a very high diversity for vascular plants, amphibians, reptiles, birds, and mammals with an estimate of more than 100 species of bats alone (Figure 1.1).

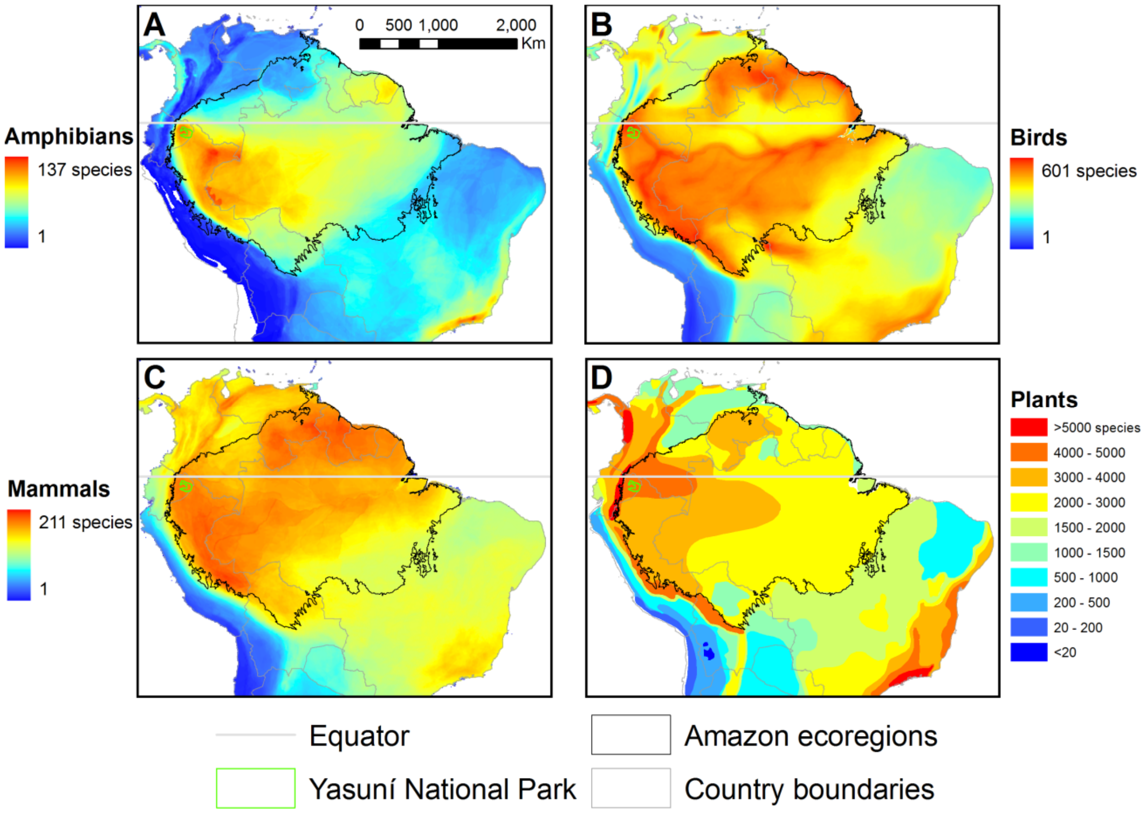

Figure 1.1: Species richness in the Amazon ecoregion for A) amphibians, B) birds, C) mammals, and D) vascular plants. Copyright by Bass *et al.* (2010) published under CC-BY 2.5.

Despite its exceptional biodiversity, the discovery of natural resources in that area has attracted the attention of extraction companies since the 1940s (Finer *et al.* 2009). Throughout decades this caused many conflicts between native people and oil companies or illegal loggers down. In 1979, the Ecuadorian government created the YNP (Finer *et al.* 2009), but in the meantime, the development of oil extraction infrastructure significantly disturbed the area. Starting in the early 1980s, the US American oil company Texaco built the Auca road approximately 120 kilometres into the YNP, attracting many settlers to colonize along the road. Later in the early 1990s, the Texan oil and gas company Maxus Energy built a gated dirt road, now known as the Maxus road, by cutting a 140 kilometres line into YNP and the Waorani Ethnic Reserve (Finer *et al.* 2009). To counterbalance these activities the Ecuadorian government extended the YNP in 1992; present day, it is with 9820 km² (Albacete *et al.* 2004) not only the largest but also the only Amazonian national park of Ecuador (Finer *et al.* 2009). But the YNP is not only a biodiversity hotspot it harbours also the country’s second largest untapped oil reserve, composed of the Ishpingo, Tambococha, and Tiputini oil fields (ITT block, Figure 1.2). The establishment of oil blocks and their associated infrastructure further boosts the speed of colonization, forest fragmentation, and deforestation. In 2007, Ecuadorian President Rafael Correa introduced a conservation effort, called the Yasuni-ITT initiative (Yasuni-ITT Trust Fund). The idea of this initiative was to seek financial compensation for leaving the oil untouched in the ground. The first step to collect US$ 100 million by the end of 2011 has been achieved, but a positive outcome of the initiative is an open question.

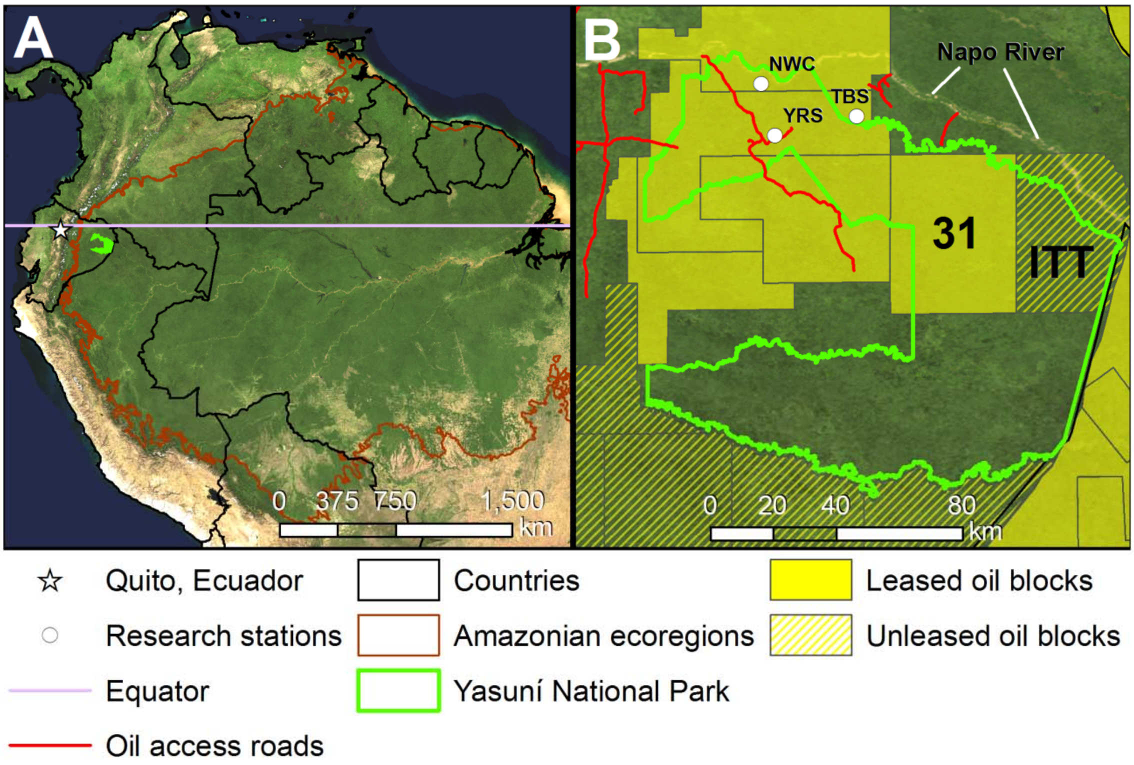

Figure 1.2: Ecuador’s Yasuni National Park and study site. A) Location of Yasuni National Park at the crossroads of the Amazon, Andes, and the Equator. B) Oil blocks and oil access roads within and surrounding the park. ITT = Ishpingo-Tambococha-Tiputini oil fields, NWC = Napo Wildlife Center, TBS = Tiputini Biodiversity Station, YRS = Yasuni Research Station. The image background is the Blue Marble mosaic of MODIS satellite images. Copyright by Bass et al. (2010) published under CC-BY 2.5.

Mineral licks and geophagy

The entire area within the YBR possesses numerous mineral licks (e.g. Blake *et al.* 2011; pers. observation). Mainly two types of mineral licks can be found in Ecuador: 1) steep river banks that are usually visited by birds (typically of the family Psittacidae such as macaws, parrots and parakeets) to directly ingest clay at the walls of the licks (Figure 1.3; Brightsmith & Muñoz-Najar 2004) and 2) muddy depressions where mostly terrestrial animals visit the licks to consume either clay or clay-enriched water (Figure 1.4; Montenegro 2004, Blake *et al.* 2011; pers. observation). Geophagy, the deliberate consumption of soil, is a commonly observed behaviour that is described for a large variety of frugivorous and omnivorous animals and, in some regions of the world, even for humans (Diamond 1999). The YBR harbours numerous animals of which a large number depend on mineral licks as a natural resource on a regular basis (Blake *et al.* 2011). Many hypotheses have been suggested to answer why animals visit these mineral licks. The two most common hypotheses are first mineral supplementation (e.g. Emmons & Stark 1979, Kreulen 1985, Brightsmith & Muñoz-Najar 2004, Brightsmith *et al.* 2008) and second detoxification of dietary toxins (Diamond 1999, Gilardi *et al.* 1999, Brightsmith *et al.* 2008).

Figure 1.3: Steep river banks function as mineral licks for birds of the family Psittacidae in Western Amazonia. A) Blue-and-yellow Macaws (*Ara ararauna*), Scarlet Macaws (*Ara macao*), Mealy Amazons (*Amazona farinose*), and Chestnut-fronted Macaws (*Ara severa*) at a mineral lick in Peru. Copyright by Brian Ralphs, published under CC-BY 2.0. B) Chestnut-fronted Macaws (*Ara severa*) Yellow-crowned Amazons (*Amazona ochrocephala*) and Dusky-headed Conures (*Aratinga weddellii*) at a mineral lick in Ecuador. Copyright by Hjalmar Gislason, published under CC-BY 2.0

However, others have additionally suggested antidiarrheal effects (Mahaney *et al.* 1995), or the use of soil as grit (Gionfriddo & Best 1995) or antacid (Davies & Baillie 1988).

In addition to many terrestrial animals frugivorous bats have also been documented to visit mineral licks in high numbers (Tuttle 1974, Voigt *et al.* 2007, 2008, Bravo *et al.* 2008, 2010), suggesting the function for the geophagy to be related to their fruit diet. The bats captured at the mineral licks are mainly from two subfamilies of the Phyllostomidae, namely Stenodermatinae and Carollinae. Interestingly, most of the bats captured at the mineral licks are female, with the majority of them being reproductively active (Tuttle 1974, Voigt *et al.* 2007, Bravo *et al.* 2008, 2010, pers. observation). While, no final conclusion for the bats' drinking behaviour could be drawn yet, a common agreement links this behaviour either to the mineral supplementation of a mineral-deficient diet (Voigt *et al.* 2007, Bravo *et al.* 2008, 2010) or to the detoxification of detrimental secondary plant metabolites of their fruit diet (Voigt *et al.* 2008).

Figure 1.4: A) Mineral lick in the forest interior in the Yasuni National Park, Ecuador. These muddy depressions are mostly visited by terrestrial mammals, such as the red brocket deer (*Mazama Americana*), the collared peccary (*Tayassu tajacu*), or the lowland tapir (*Tapirus terrestris*). B) Frugivorous bats, mostly of the subfamilies Stenodermatinae (left image: *Mesophylla macconelli*) and Carollinae (right image: *Carollia perspicillata*) visit these mineral licks in high numbers.

Bats and reproduction

Bat geophagy is thought to be important for reproductively active animals, because many of the bats visiting the mineral licks for soil or water consumption are females (Tuttle 1974, Voigt *et al.* 2007, 2008, Bravo *et al.* 2008, pers. observation). In general, the nutritional requirements of mammals are elevated in pregnant and lactating females because of the additional energy, organic nutrient and mineral demands of the growing foetuses and suckling young (Gittleman & Thompson 1988). Thus, most female mammals will consume additional food during reproduction (Cripps & Williams 1975). If food availability is restricted, however, females may reduce their daily nutritional demands by changes in physiology, behaviour or morphology. For example, some rodents and bats are less active during late pregnancy and lactation, probably as a means to reduce their energy requirements (*Mus musculus*: Speakman *et al.* 2001, *Glossophaga soricina*: Voigt 2000). In many lactating females, organs and tissues (e.g. the mammary glands, the liver (Kennedy *et al.* 1958), or the digestive tract) increase in size (Cripps & Williams 1975). Other mammals, such as the cotton rat *Sigmodon hispidus*, stores organic nutrients and minerals before pregnancy or lactation for later use during lactation (Randolph *et al.* 1977, Dominey 1984, Racey & Speakman 1987, Vernon & Pond 1997). However, storing nutrients or increasing organ size is not efficient for volant mammals such as bats because of the high energetic costs of powered flight (Speakman & Thomas 2003) and the increase of flight costs with increased wing loading (Voigt 2000). Compared to other mammals, female bats have particularly high nutrient requirements during reproduction even though they produce only a single young per year (Read & Harvey 1989, Jones *et al.* 2003, Kunz *et al.* 2009, Hood *et al.* 2011). The underlying reason for this is that female bats build up almost the entire juvenile skeleton via secreted milk, because juvenile bats cannot be weaned before they can fly which requires them to be almost adult size (Kunz 1987, Studier & Kunz 1995, Korine *et al.* 2004). Moreover, most female bats do not cease to nurse their young once they have fledged (e.g. Kunz 1973, Hoying *et al.* 1998, Koehler 1991, Kunz *et al.* 2009). In addition, many bat species feed on a low calcium diet (e.g. insectivorous *Eptesicus fuscus*: Keeler & Studier 1992) and thus lactating bats must mobilize calcium and other elements from their skeleton to meet the nutritional requirements of juvenile growth (Bernard & Davison 1996, Hood *et al.* 2006, Booher 2007). Hence, bones of the forearm in lactating bats become fragile and may even break under excessive mechanical stress (e.g. Swartz *et al.* 1992, Barclay 1994). In response to this nutritional constraint, female bats have evolved various traits to cope with the increased demands of reproduction. Some species for example forage for longer periods at night (*Eptesicus nilsonii*: Rydell 1993), which may yield a higher food intake (*Myotis lucifugus*: Kurta *et al.* 1989) but at the same time increase their risk of predation (Speakman 1991).

Aims of the study

In Western Amazonia mineral licks and their frugivorous visitors are pivotal for forest regeneration and maintenance. In spite of the possibly paramount importance of mineral licks the reasons behind the animals' visiting behaviour are still poorly understood. Frugivorous bats can be used as model organism for a better understanding of the importance of mineral licks for wildlife species and thus the ecosystem services they provide.

The three main aims of this dissertation were:

1) **To highlight the role of mineral licks as key ecological resources for frugivorous bat assemblages.**

   I studied the consumption of soil enriched water, geophagy, by frugivorous Neotropical bats and how these bats may benefit from their mineral lick visiting behaviour (**Chapter II**).

2) **To shed light on the linkage of mineral licks to ecosystem functioning and to the services provided by animals that depend on these licks.**

   Due to the essential role that mineral licks play in frugivorous bat assemblages of Western Amazonian forest ecosystems, I investigated how mineral licks can be negatively affected through disturbance caused by human activity in form of hunting or infrastructure development (**Chapter III**).

3) **To highlight the global importance of bats for ecosystem functioning and human well-being.**

   The conservation of tropical forest systems is only one of many topics that have gained attention in recent decades; this is why I end this study with a broader contemplation of the importance of bats as ecosystem service providers (**Chapter IV**).

Study site

As a threatened biodiversity hotspot, the area in the Orellana province of Ecuador was an ideal study place for this research project. In three study periods, each between October and December in the years 2008, 2009 and 2010, I worked at two research stations within the YBR. Both biological research stations are neighbouring the Tiputini River and are located at a distance of about 27 km to each other (Figure 1.2). The Tiputini Biodiversity Station (TBS, 0°38´31´´ S, 76°8´92´´ W), where I worked most of the time, can only be accessed by boat or by helicopter, while the Yasuni Research Station (YRS, 0°40´16.7´´ S, 76°24´1.8´´ W) is accessible via car. In the wider vicinity of both stations, the impact of human activities on wildlife or forest structure differs quite largely. While the surroundings of TBS are more pristine, most likely due to its isolated location (Karubian *et al.* 2005, pers. observation), the surroundings of YRS are highly affected by legal and illegal hunting practices. This is due to its vicinity to several oil blocks with associated access roads (Maxus road, established between 1991 and 1994) as well as the presence of local Waorani communities with access to a bush meat market in Pompeya (Mena *et al.* 2000, Finer *et al.* 2009, Suárez *et al.* 2009). Therefore, the north-eastern part of the YBR is more heavily affected by human encroachment than are the more pristine central and south-western parts of the reserve.

For comparative purposes that are explained in chapter II, I collected fruit samples during the spring of 2009 at “La Selva (LS) Biological Station” near Puerto Viejo de Sarapiqui in Costa Rica (10°26´N, 85°59´W). LS served as a control site in this study because no mineral licks are known to exist in Central America, although local bat assemblages include many frugivorous bats, sometimes even of the same genera or species as at YBR in Ecuador.

Outline of the study

The results of this study are presented in 3 manuscripts that comprise the following chapters:

Chapter II: Frugivorous bats drink nutrient and clay-enriched water in the Amazon rainforest: Support for a dual function of mineral lick visitations.

Geophagy is a common phenomenon among many birds and mammals. However, the underlying cause for the uptake of clay or clay-enriched water is poorly understood. In western Amazonian rainforests, pregnant and lactating fruit-eating bats visit mineral licks in large numbers. In this study, I investigated the function of this visiting behaviour in fruit-eating bats. In the Yasuni Biosphere of Ecuador, I captured bats at mineral licks to obtain faeces and blood samples for mineral analyses. With the use of ICP-MS and ICP-OES analyses, I was able to check for differences in blood or fruit mineral concentrations and to search for soil tracer minerals that are used to identify soil consumption. In this Chapter, I provide evidence that fruit-eating bats potentially benefit from their visiting behaviour in two ways.

Chapter III: Defaunation of tropical forests reduces habitat quality for seed-dispersing bats in Western Amazonia: an unexpected connection via mineral licks.

In eastern Ecuador, both oil companies and local tribe communities have a substantial negative impact on larger mammals that are essential for mineral lick maintenance. Mineral licks deteriorate over time if not kept open by larger herbivorous mammals. These mineral licks, as shown in Chapter II, are of pivotal importance for frugivorous bats. This study demonstrates that defaunation of Amazon forests affects not only large mammals directly but most likely also frugivorous bat assemblages indirectly, because reproducing female bats have less access to the nutrient-rich water of mineral licks. Thus, hunting puts the ecosystem services of mammals at risk in two ways: by eliminating seed-dispersing large mammals and by reducing habitat quality for populations of seed-dispersing bats.

Chapter IV: Increasing Awareness of Ecosystem Services Provided by Bats.

Ecosystem services provided by animals are increasingly considered to be of significant economic value to, and essential for the well-being of, humans. The relevance of bats to ecosystem functioning has been largely underestimated, probably due to their cryptic life-style and reputation as potential vectors for diseases. However, bats are the second largest mammalian taxon and contribute the largest number of species to mammalian assemblages in tropical ecosystems. This chapter reviews the available literature for evidence of how bats are ecological key players and how recent threats put bats and their ecosystem services at risk.

Chapter V: Discussion

This chapter is based on the results of all manuscripts that contributed to this dissertation. Here, I focused on the relevance of mineral licks as natural resources for bats. Today, human activity can negatively affect habitat quality and thereby the functioning of ecosystems. This is true not only for frugivorous Neotropical bats, but also for all bats that function as ecosystem service providers in various ways. Their ecosystem services are put at risk by unsustainable development combined with insufficient conservation programs.

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Chapter II

Frugivorous bats drink nutrient and clay-enriched water in the Amazon rainforest:
Support for a dual function of mineral lick visitations

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Abstract

In Central Amazonia, large mammals create water-filled puddles during soil consumption. These puddles are frequently visited by pregnant and lactating frugivorous bats; possibly for two reasons: Frugivorous bats could supplement their mineral-depleted fruit diet by drinking salty water, or they could buffer dietary secondary plant compounds by soil consumption. Using infrared cameras, we recorded bats drinking water at mineral licks. We demonstrated that frugivorous bats ingest minerals by drinking nutrient-rich water at mineral licks by confirming that blood sampled from frugivorous bats captured at mineral licks differed in physiologically relevant mineral composition (Na, K, Mg, Fe) from those captured at other sites. Further, we tested whether frugivorous bats also consumed clay by testing for soil tracers in feces. Soil tracers are insoluble in water and, thus, are not included in a strict fruit diet. Most bats from mineral licks showed higher soil tracer concentrations in their feces than bats that have never been recorded at licks, suggesting that bats take up clay material in addition to mineral nutrients at mineral licks. Our results provide evidence that frugivorous bats ingest soluble mineral nutrients and insoluble clay by consuming clay-enriched water at mineral licks, thus supporting the hypothesis that frugivorous bats of western Amazonia may derive a dual benefit from mineral lick visitation.

Key words: geophagy, nutrient supplementation, detoxification, secondary metabolites, soil tracer

Spanish abstract

En la Amazonia Central, los mamíferos grandes construyen charcos de agua durante el consumo del suelo. Estos charcos son frecuentemente visitados por murciélagos frugívoros por dos posibles razones: suplementar su dieta baja en minerales por medio de beber agua con alto contenido de sales o amortiguar compuestos secundarios provenientes de plantas. Con el uso de cámaras infrarrojas grabamos murciélagos tomando agua en saladeros. Determinamos si los murciélagos ingieren minerales al tomar agua rica en nutrientes en los saladeros comparando el contenido de minerales con relevancia fisiológica (Na, K, Mg, Fe) en la sangre de murciélagos que visitan los saladeros y aquellos que no lo hacen. La sangre de murciélagos frugívoros capturados en los saladeros difiere en su composición de minerales de la de murciélagos capturados en otros sitios. También examinamos si los murciélagos consumían arcilla buscando trazas de suelo en las heces. Dichas trazas son insolubles en agua y por lo tanto no incluidas en una dieta frugívora. Los murciélagos frugívoros que visitan los saladeros mostraron una mayor concentración de trazas de suelo en las heces que murciélagos insectívoros que nunca los visitan. Nuestros resultados proveen evidencia que los murciélagos frugívoros ingieren nutrientes minerales solubles y arcilla insoluble al consumir agua enriquecida con arcilla en los saladeros. Esto apoya la hipótesis que los murciélagos frugívoros de la Amazonia occidental obtienen un doble beneficio al visitar dichos saladeros.

Introduction

Over the last decades, consumption of soil, called geophagy, has been described for various frugivorous and omnivorous animals. Among vertebrates, examples for this widespread behavior can be found in birds (*e.g.* Diamond *et al.* 1999, Gilardi *et al.* 1999, Brightsmith & Muñoz-Najar 2004) and many mammals (e.g. ungulates: Kreulen 1985, Mahaney & Hancock 1990, Montenegro 2004; elephants: Weir 1969, Ruggiero & Fay 1994, Klaus *et al.* 1998; primates: Oates 1978, Mahaney 1987, Davies & Baillie 1988, Krishnamani & Mahaney 2000, Blake *et al.* 2010; humans: Laufer 1930, Young *et al.* 2008). Several explanations for geophagy have been suggested (reviewed in Klaus & Schmid 1998, Diamond 1999) and even though geophagy is widespread, the reasons behind this behavior are yet not completely understood (Mahaney & Krishnamani 2003). The hunger hypothesis is the simplest among all explanations, suggesting that soil provides a substitute for ingesta in times of low food availability (Bateson & Lebroy 1978, de Castro & Boyd-Orr 1952, Young *et al.* 2008). In other cases, medicinal benefit has been associated with the consumption of soil (Krishnamani & Mahaney 2000). For example, some animals consume soil for its anti-acidic function that supports a balanced stomach pH or for its anti-diarrheal function (Diamond 1999, Mahaney *et al.* 1997, de Souza *et al.* 2002). An ingestion of soil may also be tied to the support of food passage via grit in birds (Gionfrido & Best 1995). However, for nearly all animals the most common explanations for geophagy has been associated with nutrient supplementation or detoxification of secondary plant compounds (*e.g.* Abrahams & Parsons 1996, Sheppard 1998, Holdø *et al.* 2002, Izugbara 2003, Mahaney & Krishnamani 2003, Voigt *et al.* 2008). The nutrient-supplementation hypothesis assumes that animals ingest clay material for its nutrient content (Emmons & Stark 1979, Kreulen 1985, Brightsmith & Muñoz-Najar 2004). The detoxification hypothesis argues that ingested clay material may help in buffering toxic, carcinogenic, teratogenic or nutrient binding effects of secondary plant compounds such as tannins or other alkaloids (Diamond 1999, Gilardi *et al.* 1999, Brightsmith *et al.* 2008).

In the Neotropics, several species of mammals such as monkeys, tapirs, or peccaries, and also birds such as parrots visit mineral licks (also called salt licks, saladeros or collpas) to consume either soil or soil-enriched water (*e.g.* Diamond *et al.* 1999, Gilardi *et al.* 1999, Brightsmith & Muñoz-Najar 2004, Blake *et al.* 2010). Mineral licks are muddy depressions in small clearings of forested areas, which are usually connected via shallow creeks with running water or springs. Several studies have shown that frugivorous and omnivorous bats in western Amazonia (Ecuador, Peru, and Venezuela) visit these mineral licks (Tuttle 1974, Voigt *et al.* 2007, Bravo *et al.* 2008, Bravo *et al.* 2010). In these studies in particular, pregnant and lactating frugivorous bats of the subfamily Stenodermatinae (Phyllostomidae) have been observed visiting mineral licks in high numbers. During reproduction, frugivorous bats may suffer from severe nutrient stress, because many fruits are low in minerals. This nutrient stress may be more pronounced for fruit-eating bats living in nutrient depleted ecosystems, such as the Amazonian lowlands (Terborgh 1992). Here, fruit-eating bats constitute the most species rich dietary niche among mammals (Simmons & Voss 1998, Rex *et al.* 2008), but these bats most likely suffer from the combined physiological stress of reproduction and a diet depleted in mineral nutrients. Therefore, geophagy serving as mineral supplementation for frugivorous bats has been suggested by several authors (Voigt *et al.* 2007, Bravo *et al.* 2008, Bravo *et al.* 2010). However, bats may also benefit from geophagy by buffering toxic secondary plant compounds in their fruit diet, particularly when fruit consumption is increasing in times of high nutritional demands (Voigt *et al*. 2008). Thus far, no study has been able to ascertain unambiguously whether free-ranging bats consume water or clay material at mineral licks. If bats only drink water, they most likely supplement their nutrient-depleted fruit diet with essential nutrients from soil dissolved in the water. Alternatively, if bats ingest additionally clay, it is more likely that they detoxify secondary plant compounds in their diet by geophagy.

In this study, we tested the hypotheses that frugivorous bats visit mineral licks to drink water and to ingest clay. (1) To evaluate whether frugivorous bats drink water at mineral licks, we conducted video observations and analyzed chemical elements in bat blood. We predicted that frugivorous bats captured at mineral licks should have an altered blood composition in relation to frugivorous bats captured at control sites in the nearby forest (away from mineral licks). We only examined elements that are considered to be physiologically relevant, such as sodium (Na), potassium (K), magnesium (Mg) and iron (Fe). As we examined the elemental composition of available water sites in the area, we also predicted that water sampled at mineral licks should show higher values of the physiologically relevant elements than water sampled at nearby rivers, streams or ponds. Additionally, we compared the nutrient concentration in fruits from Costa Rica and Ecuador, predicting that fruits from rainforests in the Ecuadorian Amazon which grow on ancient nutrient-poor soils would be more depleted in essential nutrients than those of the more recent Costa Rican rainforests growing on nutrient-rich volcanic soils. (2) To evaluate whether bats consume clay at mineral licks, we predicted that elements in bat feces such as Aluminum (Al), Titanium (Ti), Yttrium (Y), Lanthanum (La), Cerium (Ce), and Neodymium (Nd) would indicate soil consumption. These elements are insoluble in water and thus are only sparsely contained in plant products such as fruits. Thus, they can be used as markers to detect soil consumption (*e.g.* Calabrese & Stanik 1995, Calabrese *et al.* 1997). We predicted that feces of frugivorous bats captured at mineral licks should be more enriched in these elements than feces of co-existing insectivorous bats which never visit mineral licks, if frugivorous bats consume clay or clay-enriched water at mineral licks.

Methods

Study sites – We conducted our study between October and December 2008 at the Tiputini Biodiversity Station (TBS, 0°38´S, 76°8´W), located in a lowland Amazonian primary rainforest, Orellana Province, Ecuador. For video observations and sampling of bats, we chose nine mineral licks and 15 control sites in the forest. Control sites were randomly selected at open locations such as trails or gap openings at the TBS. Additionally we collected and analyzed elements in fruits that are known to be consumed by bats.

For comparative purposes, we collected fruit samples in spring 2009 at La Selva (LS) Biological Station near Puerto Viejo de Sarapiqui in Costa Rica (10°26´N, 85°59´W). LS served as a control site in our study, because no mineral licks are known to exist in Central America, even though local bat assemblages include many frugivorous bats, sometimes even the same genera or species as at TBS (Rex *et al.* 2008).

Video observations at mineral licks – We observed bats at the mineral licks in Ecuador by using a digital video camera (Sony Digital Handycam DCR-H C39E PAL, Sony Europe) with the night shot function active. For illumination, we used an ECOLINE IR-Illuminator (Security-Center, Germany). At each of the nine licks, we recorded the behavior of visiting bats from shortly after sunset (ca. 1800 hours) until 2000 to 2400 hours, depending on battery capacity and weather conditions. We performed video observations directly via a handheld camera or as automated observations with a tripod. Focus points of observation were chosen according to one of three criteria: (1) sites were visited by other animals, such as scraping or drinking spots of spider monkeys (*Ateles belzebuth*) or tapirs (*Tapirus terrestris*); (2) sites with a good overview of the entire mineral lick; and (3) sites with high bat activity based on our netting experience.

Collection of fruit samples – We collected potential bat fruits, from a total set of 38 ripe fruits (Table 2.1), in the vicinity of the two biological stations LS (n = 18) and TBS (n = 20). All fruits were cut into pieces and dried at 50°C for about 72 h. All dried samples were kept at ambient temperature in closed ZipLock^{TM} –bags until analyses.

Table 2.1: Fruits consumed by bats and collected at the study sites in Costa Rica (CR) and Ecuador (E).

Species/Taxonomic affiliation	**Origin**	**Sample size**
Cecropia sp.	CR	3
Cecropia inflorescence	CR	1
Dipteryx	CR	1
Ficus sp. 2	CR	4
Lycianthes multiflora	CR	1
Passiflora sp.	CR	1
Piper sp. 4	CR	4
Sacoglottis sp.	CR	1
Solanum	CR	1
Virola sp.	CR	1
Cecropia sp.	E	5
Dyalium guianense	E	1
Ficus sp.	E	5
Lecythidaceae sp.	E	1
Lauraceae	E	1
Melastomatacea	E	1
Piper sp.	E	5
Virola sp.	E	1

Collection of bat blood and feces – In 31 nights, we captured bats between 1800 h and 2100 h at nine mineral licks and 15 control sites by using ground-level mist nets (length 6 to 12 m; 70 dernier/2 ply, 36 mm mesh, five shelves; R. Vohwinkel, Velbert, Germany). We identified bats based on their morphology using three field keys (Sampaio & Kalko unpublished identification key, Timm & LaVal 1998, Tirira 2007). We held all bats individually in cloth bags for approximately 1 h to collect feces. We recorded the following data using a standard protocol: species, body mass (accuracy 0.5 g; Pesola spring balance, Baar, Swiss), sex, age (juvenile, subadult, adult), and reproductive status (reproductively active, inactive, lactating, post lactating) as outlined in Handley *et al.* (1991) and Kunz and Parsons (2009). We measured the length of forearm using a vernier caliper (accuracy 0.1 mm; SPI 2000 caliper, West Chester, Pennsylvania, USA). Thirty one fecal samples were stored each in Eppendorf tubes filled with 70 percent ethanol until further analyses (Table 2.2). From each of 57 bats, we took 50-120 µl of blood, depending on body mass of the species by piercing the antebrachial vein (Kunz & Nagy 1988) using sterile 23-30 gauge needles (Microlance, Becton Dickison S.A., Spain). All blood samples were dried at 50°C for approximately 48 h and kept at ambient temperature in closed Eppendorf tubes until analyses. We released all bats at the site of capture after species identification and processing as noted above.

Table 2.2: Alphabetical list of insectivorous (I) and fruit-eating bats (F) from which fecal samples were collected at TBS.

Species	**Diet**	**Sample size**
Artibeus lituratus	F	1
Artibeus planirostris	F	1
Chiroderma trinitatum	F	3
Lophostoma silvicolum	I	2
Mesophylla maconelli	F	8
Mimon crenulatum	I	5
Phyllostomus elongatus	I	2
Sturnira lilium	F	1
Sturnira magna	F	4
Trachops cirrhosus	I	1
Uroderma bilobatum	F	1
Vampyressa thyone	F	2

Collection of water samples – We collected 50 ml samples of water from puddles at each of six mineral licks and four control sites, such as a river, stream or pond in proximity to TBS and potentially accessible for the bats. The water was stored in a PTFE vessel mixed with 1 ml of 65 wt. % ultrapure nitric acid for preservation and was kept at ambient temperature until analyses.

Measurement of elemental composition – For elemental analyses in blood, fruit, and feces samples, we dissolved the samples using a total digestion apparatus (Picotrace, Bovenden, Germany; Ruppert 1987, PicoTrace 2008). A series of 32 solid samples was simultaneously digested in polytetrafluoroethylene (PTFE) vessels using a mixture of ultrapure fluoric acid (40%), perchloric acid (70%) and nitric acid (65%) at elevated pressure and temperature (170^{o}C, all acids cleaned by sub-boiling distillation). During evaporation, acid fumes were removed directly from the samples using clean airflow. Residues of evaporation were dissolved in nitric acid and hydrochloric acid and water at 150°C. After cooling, the clear solutions were transferred into a 10 ml volumetric flask. The homogenized solutions were stored in polyethylene bottles. During the digestion procedure, we assumed minimal risk of contamination, because ultraclean, sub-boiling distilled acids were used, and because the system was closed during the pressure phase and was sheltered during evaporation. Elemental analyses of the digested samples as well as of the water samples were conducted using inductively coupled plasma emission spectrometry (ICP-OES; Optima 3300 DV, Perkin Elmer) and by inductively coupled plasma mass spectrometry (ICP-MS Elan DRC II; Perkin Elmer SCIEX). The elements sodium (Na), potassium (K), magnesium (Mg), and iron (Fe) in feces and blood samples were selected because they are physiologically relevant nutrients in mammals. Concentrations of Na, K, Mg, Fe and calcium (Ca) from fruit and water samples were also analyzed. Additionally, we used the water insoluble elements Aluminum (Al), Titanium (Ti), Yttrium (Y), Cerium (Ce), Lanthanum (La), and Neodymium (Nd) in bat feces as markers for soil consumption.

Statistics –We applied a Mann-Whitney U test to reveal significant differences in the elemental composition of fruit samples from La Selva (Costa Rica) and from TBS (Ecuador), as well as for differences in the elemental composition of water samples from mineral licks and control sites.

We transformed blood sample data using the log(x+1) function to reduce the effects of numerically dominant categories. Differences in blood composition were tested with samples of two frugivorous bat groups, collected at mineral licks and from open forest sites, using the statistical software Primer v6 (Primer-236 E 2000 Ltd., Plymouth, UK). We computed the Bray-Curtis similarities for a MDS (multi-dimensional scaling) plot to document evidence of groupings. This plot illustrates the relationship between the two frugivorous groups, by representing the samples as points in 2-dimensional space, where the relative dissimilarities of the samples are shown by the relative distances between points. We verified differences in elemental composition of blood by using an analysis of similarity (ANOSIM) permutation test (Clarke & Warwick 1994). To assess the relative contribution of elements to the dissimilarity between the two frugivorous groups, we calculated a SIMPER similarity analysis (Clarke & Warwick 1994).

We applied a Mann-Whitney U test to reveal significant differences in the elemental concentrations between fecal samples of frugivorous bats captured at mineral licks and insectivorous bats that have never been recorded to visit mineral licks (Table 2.3). We calculated the upper 95 percent confidence interval of the insectivorous group to establish threshold values that indicated soil consumption by frugivorous species. All individuals with values above the upper 95 percent confidence interval were considered to have consumed soil. Values within the 95 percent confidence interval suggest that animals had not consumed soil recently. We set the level of significance at 5 percent and used two-tailed tests.

Table 2.3: Median concentrations (µg/g of dry matter) of the soil tracer elements Al = Aluminum, Ti = Titanium, Y = Yttrium, La = Lanthanum, Ce = Cerium, and Nd = Neodymium in droppings of frugivorous bats captured at mineral licks and insectivorous bats captured at open forest sites. The 95% UL of soil tracer concentrations in the feces of insectivorous bats served as a baseline soil tracer concentrations for bats not consuming soil. We considered frugivorous bats as soil consumers, when tracer concentrations in their fecal material were above the 95% UL of soil tracer concentrations in the feces of insectivorous bats.

	Insectivorous bats		**Frugivorous bats**	
Element	Median	95% UL	Median	% of individuals with soil consumption
Al	283	487	496	50
Ti	11	0.25	15	31
Y	0.06	0.16	0.05	35
La	0.13	0.10	0.08	31
Ce	0.18	36	0.15	35
Nd	0.07	0.18	0.01	46

Results

Video observations at mineral licks – During 13 nights (total of 48 hours of recording), we never observed bats feeding directly on clay at scraping spots of other lick-visiting animals. It was difficult to obtain good overview recordings using the automated video observation, due to the size and illumination of the mineral licks. However, by focusing on smaller areas at the same mineral licks using the handheld camera, we detected and observed many bats drinking water from small depressions at the mineral licks (see Fig. 2.1 and online resource 1).

Elemental composition of fruits – The mean nutrient concentration in Costa Rican and Ecuadorian fruit samples is summarized in Table 2.4. Fruits from Ecuador showed significantly lower concentrations of P, K and Na than fruits from Costa Rica (Mann-Whitney U-Test, Phosphor: *U* = 84; *P* = 0.004; Potassium: *U* = 90; *P* = 0.008; Sodium: *U* = 100; *P* = 0.019; Fig. 2).

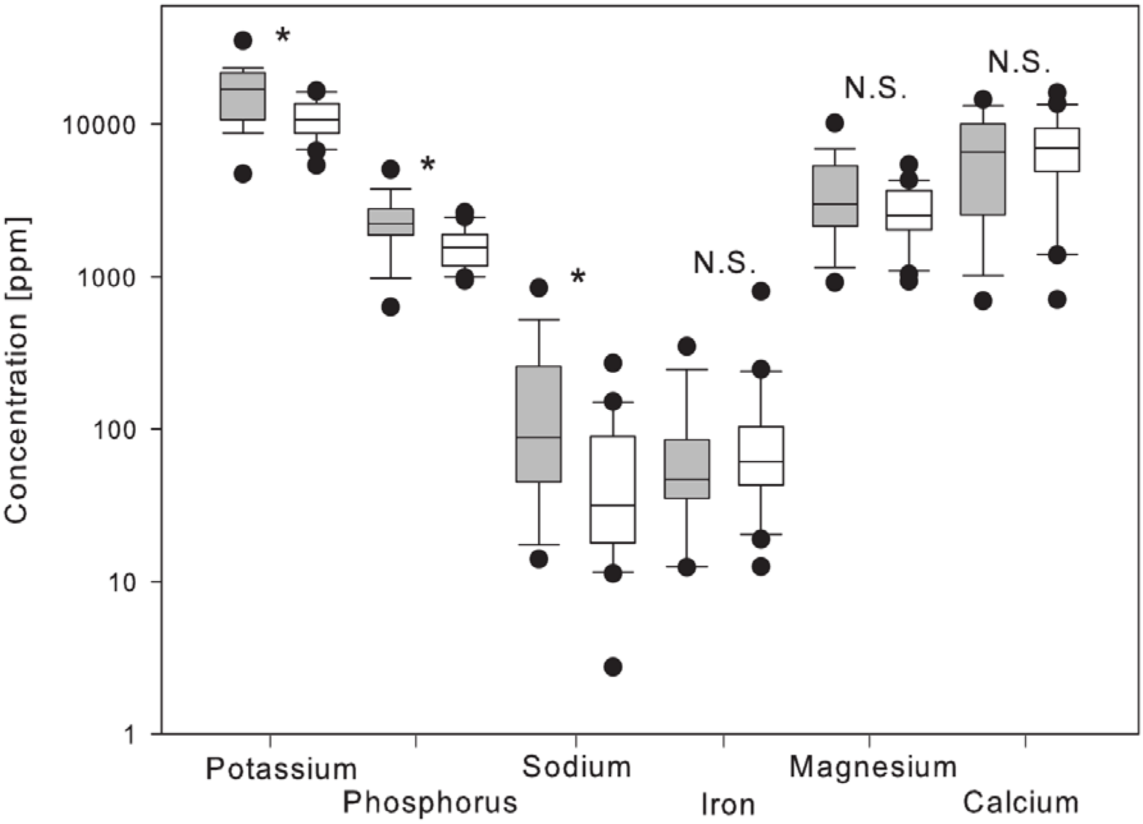

Figure 2.2: Comparison of nutrient concentration [ppm] in Costa Rican (gray, n=18) and Ecuadorian (white, n=20) fruit samples (Mann-Whitney U-Test, P: *U* = 84; *P* = 0.004; K: *U* = 90; *P* = 0.008; Na: *U* = 100; *P* = 0.019) are shown with standard box-and-whiskers with median and quartiles. * $P < 0.05$, N.S. = not significant difference. Note log scale used on y-axis.

Figure 2.1: Outtake of a video recording within a mineral lick, showing a bat approaching (from left to right) a puddle (in white margins in picture (1)). Picture (2) – (4) show the snout of the bat moving towards the water surface; see online resource 1 for full video.

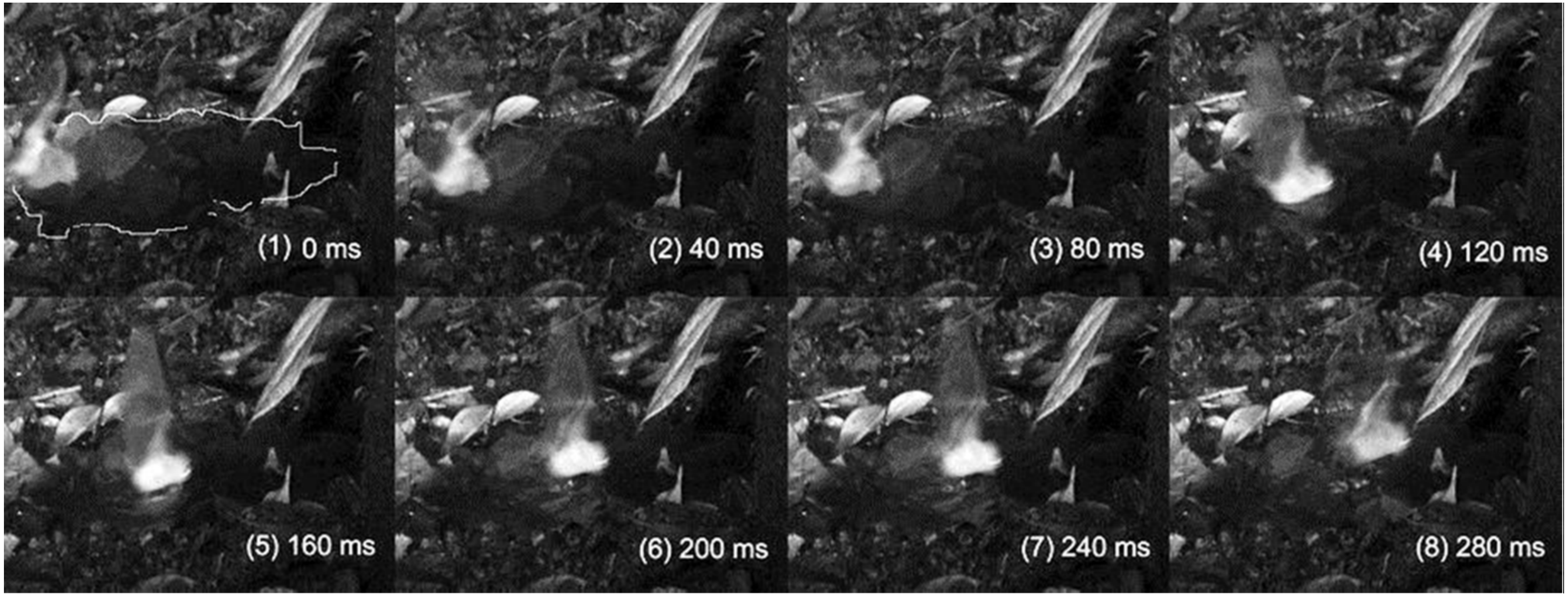

Table 2.4: Mean mineral nutrient concentrations (µg/g of dry matter) of fruits collected from Costa Rica (n = 18; CR) and Ecuador (n = 20; E). The mineral content of *Piper sp.* infructescences was used to calculate the daily mineral shortfall of *Carollia* bats when consuming exclusively *Piper* infructescences (see discussion). We estimated a daily fruit consumption of ~24 g for *C. brevicauda* and assumed that 70 percent of consumed element amounts were available to the bat's organism (70 % available). Additionally, we calculated the difference in element content (Δ) between diets of *Piper spp.* fruits in Costa Rican and Ecuador as well as the average element concentration (µg/g) of lick water (ML; n = 6 mineral licks) and control water sites (CW; n = 4 control sites) in Ecuador.

Element	All fruits		Only *Piper*		70% available		Δ	Conc. in water	
	CR	E	CR	E	CR	E	(µg/g)	ML	CW
Na	176	59	2,833	801	1,983	561	1.422	28,5	2,3
Mg	3,7	2,749	45,785	21,073	32,049	14,75	17,3	8,56	1,8
Fe	82	111	713	458	499	320	179	4,87	3,2
K	16,9	11,14	206,67	103,76	144,67	72,63	72,04	4,98	2,5
Ca	6,57	7,253	82,989	82,213	58,093	57,55	544	55,3	6,7
P	2,35	1,618	29,035	21,395	20,324	14,97	5,347	0,12	0,1

Elemental blood composition – Frugivorous bats captured at mineral licks and at control sites showed a large overlap in concentration of K, Mg, Na and Fe, with an average similarity within the mineral-lick visiting group of 99.0 percent and within the control-site group of 99.1 percent. The calculated dissimilarity between the two frugivorous groups was 1.0 percent, with most dissimilarity being explained by variations in concentrations of K (29.5 %), Mg (26.5 %), Na (24.3 %) and Fe (19.8 %). The ANOSIM revealed a significant global R value of 0.123 (*P* = 0.019), suggesting significant differences in elemental composition of blood between the two groups. Of the 999 permutations in our model, only 18 were equal to or greater than the global R, which indicates a high within-group similarity. The Bray-Curtis dissimilarity matrix among all pairs of objects was used to construct a MDS plot (Fig. 2.3), which suggests groupings according to capture site (2-dimensional stress level = 0.19).

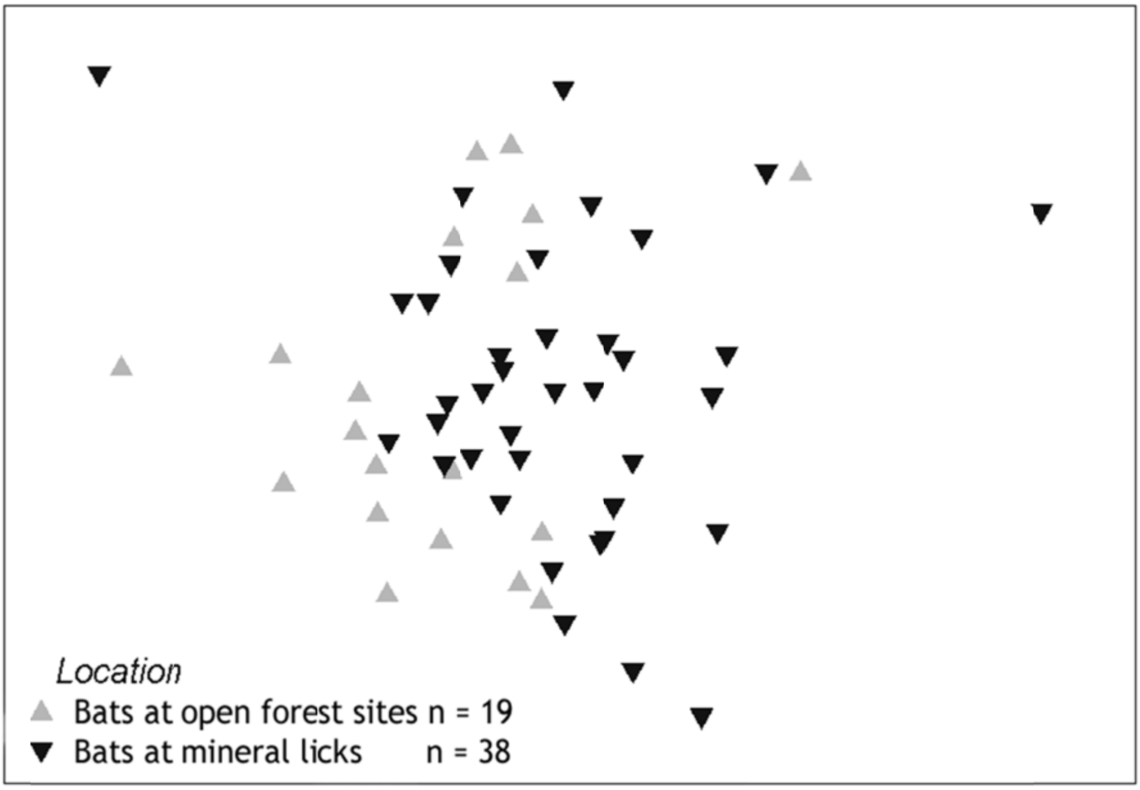

Figure 2.3: Two-dimensional MDS plots of soil tracer elements in blood of bats captured at mineral licks (black) and nearby forest sites (gray). The similarity matrix was computed using the Bray-Curtis Similarity Index (2D stress 0.19). The more similar the elemental compositions of bats, the closer the symbols appear on the plot.

Elemental Composition of water – Water collected from puddles at mineral licks showed significantly higher concentrations of Na, Mg, K, and Ca when compared to the concentrations of the control water sites (Mann-Whitney U-Test, Sodium: $U = 64$; $P < 0.001$; Magnesium: $U = 32$; $P < 0.001$; Potassium: $U = 96$; $P = 0.007$; Calcium: $U = 32$; $P < 0.001$; Table 2.4). The concentrations of Fe and P did not differ significantly (Mann-Whitney U-Test, Iron: $U = 132$; $P = 0.1$; Phosphor: $U = 93$; $P = 0.404$; Table 2.4; Fig. 2.4).

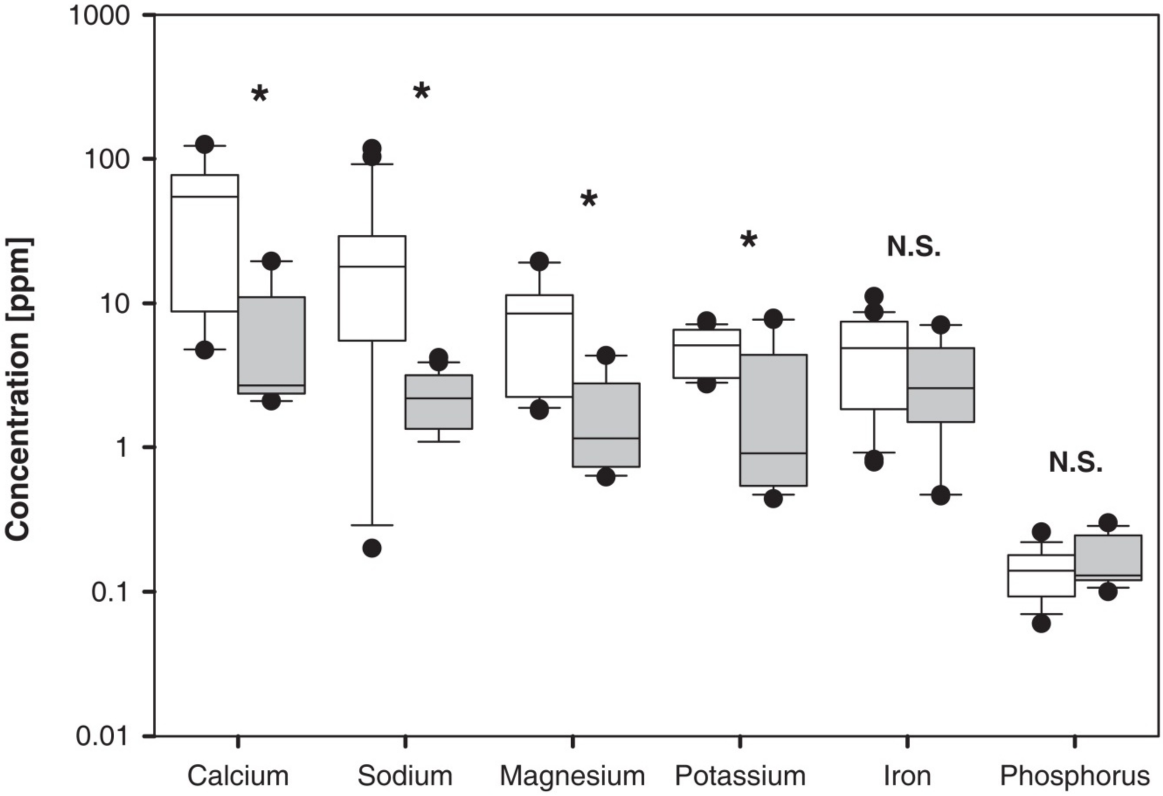

Figure 2.4: Comparison of nutrient concentration [ppm] in mineral lick (white, n=6) and control site (grey, n=4) water samples (Mann-Whitney U-Test, Na: $U = 64$; $P < 0.001$; Mg: $U = 32$; $P < 0.001$; K: $U = 96$; $P = 0.007$; Ca: $U = 32$; $P < 0.001$; Fe: $U = 132$; $P = 0.1$; P: $U = 93$; $P = 0.404$; Table 2.4) are shown with standard box-and-whiskers with median and quartiles. * $P < 0.01$, N.S. = not significant difference. Note log scale used on y-axis.

Soil markers in feces – The mean values for all soil tracers in fecal samples collected from frugivorous and insectivorous bats are summarized in Table 2.2. The calculated threshold (upper 95% CI of insectivorous group) for soil consumption revealed that 31 - 50 percent of the frugivorous species exhibited soil tracer concentrations in feces that were higher than those of insectivorous species. Feces of frugivorous species that visit mineral licks were significantly more enriched in the soil tracer aluminum than the droppings of insectivorous bats that do not visit mineral licks (Mann-Whitney U-Test; $U = 40$; $P = 0.032$).

Discussion

We tested the hypothesis that frugivorous bats ingest water for nutrient supplementation or clay for detoxification at mineral licks of the Amazon rainforest. Similar to previous studies, we captured mostly reproductively active female frugivorous species visiting mineral licks (Tuttle 1974; Voigt *et al.* 2007, 2008, Bravo *et al.* 2008, 2010). Although, we were not able to document large numbers of drinking bats with our automated camera setup, our video observations with hand-held cameras demonstrate unambiguously that bats drank water at mineral licks in the lowland Ecuadorian Amazon. We suggest that this water uptake is most likely unrelated to the daily water requirements, because frugivorous species usually consume large amounts of water when ingesting fruits (*e.g.* Morrison 1980, Ruby *et al.* 2000). The high water content of fruits is presumably sufficient for lactating bats when facing elevated water demands during milk production. Instead, frugivorous bats are probably attracted to the water-filled depressions at mineral licks, because the water is more enriched in nutrients such as sodium than water from local creeks, ponds or rivers. In support of the nutrient supplementation hypothesis, we found that the composition of physiologically relevant elements (Na, Mg, K, and Fe) differed significantly between blood collected from frugivorous bats at mineral licks and blood collected from bats at open forest sites. Based on these differences in elemental blood composition, we infer that traces of the nutrient-enriched water consumed by bats at mineral licks can be found in their blood samples, even though nutrient concentrations in blood are probably regulated within narrow ranges. This finding is interesting given that extreme deviations of elemental concentrations from the range of physiological acceptable values may be detrimental or even fatal to mammals. Our finding also provides direct support for the hypothesis that bats take up nutrients at mineral licks by drinking water from small puddles. A key question related to this is whether fruits from plants growing in the Amazonian ecosystem provide sufficient quantities of essential mineral nutrients to meet the daily requirements of frugivorous bats during reproduction. Bravo *et al.* (2010) reported that figs in Peru include less sodium than fruits of other tropical regions. Other studies in Peru showed that parrots with diets extremely low in sodium often supplement their diets by eating soils with high concentrations of sodium, most likely to meet their daily nutrient demands (Gilardi *et al.* 1999, Brightsmith & Muñoz-Najar 2004). In the present study, we compared nutrient concentrations of fruits collected from Ecuadorian and Costa Rican rain forests. Fruits from Ecuador had less sodium, potassium and phosphorus than those from Costa Rica. Our findings, in conjunction with the data of the Peruvian studies, suggest that the eastern Amazon region is generally depleted in mineral nutrients. This can be attributed to the unique geographical features of the western lowland Amazon. This region is essentially beyond coastal climate and thus marine input of sodium, because of its isolation from the Pacific Ocean by the Andes to the west, and the Atlantic Ocean to the east (Kaspari *et al.* 2008). Moreover, the soils of the Amazonian rainforest are ancient and have degraded and leached over millions of years (Terborgh 1992). Thus, low concentrations of nutrients in plants and their associated fruits may be caused by the nutrient depletion of Amazonian soils (Stark 1970, Jordan & Herrera 1981).

Based on nutrient data from the infructescences of *Pipe*r collected in Ecuador and Costa Rica, and the measured rates of water flux in *Carollia brevicauda*, a frugivorous bat species (Voigt *et al.* 2006), we estimated the nutritional deficit in this species when consuming only Ecuadorian fruits. For the daily water flux of 30 ml/d for *C. brevicauda* (Voigt *et al.* 2006), we assumed that about 20 percent of this water flux originates from the oxidation of fat as metabolic water. Thus, *C. brevicauda* must consume approximately 24 ml/d of water from fruits to maintain its daily water balance. Given that fruits are comprised of about 70 percent water, we estimated that this fruit-eating species handles approximately 31 g of fruits each day. As a conservative approach, we assumed that a bat takes up about 70 percent of the nutrients of the consumed fruits. Thus, *C. brevicauda* in Ecuador would be expected to consume about 1423 µg sodium, 543 µg calcium and 179 µg iron less than a respective Costa Rican individual on a daily basis. For sodium the daily minimum requirements of small mammals have been reported to be 600ppm on a dry matter basis (Dempsey 2004). The estimated sodium values for Ecuadorian *C. brevicauda* when consuming exclusively *Piper* infructescences lay still beneath these minimum requirements. However, our nutrient analysis of water from mineral licks suggests that a daily consumption of 1 to 2 ml of mineral lick water would be sufficient to compensate for this deficit.

A notable problem in most studies that have measured the composition of tropical fruits is that they focused on total availability of nutrients in fruits rather than on the bioavailability of mineral elements. Fruits that contain large amounts of secondary plant compounds such as phytate or oxalate can limit the bioavailability of nutrients (Kamchan *et al.* 2004). One such example can be observed in figs, a food item largely preferred by the genus *Artibeus*. While figs are known to be rich in total calcium (Wendeln *et al.* 2000), they often contain high levels of oxalate that not only bind the calcium in the fruit (Kamchan *et al.* 2004), but may also reduce the amount of calcium available to the animal when it is consumed. Thus, many fig-eating bats that consume figs may actually lack essential nutrients in their diet.

In addition to a higher demand for nutrients, reproductively active bats also have higher energy demands (*e.g.* Racey & Speakman 1987, McLean & Speakman 1999, Voigt 2003, Korine *et al.* 2004; Hood *et al.*, 2011). Thus, an increase in fruit consumption in response to these demands should lead to an increase in secondary plant metabolites absorbed. Many of these compounds negatively affect their consumers, because they can be carcinogenic, teratogenic, toxic, or they may simply bind to elements as do phytate or oxalate (*e.g.* Heiser 1969, Myers 1983, Kamchan *et al.* 2004).

The elemental analysis of bat droppings in our study revealed higher concentrations of soil tracers in feces collected from frugivorous species visiting mineral licks than in feces of those that were never observed at mineral licks. High concentrations of soil tracers provide clear evidence for geophagy in frugivorous bats of the lowland Amazonian rainforest. The soil tracer aluminum is a major structural component of clay minerals such as kaolinites or smectites (Mahaney & Krishnamani 2003). A higher enrichment of this element in feces strongly suggests that fruit-eating bats consume clay minerals while they are visiting water puddles at mineral licks. In a wide range of studies on birds and mammals, the consumption of clay minerals was linked to detoxification of secondary plant compounds (*e.g.* Klaus & Schmid 1998, Gilardi *et al.* 1999, Brightsmith & Munoz-Najar 2004). Brightsmith *et al.* (2008) and Gilardi *et al.* (1999) showed that clay minerals such as kaolinite buffer remarkable amounts of the toxin quinine, which is similar in structure to other compounds that occur in the diets of frugivorous parrots. Given these observations, it seems quite likely that bats could also benefit from the buffering and thus detoxifying effects of consumed clay minerals.

Our findings provide direct evidence that frugivorous bats obtain both essential mineral nutrients and clay at mineral licks by drinking water from these sites. Two reasons may be causal for the drinking behavior of female frugivorous bats during reproduction, apart from a demand for water: 1) female frugivorous bats may require more essential elements during reproduction than their diet of fruit can supply, and 2) possible exposure to higher levels of secondary plant metabolites may require the use of clay minerals as a detoxifying buffer. In conclusion, we suggest that the drinking behavior of frugivorous bats at mineral licks serves a dual function, namely nutrient supplementation and detoxification of secondary plant compounds in their diet.

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Chapter III

Defaunation of tropical forests reduces habitat quality for seed-dispersing bats in Western Amazonia: an unexpected connection via mineral licks

Simon J. Ghanem, Christian C. Voigt

Abstract

Hunting reduces the overall abundance of larger mammals in many tropical forests with often direct negative consequences such as reduced seed-dispersal. In Ecuador, legal and illegal hunting practices have a substantial negative impact on populations of larger mammals. Large mammals are important for maintaining so-called mineral licks; nutrient-rich muddy depressions that are also used by smaller mammals such as bats for geophagy. Mineral licks seem to play a particularly important role during the reproduction of frugivorous bats, because pregnant and lactating bats supplement their nutrient-poor diet with muddy water from mineral licks. In our study, we asked first if mineral licks deteriorate when not maintained by large mammals. Second, we tested if mineral lick deterioration reduces the visitation rate of frugivorous bats at mineral licks. For mineral licks in areas with intensive hunting, we expected to find signs of deterioration such as increased plant coverage. In addition, we expected to capture fewer bats at deteriorated licks than at natural licks. Indeed, mineral licks in forests with intensive hunting were covered by more seedlings and leaf litter than licks in pristine forests. Also, we encountered fewer bats at deteriorated mineral licks than at natural licks. We conclude that defaunation of Amazon forests affects not only large mammals directly but most likely also fruit-eating bats, because reproducing female bats may be limited in their ability to access nutrient-rich soils of mineral licks. Thus, hunting puts the ecosystem services of seed-dispersing mammals at risk in two ways, by eliminating large mammals and by reducing habitat quality for fruit-eating bats.

Key words:

Bats, ecosystem service, hunting pressure, seed dispersal, ecosystem functioning, mineral lick

Introduction

Over the past decades, wildlife populations have suffered from human encroachment in natural habitats worldwide (e.g. Redford, 1992; Bennett & Robinson, 2000; Laurance *et al.*, 2001; Finer *et al.*, 2008). Mammal assemblages, in particular, are more and more disturbed by subsistence bush meat and commercial hunting as well as the construction of roads for access to natural resources such as timber, oil or gas (e.g. Peres, 2000; Wright, 2003; Wright *et al.*, 2007a; Finer *et al.*, 2008; Suárez *et al.*, 2009). Defaunation caused by these and other human activities translates in a direct loss of ecological key species in rainforest habitats. This loss can cause a substantial shift in ecosystem functioning, for example when seeds are no longer dispersed or forest regeneration is hampered (Wright *et al.*, 2000; Forget & Jansen, 2007; Holbrook & Loiselle, 2009). While the direct, negative consequences of hunting larger mammals have been clearly documented, only few studies have evaluated the consequences for animal taxa that are not directly subject to hunting, such as smaller vertebrates and insects (e.g. Redford, 1992; Wright, 2003; Andresen & Laurance, 2007; Terborgh *et al.*, 2008). For example, dung beetle abundance in Panama decreases when dung producing mammals become rare (Andresen & Laurance, 2007). But the most prominent example of far-reaching consequences of biased hunting practice relates to the hunters' preference for large prey, such as in the red brocket deer *Mazama americana*, the collared peccary *Tayassu tajacu*, or the tapir *Tapirus terrestris* (Bodmer, 1995). This general preference for larger mammals can lead to an evident change in species composition, in which plant species with larger sized seeds are threatened to become rare. This cascading effect is related to the fact that large mammals tend to feed preferably on plants with large-sized seeds (Stoner *et al.*, 2007; Wright, Hernández & Condit, 2007b). Thus, hunting does not only lower the likelihood of seed dispersal, but also may alter plant species composition in rainforest ecosystems (Wright *et al.*, 2000).

The Northern part of the Yasuni Biosphere Reserve has suffered over the past four decades from severe ecological and social-economic changes. Following this, hunting practices of local tribal communities, such as Waorani, changed from traditional hunting with blowguns to modern and more efficient methods, for example the combined use of hunting dogs and shotguns (Franzen, 2006; Mena *et al.*, 2000; Suárez *et al.*, 2009). As predicted by Yost and Kelly (1983), modern hunting technologies and an increasing accessibility of previously remote rainforest areas promoted the hunting intensity of humans. In the Yasuni area, local hunters often chase medium and larger-sized mammals at mineral licks; muddy depressions with nutrient-enriched soils and open water. Mineral licks are often visited by larger mammals in search for essential nutrients such as sodium or potassium; a behaviour called geophagy (e.g. Abrahams & Parsons, 1996; Diamond, 1999; Holdø *et al.*, 2002; Brightsmith & Muñoz-Najar, 2004; Voigt *et al.*, 2007, 2008; Bravo *et al.*, 2008). Overall, mineral licks presumably play a crucial role for the health and nutrient supply of many frugivore assemblages in the western Amazon basin (e.g. Klaus & Schmid, 1998; Blake *et al.*, 2011).

Mineral licks are kept open by larger mammals, such as tapirs, and peccaries. These animals trample on emerging seedlings and thereby prevent forest plants from encroaching on the lick. At the same time, they create open water bodies by stamping around in the muddy soils and puddles. Therefore, large mammals are pivotal for keeping the licks accessible for smaller mammals, such as bats, and birds. Several field studies have shown that mineral licks of the Amazonian rainforests are also visited by large numbers of pregnant and lactating frugivorous bats, mostly members of the subfamily Stenodermatinae (Phyllostomidae) (Tuttle, 1974; Voigt *et al.*, 2007, 2008; Bravo *et al.*, 2008; Bravo, Harms & Emmons, 2010). Fruit-eating bats play a paramount role for the regeneration of Neotropical forest because they disperse seeds of many plant species including pioneer plants. Thus far, more than 24 frugivorous bat species have been observed to visit licks for drinking mineral and clay-enriched water (Voigt *et al.*, 2007, 2008; Bravo *et al.*, 2008, 2010). Therefore, fruit-eating bats are expected to depend on larger mammals that maintain the functionality of mineral licks.

In this study, we asked if human land use changes, such as the increase of unsustainable subsistence hunting or oil extraction, can negatively influence mineral licks and as a consequence frugivorous bat assemblages in the Yasuni Biosphere Reserve; one of the biodiversity hotspots worldwide (Bass et al. 2010). We investigated if the loss of larger mammals due to hunting and disturbance indirectly affects the relative abundances of frugivorous bats at mineral licks. We expected mineral licks to show first stirrings of deterioration in areas with intensive hunting due to the lack of large mammals that maintain licks. Accordingly, we expected leaf litter and seedling coverage to be higher while water availability was expected to be lower in disturbed compared with natural licks, leading to a reduced overall accessibility of minerals and soil to frugivorous bats. Accordingly, we expected to capture fewer frugivorous bats at disturbed than at natural mineral licks.

Methods

Study sites

We conducted our study in the lowland Amazon rainforest of the Orellana Province in Ecuador between October and December 2010. We assessed 16 mineral licks within the Yasuni Biosphere Reserve. All mineral licks were situated adjacent to two biological research stations (at maximum distance of 14.7 km). Both stations are neighbouring the Tiputini river and are located at a distance of 27 km to each other: 1) the Tiputini Biodiversity Station (TBS, 0°38´31´´ S, 76°8´92´´ W) can only be accessed by boat or helicopter and 2) the Yasuni Research station (YRS, 0°40´16.7´´ S, 76°24´1.8´´ W) is accessible via car. Thus far, no hunting or disturbance has been reported in the wider vicinity of TBS; probably due to its isolated location (pers. observation, Karubian *et al.*, 2005). In contrast, the surroundings of YRS are highly affected by legal and illegal hunting practice because of its vicinity to several oil blocks with associated access roads (Maxus road, established between 1991 and 1994) as well as the presence of local Waorani communities with access to a bush meat market (Mena *et al.*, 2000; Finer *et al.*, 2009; Suárez *et al.*, 2009). The hunting pressure has dramatically increased starting in the 1970s when Waorani hunters gradually switched from traditional hunting techniques (Blowguns and spears) to modern shotguns (Yost & Kelly 1983; Mena *et al.* 2000). Mena and his colleagues (2000) extensively discussed the problem of increasing hunting pressure in the surrounding of the Maxus road. They proposed that with their observed level of hunting larger mammals will become extirpated in the vicinity of the Waorani villages. More recent studies in the Yasuni area have reported an unchanged situation with a substantial hunting pressure (Franzen, 2006, Holbrook & Loiselle, 2009). This trend shows that the North-eastern part of the Yasuni biosphere reserve is more affected by human encroachment than the more pristine areas of central and South-western parts of the reserve.

Netting protocol

At each of the 16 mineral licks, we captured bats between 1800 and 0100 hours by using ground mist nets (length 6 to 12 m; 70 dernier/2 ply, 36 mm mesh, five shelves; R. Vohwinkel, Velbert, Germany). We identified bats according to their morphology using three field keys (Timm & LaVal, 1998; Tirira, 2007; Sampaio & Kalko, unpublished identification key). We recorded the following data using a standard protocol: species, body mass (accuracy 0.5 g; Pesola spring balance, Baar, Switzerland), sex, age (juvenile, subadult, adult), and reproductive status (reproductively active, inactive, lactating, post lactating) as outlined in Handley, Wilson and Gardner (1991) and Kunz, Adams and Hood (2009). We measured the forearm length using a handheld calliper (accuracy 0.1 mm; SPI 2000 calliper, West Chester, Pennsylvania, USA).

Data Analyses

Mineral lick quality

Building on the knowledge of the local Waorani hunters, we visited and sampled all available mineral licks in the closer surrounding of each of the stations and a road that has been built by the oil company more than 20 years ago (Maxus road) (n = 16). We assessed the level of disturbance of the 16 mineral licks based on external appearance and categorized the licks following qualitative and quantitative measurements as listed in table 3.1. During the study period, we estimated the overall coverage of a mineral lick with shrubs, saplings and leaf litter. We rated an increased coverage as a decreased quality of the mineral lick for bats because of reduced accessibility of nutrient-enriched water and soil. We further estimated the water availability with respect to muddiness and accessibility of puddles as well as the overall size of mineral licks. A large number of open, and therefore accessible, puddles and a marked muddiness accounted for high-quality mineral licks. The mineral lick quality was further described using a waterproof multi-tester (HI 98129; Hanna Instruments, USA) to measure pH, conductivity and the total dissolved solids (TDS) of the mineral lick water.

Degree of disturbance

In addition to the quality of mineral licks, we screened the existing literature for differences in hunting pressure in our study area. Especially the studies listed in table 3.2 as well as interviews with 2 indigenous hunters from close-by communities, Guiyero and Timpoka, and their hunting customs contributed most to the scoring of hunting pressure. Areas that are close to the Maxus road have been described to suffer under an increased hunting pressure for larger mammals if compared to the area around the TBS (table 3.2). In addition to the level of hunting, we measured the distances to roads, oil extraction sites and communities using ArcView GIS Software 9 (ESRI, Germany) and used the measurements to project the disturbance of light and noise to each of the licks. At each of the mineral licks, we measured the abundance of frugivorous bats by calculating their capture rate after the following equation, in order to compensate differences in netting effort (total length of used mistnet and total duration of mistnetting):

$$\text{capture rate} = \frac{\text{bats}}{\frac{netmeter}{h}}$$

Site comparisons

To search for differences in frugivorous bat assemblages at mineral licks, we used “water availability” (muddiness and open water puddles), “coverage” (seedlings, saplings, shrubs and leaf litter), “minimum distance to infrastructure” (communities, roads, oil company), “level of poaching” and “mineral lick size” as categories to rank the mineral licks (table 3.1). We calculated a regression factor analyses using PASW 18 (IBM, Chicago, USA) to reduce the number of variables. The resulting regression factor scores with an eigenvalue above 1 were used to assess the importance of individual variables in explaining the variation in quality of mineral licks. After the varimax rotation we considered variables to have a high factor loading if the loading was at minimum above 0.8. The first regression factor score was then used for a two-tailed Spearman Rho correlation with the measured capture rate of the mineral licks as the dependant variable. Furthermore, we plotted the first regression factor against the capture rate at each mineral lick. To be able to test for differences between mineral licks, we separated the licks into two groups according to the level of disturbance following the bivariate plot. We assigned all mineral licks that did not suffer from obvious infrastructural disturbance or hunting pressure as undisturbed licks (level of disturbance < 0) and all remaining licks as disturbed (level of disturbance > 0; see result section and table 3.1 for mineral lick assignment). Lastly, we used a two-tailed Mann-Whitney-U-Test to check for significant differences in mineral lick quality and in the capture rate between the two mineral lick groups.

Table 3.1: Description of 16 mineral licks in the Yasuni Biosphere Reserve according to quantitative and qualitative categories. Low values for the categories coverage, water availability, hunting score and the level of disturbance indicate low disturbance, whereas high values for the categories capture rate and the minimum distance indicate low disturbance. The level of disturbance as well as the condition resulted from a calculated factor analyses as described in the methods and results section.

Name	**Size**	**Coverage (0 - 5)**	**Water Availability (0 - 10)**	**Mininum distance [m]**	**Hunting Score (0 - 5)**	**Capture rate / net meter /**	**Level of disturbance**	**Condition**
Harpia	medium	0,5	1,5	23,087	0	49,6	-1,16	undisturbed
Yasuni1	medium	1	1,5	23,774	0	11,1	-1,1	undisturbed
Yasuni2	medium	0,5	1	19,346	0	23,1	-1,1	undisturbed
MQ21	small	2	2	25,337	0	5	-0,98	undisturbed
Corallus	medium	0	0,5	6,902	0	16,8	-0,86	undisturbed
Guacamayo	small	1	2,5	22,372	1	2,2	-0,83	undisturbed
ECO	large	0,5	0,5	1,334	0	34,8	-0,56	undisturbed
Yasuni3	small	1,5	1,5	8,627	1,5	5	-0,36	undisturbed
KM9	large	1,5	2	701	1	40	-0,05	undisturbed
Huampi	medium	1	2,5	4,469	3	2,4	0,09	disturbed
Oleoducto	small	3	4	917	3	0,7	0,62	disturbed
Roque	medium	3,5	5	555	4	1,8	1,04	disturbed
KM35	medium	4,5	5,5	925	3,5	3,5	1,16	disturbed
Benado	medium	4	6,5	755	4	0	1,27	disturbed
Bolivar	small	3,5	8,5	429	4	0,4	1,36	disturbed
Punta	small	5	7	2	4	9,6	1,46	disturbed

Table 3.2: List of references used to quantify hunting pressure in our research area.

Reference	**Area**	**Description**
Holbrook & Loiselle 2009	Yasuni Biosphere Reserve	comparison between vicinity of TBS and YRS
Franzen 2006	Yasuni Biosphere Reserve	interviews with indigenous communities in YB
Mena et al. 2000	Yasuni Bioreserve	Woarani hunting practices and their sustainability
Finer et al. 2009	Yasuni Man & Biosphere Reserve	history of the reserve and future conservation challenges
Suárez et al. 2009	Yasuni Biosphere Reserve	indirect threats of oil and gas projects

Results

Mineral lick quality

The mineral licks classified as “disturbed” (level of disturbance > 0) were more covered by leaf litter, saplings and shrubs than those mineral licks classified as “undisturbed” (level of disturbance < 0; table 3.1). Further, disturbed mineral licks showed lower water availability as well as reduced muddiness, when compared with natural licks. The comparison of pH (Mann-Whitney U-Test; $U = 14$; $P = 0.121$), conductivity (Mann-Whitney U-Test; $U = 13$; $P = 0.094$) or the total dissolved solids (Mann-Whitney U-Test; $U = 14$; $P = 0.111$) of the mineral lick water showed no significant differences among the sampled mineral licks.

Site comparisons

The factor analyses revealed two main regression factor scores with an eigenvalue above 1 (table 3.3). The resulting first regression factor (I) showed the highest factor loadings for “water availability”, “coverage”, “minimum distance „and “level of poaching” (loading > 0.8; table 3.3). This factor was labelled as “level of disturbance” because included variables either describe mineral lick disturbance or its quality. The level of disturbance accounted for 67.2 % of the total variation among the variables in our factor analyses. The second regression factor (II) showed only a high factor loading within the variable “size” (loading = 0.942; table 3.3) and accounted for 23.9 % of the total variation. The calculated Spearman Rho correlation between the level of disturbance and the capture rate was highly significant ($r_s = 0.653$; $P = 0.006$). We documented a decreasing number of frugivorous bats visiting the mineral licks with increasing levels of disturbance (figure 3.1). In total, we captured 727 bat individuals of 24 frugivorous bat species at mineral licks (table 3.4). Seventy-seven per cent of the captured bats were females with 93.7 % of them being reproductively active individuals. We captured significantly fewer bats per net meter hour at disturbed mineral licks than at mineral licks that did not suffer from obvious disturbance (Mann-Whitney U-Test, $U = 5$; $P = 0.003$). This result was robust even after re-assigning two mineral licks with intermediate level of disturbance (KM9: -0.05; Huampi: 0.09; see also figure 3.1) to the opposite category (Mann-Whitney U-Test: KM9 and Huampi grouped as disturbed: $U = 12$; $P = 0.038$; Km9 and Huampi grouped as undisturbed: $U = 6$; $P = 0.007$). Thus, higher levels of hunting or disturbance were related to a lower number of bats captured at mineral licks (figure 3.1). Further, the percentage of female bats captured at disturbed mineral licks was lower with 63.2 % compared with 82.5 % at mineral licks under natural conditions.

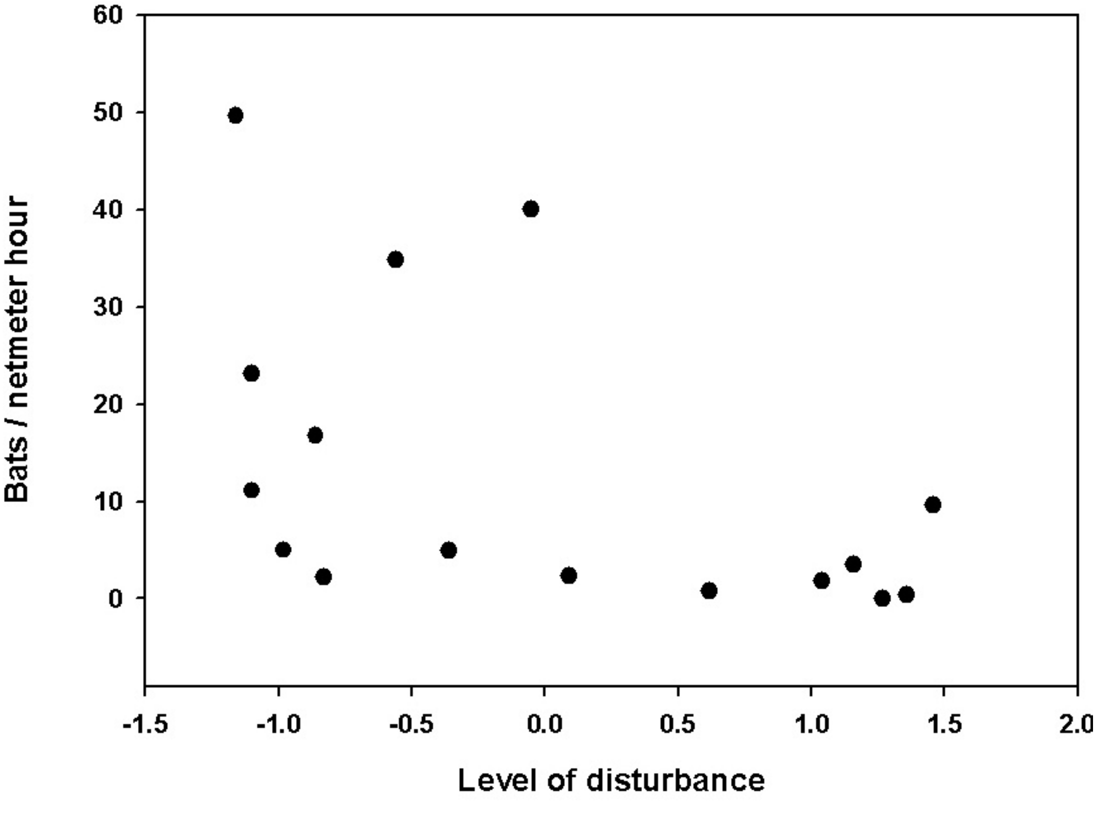

Figure 3.1: The level of disturbance at 16 mineral licks plotted against the number of bats captured per net meter hour at the corresponding mineral lick. 2-tailed Spearman-Rho correlation *rs* = 0.653; p < 0.006.

Table 3.3: The resulting factor scores of the regression factor analyses with an eigenvalue above 1 and the corresponding explained variance. All factor loadings of the variables after the performed varimax rotation.

	factor score I **“level of disturbance”**	**factor score II** **“size”**
eigenvalue	3.359	1.195
explained variation	67.1 %	23.9 %
	Variable factor loading	
size	-0.184	0.942
covering	0.912	-0.249
wateravailability	0.915	-0.290
minimum distance	0.809	0.472
hunting	0.963	-0.119

Discussion

Mineral licks deteriorate and harbor fewer bats in hunted areas

Defaunation caused by hunting and human encroachment in tropical ecosystems leads to a wide set of negative consequences; first and foremost to the direct loss of large herbivorous mammals and their ecosystem service of seed dispersal. Consequently, hunting causes shifts in ecosystem functioning (Wright, 2003; Wright *et al.*, 2007b; Terborgh *et al.*, 2008). We tested if the defaunation of forests has additional, and thus far unrecognized, negative consequences for frugivorous bat assemblages in Amazonian rainforests by lowering the quality of habitats for populations of bats. We argued that the lack of large mammals will cause the local disappearance of mineral licks, which are important for frugivorous bats during reproduction as a source for nutrients in Western Amazonia (Voigt *et al.*, 2007; Bravo *et al.*, 2008, 2010). Indeed, we found that hunting and disturbance of large mammals reduce the quality of mineral licks. In agreement with our expectation, we found more deteriorated mineral licks in areas with intensive hunting. Also, we captured fewer bats at deteriorated mineral licks than at natural mineral licks. According to our interviews with hunters from local tribal communities in the Yasuni Biosphere Reserve, mineral licks that were adjacent to villages became smaller over the past few years. Some of these mineral licks are currently close to getting lost for wildlife species, because larger mammals are either absent or reluctant to visit these sites close to human communities. In contrast, all functional licks were still visited by a large number of bats, as well as by a large diversity of larger mammals. If we take into account that mineral lick degradation is a relatively slow and gradual process, we may infer that not all of the licks fit in the dichotomic pattern of disturbed or undisturbed conditions. We documented intermediate levels of disturbance for two of the mineral licks, because not all indicator categories were consistent with the documented level of disturbance. Although the lick Km9 was rather isolated, the minimal distance to the next infrastructure was relatively small. However, our sensitivity analysis shows that results are sufficiently robust, even when switching the categories of the two respective mineral licks.

Table 3.4: Frugivorous bat species (alphabetical order) captured at 16 mineral licks in the Yasuni Biosphere Reserve, and corresponding numbers of captures. All species belong to the family (Phyllostomidae).

Species captured	**# captures**
Artibeus lituratus	16
Artibeus obscurus	10
Artibeus planirostris	32
Carollia brevicauda	9
Carollia castanea	3
Carollia perspicillata	12
Chiroderma trinitatum	55
Chiroderma villosum	9
Dermanura anderseni	7
Dermanura anderseni cf.	1
Dermanura glauca	1
Mesophylla macconnelli	40
Platyrrhinus brachycephalus	15
Platyrrhinus helleri	68
Platyrrhinus infuscus	3
Rhinophylla fischerae	3
Rhinophylla pumilio	4
Sturnira lilium	95
Sturnira magna	50
Uroderma bilobatum	34
Uroderma magnirostrum	1
Vampyressa bidens	42
Vampyressa thyone	192
Vampyrodes caraccioli	25

Mineral licks turn non-functional when accessibility is hampered or nutrient resources diminish, and thus visitors will no longer benefit from visitation. In this context, it seems most relevant that frugivorous bats probably depend on mineral licks to successfully raise their young. So far, this and several other studies have unmistakeably shown that frugivorous bats visit mineral licks especially during reproduction when nutritional demands of nursing females are elevated (e.g. Voigt *et al.*, 2007, 2008; Bravo *et al.*, 2008, 2010). The visiting behaviour of bats is probably linked to mineral supplementation (Voigt *et al.*, 2007; Bravo *et al.*, 2008, 2010) and possibly to the detoxification of detrimental secondary plant metabolites of their fruit diet (Voigt *et al.*, 2008). Our results suggest a drop in female and further in reproductively active individuals at the disturbed mineral licks. This may become problematic because chronic effects of for example low levels of sodium can have consequences for reproduction, which may affect the population dynamics of frugivorous animals (Freeland, Calcott & Geiss, 1985; Batzli, 1986). In areas with only low-quality mineral licks, frugivorous bats may suffer when not obtaining sufficient nutrients from their normal fruit diet. We found that mineral licks deteriorated with increasing disturbances. The coverage with leaf litter and saplings increased while at the same time water accessibility decreased. Thus, the observed decay in mineral lick quality is presumably responsible for lower abundances of frugivorous bat species and reproductively active females at disturbed mineral licks.

Reduced bat abundances at mineral licks may lead to forest simplification

Frugivorous bats disperse the seeds of many genera such as *Cecropia*, *Ficus*, and *Vismia* that constitute the largest plant biomass during early years of both forest succession and forest regeneration in gaps (Saldarriaga *et al.*, 1988). Frugivorous bats are therefore vital for forest regeneration and maintenance (Saldarriaga *et al.*, 1988; Gorchov *et al.*, 1993; Ghanem & Voigt 2012). The decrease in bat abundance observed in our study area may lead to a significant reduction in seed dispersal, which may ultimately lower the species richness of forests and thus simplify forest composition and structure. Klaus and Schmid (1998) proposed that the carrying capacity of frugivorous animals in some forest habitats may be influenced by the presence of mineral licks. Thus, a decrease in quality of habitat for frugivorous bats may ultimately result in a reduced carrying capacity for bat populations. Several authors have addressed a general simplification of forest structure in the Neotropics as a result of non-sustainable hunting of larger-bodied animals (e.g. Peres

& Palacios, 2007; Terborgh *et al.*, 2008). Wright and his colleagues (2007b) showed that small plants that depend on bats or birds for seed dispersal within forest ecosystems in Panama are benefiting from changes in plant species composition related to defaunation. However, there may be no such benefit for small-seeded plants in hunted areas within Western Amazonia; many frugivorous and omnivorous animals that disperse small-sized seeds of these plants depend on functioning mineral licks, which are becoming deteriorated and less accessible in hunted areas within this region. Consequently, simplification of forest structure in hunted areas of Western Amazonia may be more severe than expected, as a reduction in habitat quality may lead to declines in populations and ecosystem services of smaller seed dispersers. As a result, cumulative direct and indirect consequences of hunting will severely disturb pristine forest ecosystems and the species within them.

Conclusion

Mineral licks play an essential role not only for many larger mammals but also for bats. Medium and larger sized mammals in Western Amazonia are directly affected by human activities such as hunting or disturbance. Our results suggest that disturbance and defaunation may also affect frugivorous bat assemblages since they strongly depend on mineral licks as a supply for nutrients during reproduction. Therefore, the resulting defaunation sets ecosystem services of mammals at risk in two ways: 1) by directly eliminating seed-dispersing large herbivorous mammals and 2) by reducing the habitat quality for populations of seed-dispersing bats. The combination of these detrimental effects might lead to an extensive simplification of ecosystem functioning in Western Amazonia. Mineral licks should therefore be prioritized when habitat conservation or regeneration are considered.

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Chapter IV

Increasing Awareness of Ecosystem Services Provided by Bats

Simon J. Ghanem, Christian C. Voigt

Summary

Ecosystem services (ES) provided by animals are increasingly considered to be of economic value and essential for the well-being of humans. Yet, despite representing the second largest mammalian taxon, bats (order Chiroptera) are largely neglected in their relevance for ecosystem function. Here we review current literature concerning ecosystem services provided by bats and their behavior and highlight their economic value. Insect-feeding bats are key ecological players that control major pest insects, limit the propagation of disease vectors and provide energy via bat guano to cave ecosystems. Fruit eating and nectar drinking bats promote forest regeneration, support timber production and are essential for many food products by dispersing seeds and pollinating flowers of many tropical and subtropical plant species. Recent threats, such as the spread of white nose syndrome in North America, the construction of windmill farms, the hunting of flying foxes, and the loss of habitat have all put bats and their ES at risk.

Key words:

Disease limitation, ecosystem functioning, pest control, pollination, seed dispersal

Introduction

The 2005 synthesis report of the Millennium Ecosystem Assessment made a first attempt to summarize the relevance of animals for ecosystem services and the functioning of habitats worldwide (Millennium Ecosystem Assessment, 2005). Ecosystem services (ES) are defined as benefits to humankind derived from resources and processes supplied by natural ecosystems. The Millennium Ecosystem Assessment recognizes four categories of ES (1) provisioning services such as the production of fiber, clean water or food, (2) regulating services such as pollination or pest control, (3) supporting services such as seed dispersal, and (4) cultural services such as intellectual, academic or spiritual inspiration (Millennium Ecosystem Assessment, 2003).

In many cases, ES of wild animals such as the provisioning of food for local communities in the form of harvested fish, birds or mammals, are apparent. Other ES are more subtle but probably equally important for humans. For example, birds and insects have already been widely acknowledged for supporting ecosystems, the agricultural economy and the well-being of humans. McGregor (1976) estimated that 15 - 30% of the human diet in North America depends on pollination mediated by insects. Honey bees (*Apis mellifera*) are crucial pollinators of economically important crops such as rape (*Brassica napus*) and many fruits and vegetables. Recently, the significance of bees as pollinators became particularly apparent when populations declined due to Colony Collapse Disorder, which affected negatively the food producing industry (Klein *et al.*, 2007). Due to the loss of ES by dwindling populations of *Apis mellifera*, wild bee populations have gained recognition for being able to partially substitute the pollination services of honey bees (Greenleaf and Kremen, 2006). More than 920 species of birds also provide pollination services worldwide (Whelan *et al.*, 2008). Birds also play an important role in the control of insect and vertebrate pests. For example, many raptors, such as owls, falcons, and hawks, regulate rodent populations that may be detrimental for crop production at high densities (Whelan *et al.*, 2008).

In general, the contribution of bats to the maintenance of ecosystems is rarely acknowledged (but see e.g. Cleveland *et al.*, 2006; Kalka *et al.*, 2008; William-Guillén *et al.*, 2008; Boyles *et al.*, 2011; Kunz *et al.*, 2011). This is most likely due to their nocturnal and cryptic lifestyle and their negative reputation in many human cultures. However, bats are the second largest order of mammals (Nowak, 1994), with more than 1100 currently described species of bats (Simmons, 2005); only Rodentia have more species. Moreover, bats are the most diverse group of mammals in many tropical ecosystems (Simmons and Voss, 1998; Bass *et al.,* 2010). Recently, first attempts have been made to quantify the ES of Chiroptera in selected geographical regions such as tropical Asia (e.g. Fujita and Tuttle, 1991; Leelapaibul *et al.*, 2005), and North America (Cleveland *et al.,* 2006; William-Guillén *et al.,* 2008; Boyles *et al.,* 2011; Kunz *et al.,* 2011). Yet, the overall value of bats for human society in general and human well-being in particular has been largely underestimated (but see e.g. Cleveland *et al.,* 2006).

Bats provide all four categories of ES as listed by the Millennium Ecosystem Assessment. Cultures all over the world are intrigued by bats. In western cultures bats historically have had a negative connotation, as in the story of Dracula or as an ingredient in witches' potions. However, in eastern cultures the reputation of bats was substantially better; in these cultures bats are often represented as a symbol of luck and fortune (Allen, 1962; Kunz et al 2011). Today, bats provide cultural ES through their appearance in Blockbuster movies, TV series, and books. While bats are not always seen in a positive light, they leave an imprint on the hearts and minds of people all over the world. However, in this review we focus primarily on ES that are provisioning, regulating or supporting services, because they are closely related to the daily life and behavior of bats and because they are directly linked to the health and benefit of ecosystems and humankind. The feeding behavior of insectivorous and frugivorous bats, for example, leads to the consumption of insects or fruits and thereby to pest control or seed dispersal. The guano production of many cave dwelling bats is a direct result of their roosting behavior. As the guano of the roosting bats provides and supports cave ecosystems for many other vertebrate and non-vertebrate species. Moreover, the pollination of plants and the dispersal of their seeds just become effective precisely because of the bats' ranging behavior together with their usually large home ranges.

Here we review information about ES of bats in relation to three main ecological functions: the regulation of insect populations, dispersal of seeds and pollination of plants.

Insectivory

Insectivory is considered to be the ancestral diet for bats (Simmons *et al.*, 2008). Insectivorous bats are abundant and distributed throughout all continents, except Antarctica and small and remote oceanic islands (Figure 4.1 A-B). In some locations, such as caves, they form the largest aggregations of any wild mammal. For example, about 2.6 million wrinkle-lipped free-tailed bats (*Chaerephon plicata*) roost in the Khao Chong Pran Cave in Thailand (Hillman, 1999) and about 100 million Brazilian free-tailed bats (*Tadarida brasiliensis*) roost in a few caves in Mexico and southern U.S.A. (Wahl, 1993; McCracken, 2003). The most important ES of insectivorous bats is probably the control of herbivorous arthropods including pest insects, the control of arthropod disease vectors and the provisioning of bat guano (figure 4.2, table 4.1).

Pest control

Insect herbivory is a major problem affecting plant reproduction and reducing plant biomass production, diversity and distribution (e.g. Fine *et al.*, 2004). The top-down control of populations of herbivorous insects is a valuable ES of insectivorous animals by directly increasing the monetary gain of crop farmers and supporting the food production industry (e.g. Leelapaibul *et al.*, 2005; Federico *et al.*, 2008; Kalka *et al.*, 2008; McCracken *et al.*, 2008; Williams-Guillen *et al.*, 2008). Recently, bats have been identified as important top-down regulators of herbivorous insect populations (Kalka *et al.*, 2008; Williams-Guillén *et al.*, 2008; Böhm *et al.*, 2011). Bats have also been identified as important agents for biological pest control on farmland (Leelapaibul *et al.*, 2005; Williams-Guillén *et al.*, 2008). Interestingly, previous studies on the top-down limitation of insect populations have solely looked at bird predation and have even overestimated the impact of insectivorous birds on insect pest populations by ignoring the additional nocturnal pest control services of bats. For example, researchers have used cage-like exclosures around plants to quantify changes in the rate of herbivory when birds are prevented from feeding on phytophagous insects. However, by excluding vertebrate predators from a given plant or plant community both during the day and night, researchers have quantified accidently the combined effect of birds and bats on herbivorous insect populations and have falsely assigned this effect exclusively to birds (e.g. Holmes *et al.*, 1979; Greenberg *et al.*, 2000; Van Bael *et al.*, 2003). To determine the taxon-specific effect of insectivorous vertebrates on insect populations, it seems more appropriate to conduct night and daytime exclosures separately. Following this experimental protocol, recent studies have highlighted that bats are as important as birds for controlling populations of herbivorous insects (Kalka *et al.*, 2008; William-Guillén *et al.*, 2008; Böhm *et al.*, 2011). Moreover, Kalka *et al.*, (2008) provided substantial evidence that bats even have a larger impact on insect populations than birds. They could show that arthropod herbivory increased significantly in plants protected by nocturnal exclosures from foraging bats compared to those protected by diurnal exclosures that only preclude birds from feeding on arthropods.

Worldwide, humans are in competition with a multitude of pest animals for food, fiber and timber. These pest animals cause large monetary losses when not controlled (Daily, 1997). Losing insect-feeding bats due to habitat destruction or global climate change may put the natural pest control services of bats at risk, and thus, may cause large economic, environmental or human health repercussions. Chemical pest control could function as an alternative technological approach to natural pest control (Cleveland *et al.*, 2006); yet more than 500 insect and mite pest species have already developed resistance against insecticides. In addition, chemicals that act in a non-specific way towards a variety of animal species may not only affect insects, but also vertebrates, including humans. Thus, insectivorous bats can help to reduce the use of chemical pesticides in forestry or agricultural ecosystems (e.g. Cleveland *et al.*, 2006). Moreover, bats can help to keep insect populations below the so-called ‘economic injury level’ (e.g. Leelapaibul *et al.*, 2005; Federico *et al.*, 2008). The term ‘economic injury level‘ depicts the threshold value of lowest pest population density that causes significant economic damage to a crop yield (Stern *et al.*, 1959; Pedigo *et al.*, 1986). Yet, the large-scale application of toxins as well as the use of transgenic crops may lead to a decline in insect populations that may become too small to attract bats to feed on them (Federico *et al.*, 2008). Federico *et al.* (2008) suggested that bats, together with pesticide application, could have important long term economic benefits for crop producers. Insects that survive transgenic crops or pesticide toxins may either be resistant or survive by luck. Partially intoxicated insects are possibly more prone to bat predation when their natural behavior is unfavorably influenced. If insectivorous bats feed on these and potentially resistant insects, pesticide resistance may develop and spread at a slower rate in insect populations than without additional bat insectivory (Federico *et al.*, 2008). Therefore, bats may have an impact on crop profitability even when insect populations are low.

Figure 4.1: Five bat species representing the three major feeding guilds and their main ecological function. Insectivorous bats (A-B) primarily provide regulating and supporting ES by controlling arthropod populations. Frugivorous (C-D) and nectarivorous bats (E-F) mainly provide provisioning and supporting ES by pollination and dispersal of seeds. A lesser bull dog bat (*Noctilio albiventris*) feeding on a moth (A). An aerial hawking bat (*Centronycteris centralis*) (B). Seba’s Short-tailed bat (*Carollia perspicillata*) approaching an infructescence of *Solanum rugosum* (C). A Pygmy Fruit-eating bat (*Dermanura phaeotis*) pollinating a *Calyptrogyne ghiesbreghtiana* palm while feeding on its flowers (D). A Pallas's Long-tongued bat (*Glossophaga soricina*) pollinating an inflorescence of a Chupa-chupa tree (*Matisia cordata*) (E) and feeding on a neotropical succession plant (*Piper auratum*) (F).

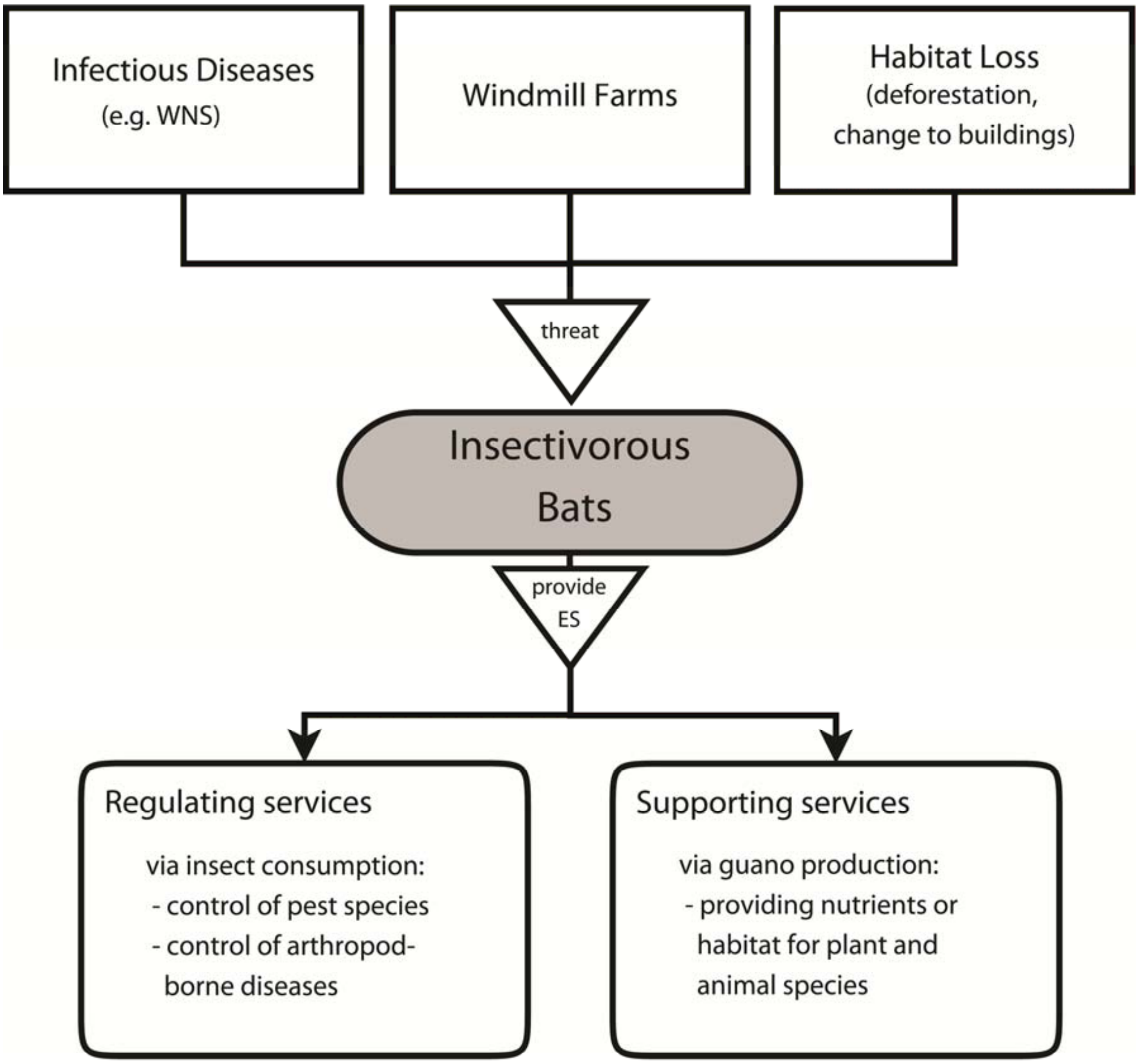

Figure 4.2: Illustration of the key ES provided by insectivorous bats including the major threats that put these services at risk.

Insectivorous bats eat a large variety of insects such as Homoptera, Lepidoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Orthoptera and Psocoptera (e.g. Lee and McCracken, 2005; Leelapaibul *et al.*, 2005). Some of these comprise the most destructive and costly forest and agricultural pests, like the cabbage looper (*Trichoplusia ni*, Lepidoptera), the army worm (*Spodoptera frugiperda*, Lepidoptera), the tobacco budworm (*Heliothis virescens*, Lepidoptera), the corn earworm or cotton-bollworm (*Helicoverpa zea*, Lepidoptera) and the white-backed or brown plant hopper (*Sogatella sp.*, Hemiptera), as well as many Dipterans. However, not all insect species consumed by bats can be considered as pests. Thus, it is probably safe to say that bats have a potential negative effect on insect populations.

Table 4.1: Examples of ecosystem services provided by insectivorous bats, their uses and occurrences with the yearly estimated economic value of the respective services. PC = pest control; BG = bat guano.

Service	**Pest or Service function**	**Service Provider**	**Land or reference**	**Common usage**	**Approx. yearly value**	**Source**
PC	Prolongation of insect toxin resistance	All insectivorous bats (e.g. *Tadarida sp.*)	Worldwide	Reduction of insecticide use	N.A.	Federico *et al.* 2008
PC	Cotton bollworm larvae (*Helicoverpa zea*)	Brazilian free-tailed bat (*Tadarida brasiliensis*)	South-central Texas	Insect pest control	500,000 US$	Betke *et al.* 2008
PC	Many insect pest species	All insectivorous bats (e.g. *Tadarida brasiliensis*)	North America	Insect pest control	22.9 billion US$ (range 3.7 - 53 billion US$)	Boyles *et al.* 2011
PC	Plant hopper (*Sogatella sp.*)	Wrinkle-lipped Free-tailed Bat (*Chaerephon plicata*)	Thailand	20,000 MTs of insect prey yearly	N.A.	Leelapaibul *et al.* 2005
BG	Bat guano as energy resource for cave ecosystems	E.g. grey bats (*Myotis grisescens*)	North America	Energy source	N.A.	Fenolio *et al.* 2006

On a daily basis, bats are able to consume insect masses equal to about two-thirds of their body mass, especially during pregnancy and lactation when energy requirements increase drastically (Barclay, 1994; Williams-Guillén *et al.*, 2008). Since juvenile bats cannot be weaned before they are almost fully grown, female bats have to build up almost all of the juvenile body via milk (e.g. Studier and Kunz, 1995; Korine *et al.*, 2004). Moreover, most female bats continue to nurse their young after fledging (Jones 1967).

So far, most of the studies on the effect of bats as pest control have focused on the North American continent, where for example Brazilian free-tailed bats, *Tadarida brasiliensis*, offer a large-scale service as natural pest controllers for the agricultural industry. For cotton farmers and related industry, Cleveland and co-authors (2006) estimated the economic value of pest control services provided by Brazilian free-tailed bats in south-central Texas as 741,000 US$ (range of estimates: 121,000 - 1,725,000 US$), which is substantial considering that the annual harvest of agricultural goods amounts 4.4 – 6.4 million US$ each year for the same area. More recently, Betke *et al.*, (2008) recalculated the annual monetary savings of farmers having to use fewer pesticides due to the consumption of pest insects by bats. Based on more recent estimates of populations of Brazilian free-tailed bats (4 million to 6 million as compared for six major caves in the U.S.A.), the agricultural industry of south-western U.S.A. saves about 500,000 US$ each year due to the ES provided by *Tadarida* bats. However, the populations of *T. brasiliensis* have dropped since 1957 when about 54 million bats were estimated to inhabit the same caves. Thus, ES provided by *Tadarida* bats are already on the decline in North America and conservation efforts have to be installed to preserve the regulative function of these insectivorous bats.

In a second example from the North American continent, Whitaker (1995) estimated the total insect consumption of an average maternity colony of 150 big brown bats (*Eptesicus fuscus*) based on their foraging days per year, dietary composition and the number of insects they found in guano pellets. According to this assumptions, colonies of big brown bats may consume up to 600,000 cucumber beetles (*Diabrotica sp.*, *Acalymma sp.*, Coleoptera), 194,000 june bugs *(Phyllophaga sp.*, Coleoptera), 335,000 stink bugs (Heteroptera), and 158,000 leafhoppers (Cicadellidae, Homoptera) during each growing season (Whitaker, 1995). Based on this article, Kunz and co-authors (2011) extrapolated, that the consumption of large numbers of adult cucumber beetles protects American farmers from about 33 million larvae, which could have a devastating effect on cultivated cucumber and cause million US$ losses to North American farmers. For 2010, Boyles and co-authors (2011) estimated that ES provided by insectivorous bats to the US agricultural industry amount about 22.9 billion US$ (range 3.7 billion US$ to 53 billion US$, annually). Consequently, more and more homeowners and farmers are requesting detailed information about how to attract bats to their land (California Agriculture, 1998). Optimal management of artificial roosts for insectivorous bats may promote bats as key actors in integrated pest control.

Insectivorous bats have not only a local effect but also a large scale effect on pest insects. This is because many bat species, such as *Tadarida brasiliensis*, fly up to an altitude of 3,000 m above ground and cover distances of more than 100 km each night (Davis *et al.*, 1962; Williams *et al.*, 1973; McCracken *et al.*, 2008). Many bats such as *Tadarida* and *Chaerephon* feed on high altitude windborne insects (McCracken, 1996; Fenton and Griffin, 1997; Leelapaibul *et al.*, 2005). The large feeding ranges of these and other bats, in conjunction with a long distance aerial drift of some insect pests are the main reasons why bats may influence insect populations beyond their actual home range (McCracken *et al.*, 2008). For example, the seasonal high-altitude migration of billions of moths emerging from agricultural crops of northern Mexico and southern Texas towards the north has been well documented (e.g. Wolf *et al.*, 1990). Several studies observed a striking coincidence between the seasonal availability of migratory moths and the relative contribution of moths to bat diets (e.g. Whitaker *et al.*, 1996; Lee and McCracken, 2002, 2005). Cleveland *et al.*, (2006) reported that the activity of *T. brasiliensis* is closely linked in time and space to the major emergence of bollworm moths (*Helicoverpa zea*), and recent radar monitoring of bats revealed that bats fly actively towards swarming insects over relatively large distances, which implies that they search for and specifically hunt for airborne insects on a large geographical scale (McCracken *et al.*, 2008).

The ES of insectivorous bats may apply to all regions where bats live. In Thailand, the wrinkle-lipped free-tailed bat *Chaerephon plicata* is a known control agent for plant hoppers, *Sogatella sp.* (Hemiptera), a biological pest insect of rice (Leelapaibul *et al.*, 2005). The 2.6 million *Chaerephon* bats inhabiting the Khao Chong Pran Cave consume at least 17.5 metric tons (MTs) of insects every day (Leelapaibul *et al.*, 2005). For the whole of Thailand, the total mass of insects consumed by *C. plicata* amounts to 20,000 MTs per year. Populations of plant hoppers boom every 8-10 years, often with drastic consequences for local settlements and national economies. In 1990, for example, brown plant hoppers (*Nilaparvata lugens*, Hemiptera) caused damages of up to 200-240 million US$ to the agricultural industry of Thailand (Vungsilabutr *et al.*, 2001).

Even though current information on ES of insectivorous bats is missing for ecosystems in Europe and Africa, bats can be expected to have a positive impact on crop production or silviculture in these regions as well. For example, Böhm and his colleagues (2011) recently reported on the impact of vertebrate exclosures on leaf damage in temperate oak (*Quercus robur*) forests in Germany. They showed that the top-down control of herbivory by bats and birds significantly reduced leaf damage and biomass loss in the oak forest canopy. This and other studies highlight that bats are not only essential members of intact ecosystems, but also central agents for functional diversity, which is central to the maintenance of ES of ecosystems (Tilman *et al.*, 1997). This need for functional diversity is compromised by the decline of bat species in many areas with often unforeseen consequences for pest insect populations in particular and the agricultural economy in general. Down to the present day, the overall impact of many insectivorous bat species on arthropod pests remains unclear. Recently, DNA-barcoding analyses of feces collected from little brown bats (*Myotis lucifugus*, Clare *et al.*, 2011) and eastern red bats (*Lasiurus borealis*, Clare *et al.*, 2009) did not reveal a pronounced consumption of potential arthropod pest species. Thus, until more evidence exists for pest control by species other than *Tadarida sp.*, *Eptesicus sp.* or *Charephon sp.*, we have to remain careful not to overstate the global impact of bats on pest insects. There is no doubt that bats need protection whether or not they consume arthropod pest species, but one has to be careful to extrapolate ES across all insectivorous bats.

Control of arthropod disease vectors

Many airborne and nocturnal insects are vectors for pathogens that are relevant for human health, such as the *Anopheles* mosquito which is the vector for the malaria pathogen *Plasmodium*. By feeding on these insects, insectivorous bats may have an indirect impact on disease outbreaks and pathogen prevalence. Up to now, we lack empirical data on how important bats are for controlling insect borne diseases. Around 1900, Charles Campbell established the first artificial daytime roosts for bats with the ultimate goal of controlling mosquito populations in the San Antonio area in Texas. Unfortunately, it is unclear to what extent the disappearance of malaria from this area was supported by his efforts (Murphy, 1989). Until now, only a few studies have demonstrated that free ranging bats are foraging on mosquitos. Reiskind and Wund

(2009) were among the first to show quantitatively that bats affect populations of mosquitoes (*Culex spp.*). Based on enclosure experiments, the authors demonstrated that aerial predation by northern long-eared bats (*Myotis septentrionalis*) reduced the nightly oviposition rate of mosquitoes by 32 %. In a recent study, Bohmann and her colleagues (2011) documented mosquito consumption of the African Free-tailed bat *Chaerephon pumilus* using DNA-barcoding of fecal samples. The authors revealed that 16 out of the 59 sampled fecal pellets (27.1 %) contained members of the family Culicidae (mosquitoes). Given these numbers, an impact of bats on disease-carrying mosquito populations seems plausible under certain conditions. Nonetheless, further dietary investigation, such as DNA Barcoding of bat feces, is needed to document the large-scale consumption of mosquitoes by bats under natural conditions.

Bat guano

Cave roosting bats produce large amounts of guano and this has been extensively used in many countries as natural fertilizer. In historical times, bat guano was also used for gun-powder production; a highly profitable business during those days. Between 1903 and 1923, companies removed at least 100,000 tons of bat guano from Carlsbad Caverns in New Mexico and used this guano mostly for fruit production in California. Some bat guano is still sold commercially as a natural fertilizer. In the Bracken Cave in Texas, which is now protected by Bat Conservation International, around 85 tons were exploited annually until the late 1980s. The provisioning of guano is not restricted to insectivorous bats, for example in Thailand or Egypt guano of fruit bats has been and is still harvested and used as fertilizer. The millions of bacteria and microorganisms in bat guano have not yet been thoroughly monitored for potential use in biotechnologies. However, Tanskul *et al.* (2009) recently isolated an alkaline proteinase from *Bacillus sp.* that originated from bat feces collected at the Wat Suwankuha cave in Thailand. The authors presumed that this alkaline serine-proteinase has a potential use as a detergent additive, due to its high stability against detergents. Thus, some of the unknown guano microorganisms could produce enzymes useful in detoxifying industrial wastes, producing natural insecticides, improving detergents or developing new antibiotics. Numerous of these organisms may be endemic, and for most of them we still lack detailed information about their biotechnological potential. Bat guano is also the main energy source in many temperate cave ecosystems, influencing trophic dynamics and community structure of cave specialists (Harris, 1970; Poulson, 1972; Gnaspini and Tranjano, 2000; Fenolio *et al.*, 2006). The endemic cave–living salamander *Eurycea spelaea* (Caudata), like many other species, depends directly on the food web based on bat guano (Fenolio *et al.*, 2006). Overexploitation of bat guano or a decline in bat populations may put these cave specialists at risk of local extinction.

In summary, insectivorous bats provide pest control services that can be seen as a direct contribution of bats to agricultural production since they substitute agricultural machines, labor, pesticides or fertilizers (Cleveland *et al.*, 2006). The monetary benefits for human society may be large, but have yet to be quantified.

Plant visiting bats

Mammals are efficient pollinators and seed dispersers and thus have a positive effect on plant reproduction in many habitats worldwide (Fleming and Sosa, 1994). In total, about 250 species of New World leaf-nosed bats (Phyllostomidae) and Old World fruit bats (Pteropodidae) utilize more than 500 species of trees and shrubs in tropical and subtropical ecosystems from which they consume fruits or nectar (Thomas, 1991).

Seed dispersal

By dispersing seeds from pioneer plants, neotropical bats promote the quick reforestation of areas such as large cleared areas within forests (Figure 4.1 C-D; e.g. Gorchov *et al.*, 1993). For example, trees and shrubs of the genera *Cecropia*, *Ficus*, *Vismia* and others constitute the largest plant biomass in the early years of forest succession (e.g. Saldarriaga *et al.*, 1988; Mesquita *et al.*, 2001). Seeds of these species are predominantly dispersed by phyllostomid or smaller pteropodid bats. Many bats swallow entire fruits, which facilitates the dispersal of several seeds per meal, sometimes even hundreds as in the case of fig fruits (Hodgkison e*t al.*, 2003). A fast transit time of about 20 to 30 minutes through the bats' digestive tract in combination with the relatively large feeding ranges of bats ensure that seeds are carried far away from their parent plant, which prevents intense seed predation by insects or mammals on the forest floor underneath the parent plant (Heer *et al.*, 2010). The dispersal of seeds by bats is distributed more evenly and over larger areas than that mediated by frugivorous birds. This difference is related to the specific foraging and feeding behavior of bats and birds. While birds often deposit the majority of seeds from a perched position under canopy trees, bats often defecate seeds while flying and thereby rather scatter the seeds along their flight paths (Charles-Dominique 1986; Thomas *et al.*, 1988; Gorchov *et al.*, 1993; Galindo-González *et al.*, 2008).

The influence of fruit-eating bats on the early succession of forests in the New and Old World was recently reviewed by Muscarella and Fleming (2007). In the Old World, the impact of bats on forest regeneration is thought to be less pronounced than in the New World (Muscarella and Fleming, 2007). This discrepancy stems from the fact that Old World pteropodids consume fruits mostly from trees or shrubs that are considered climax plant species, whereas New World phyllostomids consume fruits from both climax and pioneer plant species.

The important ES provided by Old and New World bats become particularly apparent when fruit, vegetable or timber products are considered (figure 4.3, table 4.2). Fujita and Tuttle (1991) reported that 23 % of the total plant related products in the Old World tropics depend on services provided by flying foxes. In Africa, about 34% of economically relevant timber species belong to families whose fruits are dispersed by pteropodid bats (Muscarella and Fleming, 2007). Even if tropical timber exploitation is declining, bats will have a crucial impact on the regeneration of populations of timber tree species in natural forests and the preservation of ecosystems. Indeed, entire ecosystems depend largely on bat mediated pollination or seed dispersal. In particular, bats play a crucial role for plants on island ecosystems, where the paucity of alternative efficient pollinators and seed dispersers results in a strong dependency of plants on bats for seed dispersal. Flying foxes are the only vertebrate pollinators and seed dispersers for plants on many islands of the Indio-Pacific Ocean (Cox *et al.*, 1991), which contrasts with tropical mainland areas, where monkeys, opossums, rodents or to a large extent birds usually occupy this niche as well (Thomas, 1991). Bat-dependent plants support the animal diversity of islands by providing food and habitat.

The relevance of bats as seed dispersers is well documented for Mango trees, *Mangifera indica*, and Shea trees, *Butyrospermum parkii*. The seeds of both species are dispersed by various pteropodid bat species (Fujita and Tuttle, 1991). The Shea Belt region in sub-Saharan Africa is known for the production of shea butter that originates from the fruit kernel. In Western Africa, the dominant variety of Shea tree, *Vitellaria paradoxa*, has a yearly production volume of 800,000 metric tons (MTs). In 2007, this volume accounts for an estimated monetary value of 115 million US$ for the top seven producing countries (FAO export statistics, 2007). Lovett (2005) estimated the total production of this tree species, based on 500 million productive trees, to be 2.5 million MTs with a value of 360 million US$. This economic value highlights the significance of bats as key seed dispersers in many ecosystems.

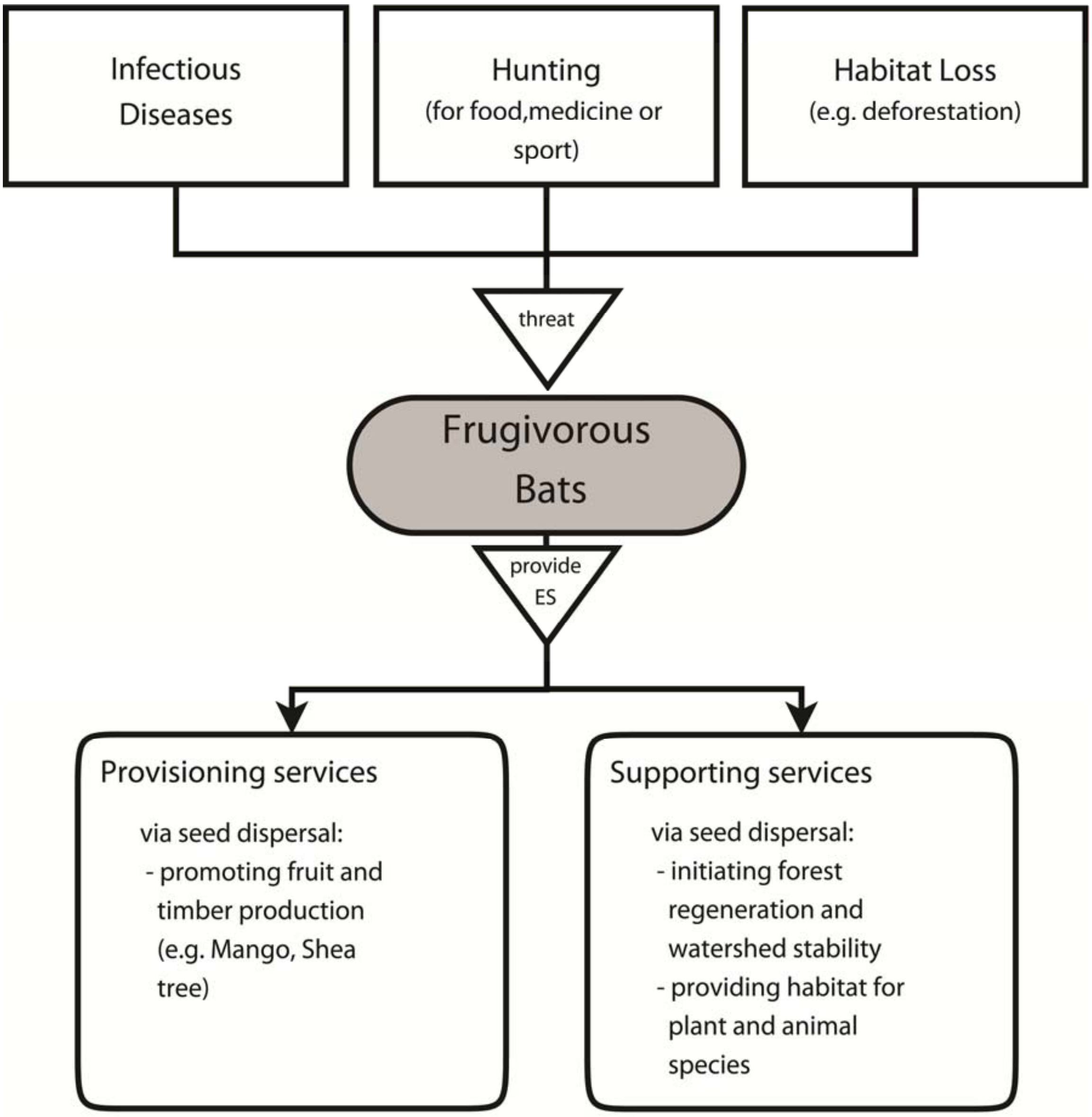

Figure 4.3: Illustration of the key ES provided by frugivorous bats including the major threats that put these services at risk.

Table 4.2: Examples of ecosystem services provided by fruit-eating and nectar feeding bats, their uses and occurrences with the yearly estimated economic value of their respective services. P = pollination; SD = seed dispersal.

Service	**Product**	**Service provider**	**Land or reference**	**common usage**	**Approx. yearly value**	**Source**
P	Durian fruit (*Durio spp.*)	Dawn Bat (*Eonycteris spelaea*)	World Market	Fruit, vegetable	1 billion US$	Biz Dimension Co., Ltd.
P	Agave (*Agave sp.*)	Curaçaoan Long-nosed Bat (*Leptonycteris curasoae*), Mexican Long-tongued Bat (Choeronycteris mexicana)	Mexico	Tequila, alcoholic beverage	Multi-million US$ market	López-López *et al.* 2010
SD	Shea tree (*Vitellaria paradoxa*)	Various pteropodid bat species	Africa, Shea Belt region, total production	Charcoal, timber, fuel, oil	360 million US$	Lovett, 2005
SD	34% of economically relevant timber species	Various pteropodid bat species	Africa	E.g. timber, food, cosmetics	N.A.	Muscarella and Fleming, 2007
SD	23 % of the total plant related products	Various pteropodid bat species	Old World Tropics	E.g. timber, food, cosmetics	N. A.	Fujita and Tuttle, 1991
SD	Pioneer plants (e.g. *Cecropia, Ficus, Vismia*)	Various Phyllostomid species (e.g. *Carollia*)	Neotropical Forest	Promote quick reforestation	N. A.	Gorchov et al. 1993

An overall calculation of ES by New and Old World seed dispersing bats is still lacking. The economic value of goods originating from bat-dispersed plants either grows or declines as local and global ecological conditions change. These global trends are influenced by habitat fragmentation, urbanization and changes in land use, or simply by fluctuating market structures that are driven by economic demands of the human society. These changing conditions make it necessary to recalculate the monetary benefits provided by bats at regular intervals.

Pollination

Many plant species require animal-mediated pollination for a successful seed set. The floral syndrome of pollination by bats is well documented and has been reviewed extensively by several authors (e.g. Baker, 1973; Dobat and Peikert-Holle, 1985). The flowers of bat-pollinated plants are usually large, open at dusk, provide large nectar volumes, and can be recognized by a white or pale-yellow color and a musky scent (Dobat and Peikert-Holle, 1985). The different genera of nectarivorous bats are generally characterized by long and narrow muzzles, delicate mandibles, reduced dentition, and long tongues (Figure 4.1 E-F, Freeman, 1995).

Human society benefits from the products of many bat-pollinated plants both in a direct way and in many indirect ways. The successful reproduction of plants pollinated by bats may provide other ES such as soil stabilization to maintain water catchment areas, or simply habitat for other plant and animal species. Several nectar-feeding and fruit-eating bats in the Old and New World tropics and subtropics are known to provide these valuable ES (figure 4.4, table 4.2). Bat pollination (Chiropterophily) can be found in numerous plant families, but it has mostly been studied in Bombacaceae, Passifloraceae, Mimosaceae, Caesalpiniaceae (reviewed in Bawa, 1990). Chiropterophily is restricted to the tropical and subtropical zone within 30° latitudinal from the equator (Dobat and Peikert-Holle, 1985). Many obligate nectarivorous bat species depend on the continuous phenology of flowering plants throughout the year or are known to migrate seasonally when flowering plants are not available (Fleming *et al.*, 1993).

Flying foxes and phyllostomid bats are capable of carrying large amounts of pollen over long distances, which is one of the criteria for efficient pollination (e.g. Law and Lean, 1999). Consequently, bats are able to connect remote plants and forest fragments by covering longer distances than terrestrial animals. In the Mesoamericas, about 60 species of agave plants are pollinated by the lesser long-nosed bat *Leptonycteris* *curasoae* and the Mexican long-tongued bat *Choeronycteris mexicana* (Ducummon, 2000). The juices of agave plants are fermented and distilled to the alcoholic beverage tequila. In 2008, a total of 227 million liters of tequila were produced in Mexico (López-López *et al.*, 2010), thus linking the ES of bats to a multi-million dollar market.

In contrast to many islands where flying foxes are the only vertebrate pollinators and seed dispersers, most of the pollination provided by bats in mainland areas should be considered as supporting ES, because bat pollinated plants are often pollinated by other taxa like insects, birds and other small mammals as well. In a recent review, the economic value of the pollinating service of all animal taxa was estimated to vary between 112 and 200 billion US$ globally (Kremen *et al.*, 2007). The specific economic value of pollination services by bats has not yet been quantified. Currently, we know of only a few examples where plant species depend entirely on a single pollinating bat species. In addition, the exact number of plant species pollinated by bats is yet unknown. ES of bats become most apparent when bat pollinated plants have a high economic value. The Durian Fruit *Durio spp.*, also known as King of Fruits, is a popular fruit from Southeast Asia that can be either consumed fresh or frozen, or processed to chips, powder, paste, cake, or other products. The dawn bat *Eonycteris spelaea* is the only effective pollinator of Durian trees, apart from the honey bee *Apis dorsata* (Bumrungsri *et al.*, 2009). Consequently, this bat species is responsible for the successful cultivation and maintenance of the semi-wild *Durio zibethinus* trees. Durian fruits play an increasing role in the Asian agricultural economy. In 2000, Thailand was the largest producer of Durian fruits with a production volume of more than 826,000 tons and a market value of about 575 million US$ (Biz Dimension Co., Ltd., 2011). The world production of Durian amounted 1,400,000 MTs in the same year. We estimate a hypothetical world market value of nearly 1 billion US$ for the ES of *Eonycteris spelaea*, when extrapolating the monetary value of Durian fruits in Thailand to other countries. In other markets such as Indonesia, the production and export volumes of Durian are still rising due to the fruit’s increasing popularity. Thus, our estimates are probably conservative. Overall, pollination of Durian trees by bats is essential for a significant sector of the Southeast Asian food economy. Therefore, conservation programs should support Asian bats so that they can continue to provide ES by pollination.

Threats such as habitat fragmentation are problematic for many bat species and consequently pollinating services of bats are at risk in many countries. A lack of pollinators in disturbed forest patches impedes the exchange of pollen between forest fragments and may consequently reduce the reproductive output of plant species (Quesada *et al.*, 2004).

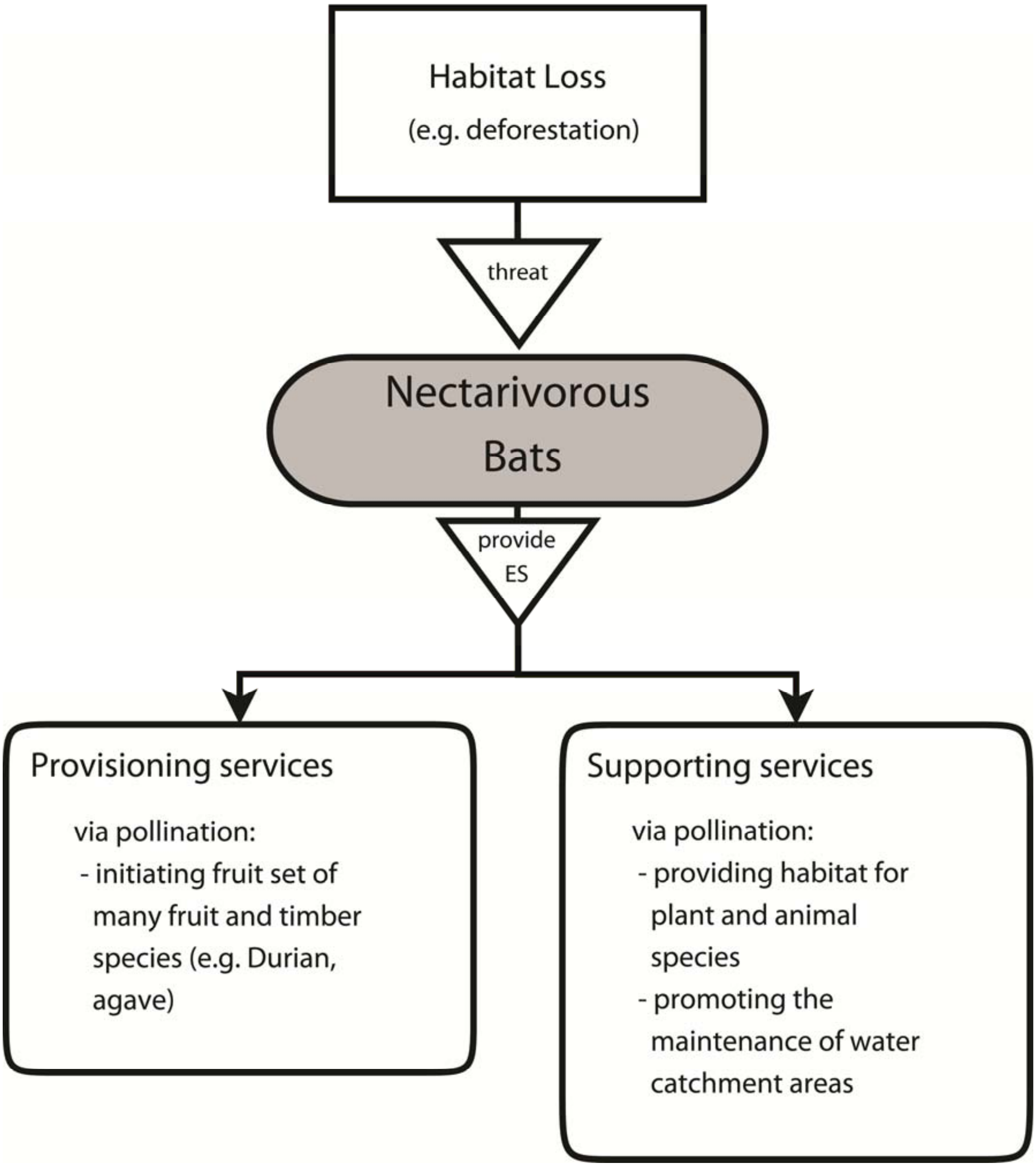

Figure 4.4: Illustration of the key ES provided by nectarivorous bats including the major threats that put these services at risk.

What can be done to preserve and promote ecosystem services by bats?

Despite their crucial role as ES providers, bats are under severe threats. For example, bat populations are rapidly declining in the Old World due to hunting for sport, adventure or meat, to control them as crop pests, or to use them for medical purposes (e.g. Fujita and Tuttle, 1991; Epstein *et al.*, 2009). In addition to hunting and poaching, global bat populations are also suffering from indirect poisoning through the over-use of agricultural pesticides, from habitat fragmentation, from changes in house construction and the related impact on bat roosts, and from recently emerging infectious diseases such as White Nose Syndrome (WNS). In the north-eastern USA, white-nose Syndrome is responsible for high rates of bat mortality (>75%) in hibernacula (Blehert *et al.*, 2008; Frick *et al.*, 2010b). Many of these diminishing populations may be key contributors to ES (e.g. *Myotis lucifugus* Frick *et al.*, 2010a). In a recent article Boyles and colleagues (2011) estimated that between 660 and 1320 metric tons of insects are no longer being consumed each year, due to the one million bats that have already died of WNS. Thus, a continuation of the epidemic spread of WNS throughout the USA will probably produce significant detrimental effects on the ecology of the whole continent. An improved understanding of the conservation status of bat species is therefore pivotal (Williams-Guillen *et al.*, 2008). The current threat of massive population declines in many species around the globe has raised awareness of their importance.

A significant drop in population sizes may put the ES of bats at risk even when bats may still persist at low densities. For example, ES of island flying foxes have been observed to collapse when critical thresholds in population numbers have been reached (McConkey and Drake, 2006). Sudden and drastic population declines are particularly problematic for bats since most species produce only one or two offspring each year (Wilkinson and South, 2002; Barclay and Harder, 2003). Such a low reproductive rate delays a recovery from population collapses substantially, and regeneration of disturbed ecosystems may require more time than anticipated (McConkey and Drake, 2006). Thus, it is vital to respond quickly before bat populations become functionally extinct in ecosystems.

There are many practical ways to respond effectively to decreasing bat population sizes and declining ES of bats. Ecologically important seed dispersers can be attracted to fragmented habitats by offering natural or man-made forest fragments that are planted with the goal of facilitating reforestation in the surrounding area (Guevara *et al.*, 2004, Zahawi and Augspurger, 2006). The survival of plants in such forest fragments could promote the input of plant species into species depleted areas, leading ultimately to an increase in the biological diversity of larger areas (Muscarella and Fleming, 2007). Kelm *et al.* (2008) suggested the use of artificial bat cavities to attract and keep important seed dispersers at disturbed areas. Such artificial roosts encourage bats to fly over areas which have been cleared of trees and thus promote seed dispersal into fragmented habitats. Efficient protection of daytime roosts of Old World flying foxes is also of great importance. Although many species are protected in most countries, bats are still vulnerable to illegal hunting, habitat loss and also to invasive species (Allen-Wardell *et al.*, 1998; Nyhagen *et al.*, 2004; Epstein *et al.*, 2009). In the Eastern Amazon lowlands, mineral licks support populations of frugivorous animals, including over 25 bat species (e.g. Voigt *et al.*, 2007). Protection of such hotspots of bat activity may lead to higher abundances of tropical fruit-eating bats, which are essential for forest regeneration (Montenegro, 2004). In an attempt to prevent the decline of insectivorous bat species, protection of cave ecosystems and reduction in the use of agricultural pesticides have also been suggested. At the same time, emerging diseases such as WNS should be studied, and strategies developed to mitigate the negative effects of diseases on bat populations. Most importantly, local people have to be educated to value the importance of bats as providers of ES. Education and the provisioning of scientifically sound information are crucial in order to maintain and increase awareness of the importance of bats for the global ecosystem.

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Chapter V

General Discussion

The general purpose of this dissertation was to gain insight into geophagy, or the consumption of soil enriched water, by tropical fruit-eating bats. Mineral licks, at which geophagy takes place, function as an ecological key resource for many frugivorous and omnivorous animals such as bats. The role of bats in ecosystem functioning is usually undervalued due to their cryptic lifestyle, as they are mostly active during the night. In this study, I focused on bat geophagy and the link between mineral licks and ecosystem functioning.

Geophagy - mineral licks as key ecological resource for many taxa

The consumption of soil or soil-enriched water has been described to be of essential importance for a wide range of animals. Examples for this behaviour can be found at mineral licks in the form of steep river banks (Figure 1.3) that are mostly visited by birds (e.g. Diamond *et al.* 1999, Gilardi *et al.* 1999, Brightsmith & Muñoz-Najar 2004, Lee *et al.* 2009) and at mineral licks in the form of muddy depressions farther inside the forest (Figure 1.4) that are mostly visited by animals such as hoofed mammals like tapir and manzana deer (Kreulen & Jagaer 1984, Mahaney & Hancock 1990, Lizcano *et al.* 2000, Montenegro 2004, Tobler *et al.* 2009), primates (e.g. Oates 1978, Blake *et al.* 2010, Blake *et al.* 2011) and bats (Tuttle 1974, Bravo *et al.* 2008, 2010, Voigt *et al.* 2007, 2008). More than a few explanations for mineral lick visitation and geophagy have been summarized (e.g. Klaus & Schmid 1998, Diamond 1999), but ultimate reasons behind this widespread behaviour are not completely unveiled (Mahaney & Krishnamani 2003). Nevertheless, the uptake of soil material is attributed to some medicinal use in nearly all studied species (Krishnamani & Mahaney 2000), suggesting that mineral licks are indispensable for many frugivorous species. The mineral supplementation hypothesis and the detoxification hypothesis are the two most common explanations for the observed visiting behaviour at mineral licks. The mineral supplementation hypothesis describes the need for essential minerals, such as sodium, calcium or potassium, for many taxa that cannot meet their daily requirements solely from nutrition (Jones & Hanson 1985, Powell *et al.* 2009). One example is the cross-taxonomic need for sodium, especially in the Western Amazon region, where mineral licks are used to minimize the nutritional deficit (Dudley *et al.* 2012).

The detoxification hypothesis assumes that the diet of birds and mammals requires the buffering of possible dietary toxins to prevent health damage or other disadvantages for the animals (Oates 1978, Gilardi *et al.* 1999, Voigt *et al.* 2008). The results of many of these studies clearly show that mineral licks are of unique value for a tremendous number of different species. The mostly frugivorous animals highly depend on the licks for the well-being of themselves and their young. In this study, I was particularly interested how frugivorous bats benefit from this visiting behaviour and how mineral licks can contribute to the bats' well-being. To gain insight into the ecological relevance of mineral licks to bats, I focused particularly on the two major hypotheses: mineral supplementation and detoxification of their fruit diet.

Geophagy – frugivorous bats visit mineral licks

During this study, the recurring bat-capturing in the Yasuni region in Ecuador showed that frugivorous bats, mainly of the subfamilies Sturnirae and Stenodermatinae, are visiting mineral licks in high numbers. Only 8 insectivorous bats have been captured at mineral lick sites, while more than 1063 frugivorous bats visited the mineral licks. Interestingly, about 80 per cent of the captured bats at the licks were females, with 79 per cent of them being reproductively active (over two thirds of all captured bats). These results are in concordance with earlier studies (Tuttle 1974, Voigt *et al.* 2007, 2008, Bravo *et al.* 2008, 2010), indicating a general importance of mineral licks for the reproductive output of frugivorous bat assemblages. Using video observations, I documented that bats drink water from small puddles at the mineral licks (**Chapter II**). As these mineral lick waters contain high levels of suspended solids and clay minerals, this drinking behaviour could clearly be linked to an intentional uptake.

In the west of the Andes, frugivorous animals have to cope with a diet that is low in nutrients but at the same time possibly enriched with secondary plant compounds that have negative consequences when eaten, such as intoxication effects. The reason for the scarcity in nutrients lies at least partly in the geographical isolation of the region from costal climate and marine input of, for example, sodium (Kaspari *et al.* 2008). Thus, the nutrient depletion of Amazonian soils over time may be the cause for low concentrations of nutrients in plants and their associated fruits (Stark 1970, Jordan & Herrera 1981). To reveal a shortcut in essential nutrients in the diet of frugivorous bats of the western

Andes region, I compared potential bat fruits from our study site in Ecuador with fruits from Costa Rica (**Chapter II**).

I could document that fruits from Ecuador have lower concentrations in sodium, potassium and phosphorus compared to fruits from Costa Rica, which is in conjunction with the study of Dudley and colleagues (2012). In addition to the diet analyses, I collected blood samples of frugivorous bats at mineral licks and open forest sites to compare their elemental blood composition with multi element analyses (ICP-MS and ICP-OES; for sodium (Na), potassium (K), magnesium (Mg), and iron (Fe)). Even though the elemental composition of blood in the body is highly buffered, I found differences in the elemental composition between blood from bats captured at mineral licks and at control sites, suggesting a supplementary nutrient consumption by bats. The observed higher values of Sodium, Potassium and Phosphorus in the elemental blood composition of mineral lick visiting bats, together with the reduced nutrient availability in their fruit diet, are in concordance with the mineral supplementation hypotheses. Thus, bats do supplement their fruit diet, at least in times of high demands.

I was further interested in studying if detoxification is a possible explanation for the visiting behaviour of frugivorous bats, since other authors have already proposed that detoxification is evident in birds (Gilardi *et al.* 1999) and mammals (Oates 1978). The faecal analyses in my study showed higher concentrations of non-plant-available soil minerals (aluminium (Al), titanium (Ti), yttrium (Y), lanthanum (La), cerium (Ce), and neodymium (Nd)) in faeces of frugivorous bats captured at mineral licks than in faeces of co-existing insectivorous bats that never visit mineral licks. These elements are insoluble in water and thus can be used as markers to detect soil consumption (*e.g.* Calabrese & Stanik 1995, Calabrese *et al.* 1997). The higher values allow me to conclude that frugivorous bats are able to take up soil minerals and suspended solids, which is a prerequisite to enable detoxification. Follow-on studies that have been running in Braunschweig University could document humic acids as well as clay minerals in the mineral lick water samples (unpublished data; **Chapter II**). Both compound classes are well known to detoxify secondary plant compounds (Gilardi *et al.* 1999, Slamova *et al.* 2011, Scheffer *et al.* 2002).

Thus, I provided evidence that frugivorous bats are benefiting at least from a dual function of their visiting behaviour at the mineral licks. Bats drink the mineral enriched water and thereby supplement their fruit diet with essential nutrients. Further, they are able to consume clay minerals and humic acids that have already been proven to detoxify secondary plant compounds of their fruit diet that are potentially toxic, carcinogenic or teratogenic. In areas where minerals and nutrients are difficult to obtain to fulfil their daily demands, negative consequences, such as a reduced reproductive output or survival-chance, can be assumed. As the function of mineral licks for frugivorous bats is at least partially solved, the importance of mineral licks for the well-being of frugivorous bat assemblages becomes obvious.

Mineral licks under threat – disturbance and poaching

A conservation-oriented question of this thesis was the role of mineral licks for frugivorous bat assemblages that are, as important seed dispersers, massively involved in forest regeneration (e.g. Gorchov *et al.* 1993, Ghanem & Voigt 2012). This study draws attention to the important role of mineral licks in habitat conservation and ecosystem functioning.

Tropical ecosystems are under threat in various ways. Many studies in the South and Central American tropics have focused on the direct negative influence of hunting on larger-bodied animal populations. Poaching in Amazonian forests affects mostly medium and larger sized mammals directly, because hunters prefer larger prey species (Bodmer 1995). Such species include the red brocket deer *Mazama americana*, the collared peccary *Tayassu tajacu*, or the lowland tapir *Tapirus terrestris*. In the last decade, after years of research on the direct effects of hunting, researchers started to focus on indirect effects caused by the defaunation of larger-bodied forest animals (Redford 1992, Wright 2003, Andresen & Laurance 2007, Terborgh *et al.* 2008). Hunters' general preference for larger prey can lead to an evident shift in species composition because with the disappearance of large bodied mammals, plant species with larger-sized seeds are also becoming threatened, as only larger mammals can disperse their seeds. Several authors have addressed the possibility of a general simplification of the forest structure in the Neotropics as a result of non-sustainable hunting of larger-bodied animals (e.g. Peres & Palacios 2007, Terborgh *et al.* 2008). Lower abundances of frugivorous animals may lead to significantly reduced seed dispersal, which may ultimately lower the species richness of forests and thus simplify forest composition and structure, with long term negative effects for forest biodiversity and ecosystem function (Peres & Palacios 2007, Terborgh *et al.* 2008). In addition, larger-sized animals are of pivotal importance to mineral lick accessibility, as they prevent seedlings from overgrowing the mineral licks. My results of this study unequivocally show that disturbance and defaunation of larger-sized animals will indirectly affect frugivorous bat assemblages since they especially depend on mineral licks in times of reproduction (**Chapter II & III**). In addition to hunting, infrastructure construction or community life may negatively influence ecosystem functioning. All over the world roads are built to link communities with often devastating side effects. In tropical rainforests every road not only disturbs the actual area it is built on, but also affects the surrounding forest area (Johnson & Cabarle 1993, Kummer & Turner 1994, Chomitz & Gray 1996, Laurance *et al.* 2002). With new roads in formerly pristine areas, humans become encouraged to cultivate plantations and to settle and build new communities along the road (Greenberg *et al.* 2005), with often severe impacts such as illegal logging (Aguirre 2007) or unsustainable hunting (Dew *et al.* 2003, Franzen 2006).

Over the course of this study it became clear that ecosystem functioning is put at risk by disturbance or hunting in areas where mineral licks support a large number of frugivorous and omnivorous animals. The carrying capacity of some forest habitats for frugivorous animals may be influenced by mineral lick presence (Klaus & Schmid 1988). I was able to document a reduction in habitat quality for frugivorous bats in the surrounding of the oil extraction sites (Maxus road) in the Yasuni National Park. My results unambiguously show that the long-term defaunation caused by disturbance and poaching lead to mineral licks that are inoperative as they become overgrown by plants (**Chapter III**). Thus, the overall accessibility of mineral licks was reduced in areas that suffer from constant negative impacts such as poaching of larger-bodied animals as well as oil extraction and its related facilities. This drop in habitat quality may ultimately result in a reduced carrying capacity for bat populations in the forest. The lower bat abundances I observed in my study area may lead to significantly reduced seed dispersal, which may ultimately lower the species richness of forests and thus simplify forest composition and structure. Consequently, the expected forest structure simplification in hunted areas could largely outweigh its proposed extend, simply because a reduction in habitat quality may impair smaller seed dispersers and their ecosystem services as well.

Therefore, direct and indirect consequences of hunting will add up with a general disturbance to the overall negative human impact on pristine forest ecosystems. The subsequent defaunation puts ecosystem services of mammals at risk in two ways: 1) It eliminates seed-dispersing large and medium sized mammals, and 2) It reduces the habitat quality for populations of seed-dispersing bats. Both could cause an intensified simplification of ecosystem functioning in western Amazonia, as frugivorous bats and other smaller mammals are dispersing seeds of usually small-seeded pioneer plants.

Field studies - Implications for science and conservation

Fundamental research in ecology, as carried out in this thesis, is an important element for the justification of conservation projects. The **chapters II** and **III** provide insight into the visiting behaviour of frugivorous bats at mineral licks. The bats’ dependence on that resource, along with many studies reporting of a similar dependence by animals of other taxa, supports the idea of mineral licks as a key resource for a variety of herbivorous species. This valuable fact as well as information on the ecology of many species could only be obtained at the actual place where the animals live. Due to the extensive and reoccurring capturing of bats in this study, I could document many rare species that exist in the Yasuni region. Thus, ecological field studies will help to achieve information on animals that is usually difficult to collect, for example for rarely captured species such as the *Uruderma magnirostrum* or some *Vampyressa* species. The information that is gained via field studies is vital to be able to propose national parks or other protected areas. This information will be useful for the awarding or rejection of construction projects in the future, as well as for concessions or licenses, for example for mining, oil extraction, forestry rights, energy and water supply or even waste removal. Conservation plans or the proposal of protected areas that is not based on scientific data will lead to a squandering of money or even worse to ineffective conservation. Field studies are a cost and time consuming way to obtain data, especially at a time when cost effective computer supported models are able to predict many things, ranging from species’ home ranges to climate change. But even today, data-supported field work is necessary to finally validate these models.

Bats as ecosystem service provider – the importance of bats

The knowledge of an animal’s ecology is essential to appropriately react to conservation challenges. As frugivorous bats disperse seeds and pollinate the flowers of numerous plant species, they become vital for forest regeneration and maintenance (Saldarriaga *et al.* 1988, Gorchov *et al.* 1993, Fleming & Sosa 1994). The link between frugivorous bats, the ecosystem services they provide, and their dependence on operational mineral licks highlights the need for bat and mineral lick conservation to protect a functioning ecosystem. Because bats do not only provide ecosystem services in the Western Amazon region but worldwide, I broadened the scope of this present study to the general importance of bats on a global scale. Bats do provide ecosystem services nearly all over the globe by controlling insect pest species, dispersing seeds and pollinating flowers of plants. Their vast importance to ecosystem functioning and human well-being has been elaborately discussed in **Chapter IV**.

Despite their crucial role as ecosystem service providers, bats all over the world are under severe threats. In the Old World, bat populations are rapidly declining as bats are hunted for sport, adventure or meat, to control them as crop pests, or to use them for medical purposes (e.g. Fujita & Tuttle 1991, Epstein *et al.* 2009). In Western Amazonia, bats are not hunted, but for their long-term survival they depend on operational mineral licks. In addition to the negative effects of hunting and poaching, global bat populations are also suffering from habitat fragmentation and the related impact on bat roosts, from changes in house construction, and from recently emerging infectious diseases such as White Nose Syndrome (WNS). In the north-eastern USA, WNS is responsible for high rates of bat mortality (>75%) in hibernacula (Blehert *et al.* 2008, Frick *et al.* 2010b). Many of these diminishing populations may be key contributors to ecosystem services (e.g. *Myotis lucifugus* Frick *et al.* 2010a); an improved understanding of the conservation status of bat species is therefore pivotal (Williams-Guillen *et al.* 2008). Decreases in population size can jeopardize ecosystem services even when bats may still persist at low densities. The ecosystem services of island flying foxes, for example, have been reported to collapse when a critical threshold in population numbers has been reached (McConkey & Drake 2006). Sudden and drastic population declines can be particularly problematic for bats since most species produce only one or two offspring each year (Wilkinson & South 2002, Barclay & Harder 2003). Thus, a possible recovery from population collapses will be delayed by such low reproductive rates, and regeneration of disturbed ecosystems may require more time than anticipated (McConkey & Drake 2006). It is therefore vital to respond rapidly before bat populations may become functionally extinct in ecosystems.

Conservation challenges in the Yasuni region

Conservation and sustainable management of tropical rainforests has become increasingly challenging over the last decades. This is true because many emerging market countries such as Ecuador heavily depend on natural resources as oil or gas for industrial and infrastructural progress. In Ecuador, half of the total export earnings and one-third of the annual federal budget depend on the oil industry (United States Energy Information Administration 2009). These natural resources often overlap with ecologically important areas, such as proposed indigenous reserves, natural reserves or other protected or unprotected forest areas, as is the case for my study site – the Yasuni region. Multiple on-going and planned large-scale projects in the Napo Moist Forest terrestrial ecoregion make it difficult to protect this outstanding biodiversity hotspot (Bass *et al.* 2010). A vast and quickly advancing set of oil blocks with associated roads and infrastructure are being established and finally exploited in this area (Figure 5.1). In the time leading up to spring 2012, the Ecuadorian Government has made no decision on the Yasuni - ITT initiative. Whether the initiative will succeed by convincing donors and policy makers to leave Ecuador's largest oil fields untouched for financial compensation (Yasuni-ITT Trust Fund) remains an unanswered question. In addition, construction sites on parts of Trans-Amazonian Highway are still running (IIRSA Eje Manta-Manaus). This waterway and road combination was originally planned to link Brazil to the Western part of the Amazon and the Pacific Ocean. Furthermore, many parts of this ecoregion suffer from legal and illegal logging. This is especially evident on the Peruvian side of the Yasuni area, where large logging projects are advancing (e.g. Aguirre 2007, Bank Information Center 2009). These and many other projects will speed colonization, forest fragmentation, and ultimately deforestation in the region as well as its rainforest ecosystems. These conservation conflicts inevitably lead to ethical problems that cannot be solely solved by scientists or policy makers. This dissertation identifies mineral licks as keystone ecosystem players, as their visiting frugivorous ecosystem service providers, particularly bats, are pivotal for forest regeneration and maintenance. Based on this and on the findings that have been collected in several research projects over the last years (e.g. Franzen 2006, Finer *et al.* 2008, 2009, Holbrook & Loiselle 2009, Bass *et al.* 2010) policy makers are to be called to improve their management for sustainability and protection in large intact pieces of this forest area. The overall aim needs to be to maintain the high biodiversity ecosystems that are still functioning.

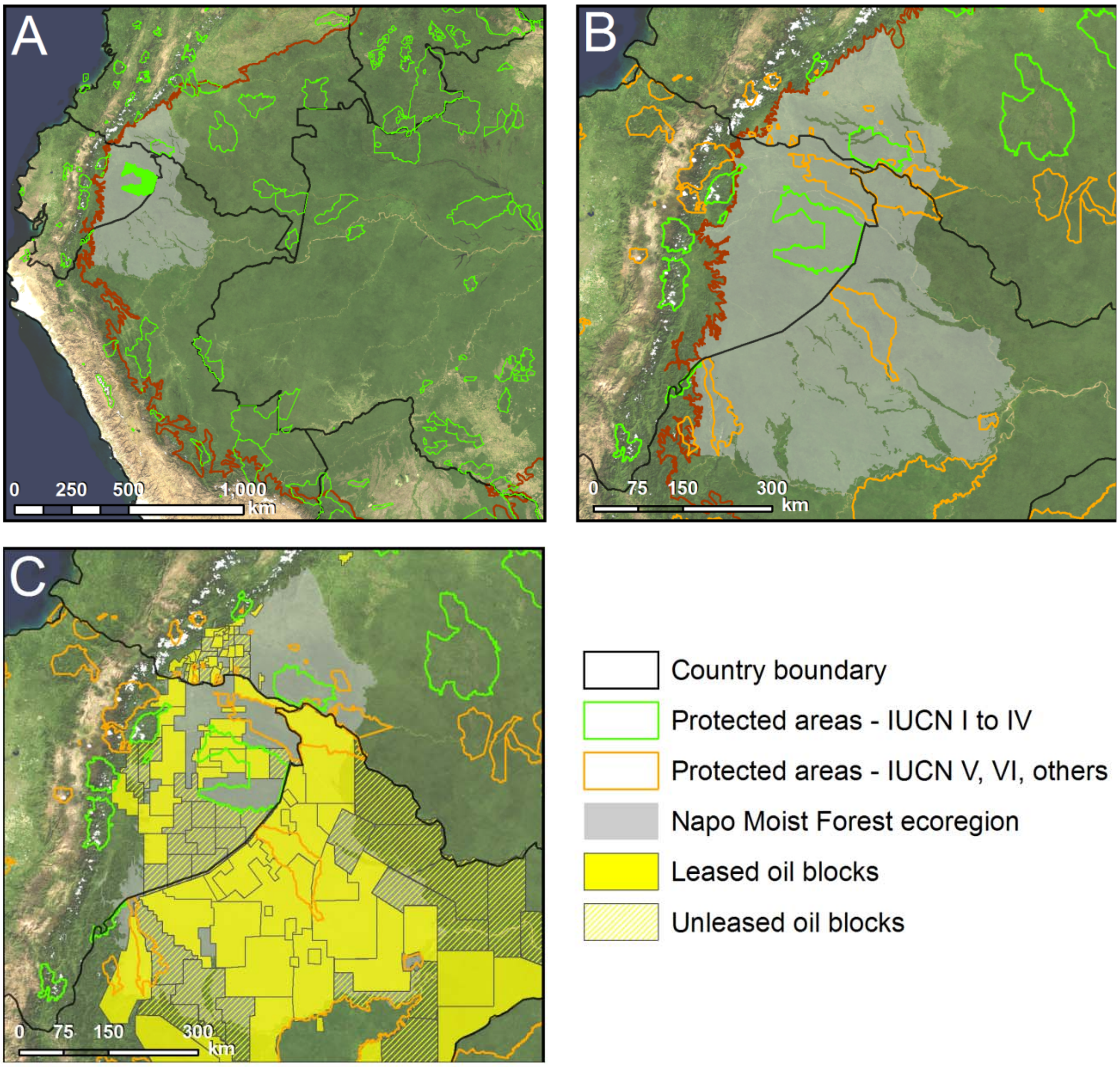

Figure 5.1: The greater Napo Moist Forest ecoregion with protected areas and oil blocks. A) Strict protected areas (IUCN categories I–IV) in the western Amazon. B) All protected areas within the Napo Moist Forests ecoregion. C) Oil blocks covering the Napo Moist Forests ecoregion. Copyright by Bass et al. (2010) published under CC-BY 2.5.

Conclusive remarks

In the “United Nations decade on biodiversity (2011-2020)”, governments from all nations are advised to support the conservation of important biodiversity hotspots such as the Napo Moist Forest terrestrial ecoregion. The results of my thesis highlight the importance of mineral licks as a key ecological resource for frugivorous bat assemblages, as frugivorous bats – mainly reproductively active females – visit the mineral licks to fulfil their nutritional demands and to detoxify their fruit diet. The knowledge of the ecology behind the bats and many of the other animals visiting mineral licks will be useful for the preservation of this biodiverse region. By identifying keystone ecosystem players, field studies such as this study are a prerequisite to plan and to coordinate on-going and future conservation efforts. As mineral licks and their visiting frugivorous ecosystem service providers are pivotal for forest regeneration and maintenance, their conservation should be considered a major goal for Western Amazonia. Another very important component in the long–term success of conservation efforts is the direct involvement of the local inhabitants. It is key to raise the awareness for the value of biodiversity and ecosystem functioning. Education and the provisioning of scientifically sound information are crucial in order to maintain and increase awareness of the importance of biodiversity and the services nature can provide for the global ecosystem.

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Curriculum Vitae

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Selbstständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Doktorarbeit eigenständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe.

Berlin, den 30.03.2012

Simon Ghanem