Impact of habitat fragmentation on selected amphibian species in the fragmented landscape of the Mata Atlântica at the Atlantic Plateau of São Paulo, Brazil

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The frog does not drink up the pond in which it lives.

Chinese proverb

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1.1 Einleitung

Biologische Diversität oder Biodiversität ist, vereinfacht ausgedrückt, die Vielfalt des Lebens auf der Erde (WILSON 1997). Seit Beginn der systematischen Forschung konzentrieren sich Biologen auf die Inventarisierung von Arten. Aktuelle Schätzungen für eukaryote Spezies besagen, dass heute ca. 300.000 Pflanzenarten, 45.000 Wirbeltierarten und mehr als 3.000.000 Invertebratenarten beschrieben sind. Die genaue Zahl ist unklar. Konservative Schätzungen und Voraussagen gehen von einer Gesamtzahl von insgesamt sieben Millionen Eukaryotenarten weltweit aus, beschriebene und bisher unbeschriebene (MAY 1997). Die Mehrzahl dieser sieben Millionen Arten sind Tiere und davon ca. 85% landlebend (PIMM und RAVEN 2000). Ungefähr zwei Drittel aller heute bekannten Eukaryotenarten leben in den tropischen Regionen der Welt. MYERS et al. (2000) identifizierten 25 so genannte "Hotspots" der Biodiversität der Welt. Insgesamt befinden sich demnach 44% der Gefäßpflanzenarten und 35% aller bekannten Säuger-, Reptilien-, Amphibien- und Vogelarten innerhalb dieser Hotspots. Dennoch bedecken diese Schwerpunkte der Artenvielfalt nur ca. 1,4% der Landmasse der Erde. Von den 25 identifizierten Diversitätsschwerpunkten befinden sich 19 in tropischen Regionen.

Innerhalb der hochdiversen Artengruppen nehmen Amphibien eine herausragende Stellung ein. Der Wissenschaft sind heute mehr als 6000 verschiedene Amphibienarten bekannt (FROST 2006). Es sind demnach weltweit mehr Amphibienarten als Säugerarten beschrieben (GLAW und KÖHLER 1998). Wie im Allgemeinen für Eukaryotenarten gültig, so gilt auch im Speziellen für Amphibien, dass die tropischen Regionen der Erde, im Fall der Amphibien insbesondere die Tropen der neuen Welt, Diversitätsschwerpunkte darstellen (DUELLMANN und HEATWOLE 1999). Legt man jährliche Neubeschreibungen zu Grunde, sind mit hoher Wahrscheinlichkeit noch immer viele Arten unbeschrieben. Zwei Drittel aller neu beschriebenen Amphibienarten sind neotropische Arten (GLAW und KÖHLER 1998). Doch diese extreme Diversität der Amphibien ist aus verschiedenen Gründen besonders bedroht. Durch ihre besonderen Reproduktionsmodi, den Lebenszyklus und die Besonderheiten der Morphologie sind Amphibien in erhöhtem Maße sensibel gegenüber Umweltveränderungen und Umweltverschmutzungen. Aufgrund dieser erhöhten Sensibilität werden Amphibien häufig als Indikatoren für die Anzeige und den Grad von Umweltveränderungen genutzt (MYERS 1993; BLAUSTEIN et al. 1994; TYLER 1994; ALFORD und RICHARDS 1999; PINEDA und HALFFTER 2004). Allerdings führte diese besondere Exponiertheit der Amphibien aufgrund massiver globaler Umweltveränderungen in den vergangenen Dekaden zu einem weltweiten Amphibiensterben (ALFORD und RICHARDS 1999; HOULAHAN et al. 2000; HOULAHAN et al. 2001; STUART et al. 2004). Als Folge ist heute ein Drittel aller bekannten Amphibien der Welt bedroht (MENDELSON et al. 2006). Dieser Rückgang der Amphibien weltweit geht einher bzw. ist Teil eines globalen Verlusts an Biodiversität. Insbesondere die tropischen Regionen der Erde sind vom allgemeinen Verlust der Artenvielfalt betroffen (PIMM und RAVEN 2000). Da die Tropen einen Großteil der Schwerpunkte der Biodiversität beherbergen (MYERS et al. 2000), ist dieser Verlust besonders verheerend. Einer dieser besonders betroffenen Schwerpunkte ist der brasilianische atlantische Regenwald oder "Mata Atlântica".

Mata Atlântica ist der Sammelbegriff für alle Waldtypen des ursprünglichen Areals zwischen 8° und 28° südlicher Breite und 100km landeinwärts im Norden bis zu 500km im Süden (DEAN 1995). Der atlantische Regenwald erstreckte sich ursprünglich über 1,3 Millionen km^2. Mit einem Anteil von insgesamt 1,1 Millionen km^2 beherbergte Brasilien dabei den größten Teil. Nur kleinere Ausläufer der Mata Atlântica reichen bis nach Paraguay und Argentinien (MORELLATO und HADDAD 2000; OLIVEIRA und FONTES 2000). Das gesamte Biom ist durch außerordentlich hohe Endemiegrade von Wirbeltierarten geprägt: ca. 30% bei Vogel-, Säuger- und Reptilienarten. Die hier vorkommenden Amphibienarten sind zu 90% endemisch (MYERS et al. 2000). Das Gebiet der Mata Atlântica beherbergt heute ca. 60% der brasilianischen Bevölkerung. Das entspricht ca. 110 Millionen Menschen (IBGE 2001). Die ehemaligen Bereiche der Mata Atlântica gehören zu den am stärksten entwickelten und industrialisierten Gebieten Südamerikas. Diese Entwicklung führte dazu, dass heute weniger als 7,6% der ursprünglichen Fläche der Mata Atlântica noch von natürlichen Wäldern bedeckt sind (SOS MATA ATLÂNTICA und INPE 2002). Die verbliebenen bewaldeten Gebiete sind meist kleinräumige, gestörte Waldfragmente oder befinden sich in unzugänglichen, steilen Höhenlagen (OLIVEIRA und FONTES 2000). Habitatzerstörung und –fragmentierung durch Sammeln von Feuerholz, illegalen Einschlag und das Eindringen fremder Arten bedrohen die Mata Atlântica und ihre Fauna heutzutage besonders (TABARELLI et al. 2005).

Generell gehören die Zerstörung und Fragmentierung des Lebensraumes zu den wichtigsten Ursachen für das Aussterben von Arten (HENLE und STREIT 1990; SARRE et al. 1996; PIMM und RAVEN 2000; SALA et al. 2000; YOUNG et al. 2001; HENLE et al. 2004b; ETEROVICK et al. 2005). Die fortschreitenden weltweiten Veränderungen der Landnutzung, die in besonderem Maße in der Mata Atlântica zu beobachten sind, haben zu einem verstärkten Lebensraumverlust bzw. zu einer zunehmenden Isolation verbliebener Habitate geführt. Hauptfaktoren, die im Bezug auf Habitatfragmentierung die Artenvielfalt oder Biozönose beeinflussen, sind 1) die räumliche Struktur einer Landschaft wie beispielsweise Habitat-größe und –isolation, 2) Habitatcharakteristika bzw. –qualität und 3) biologische Eigen-schaften der betroffenen Arten (WITH and CRIST 1995; HENLE et al. 2004a). Allerdings sind nicht alle Tier- und Pflanzenarten in gleichem Maße von der Zerstörung und Fragmentierung ihres Habitats betroffen (HENLE et al. 2004a). Die biologischen Eigenschaften betroffener Arten wie Ausbreitungsvermögen, Reproduktionspotential oder Habitatpräferenzen spielen eine herausragende Rolle für die Empfindlichkeit gegenüber Habitatfragmentierung (HENLE et al. 2004a). Ein besseres Verständnis dieser unterschiedlichen Sensibilität von Arten gegenüber Änderungen des Habitats ist ein unverzichtbarer Beitrag sowohl zur Verbesserung ökologischer Theorien und der Interpretation evolutionärer Entwicklungen, als auch für die Prioritätenfindung und die Identifizierung von Zielarten in der angewandten Naturschutzforschung (HENLE et al. 2004a). Detaillierte Kenntnisse der durch Fragmentierung hervorgerufenen Änderungen in der Ökologie betroffener Arten bzw. innerhalb einzelner betroffener Populationen sind dabei für das Verständnis der Prozesse, die sich beim Aussterben von Arten innerhalb eines Ökosystems abspielen, essentiell (HENLE et al. 2004a). Die Mehrzahl der in den Tropen lebenden Arten lässt derartig detailliertes Wissen vermissen

(YOUNG et al. 2001). Weitergehende Studien zur Ökologie einzelner Arten sind daher eine der Schlüsselprioritäten in der Fragmentierungsforschung in tropischen Ökosystemen (BIERREGAARD et al. 1997).

Insbesondere zur Ökologie tropischer Amphibien in fragmentierten Landschaften ist bisher wenig bekannt. Dabei hat die Fragmentierung des Lebensraumes für Amphibien und andere Arten mit geringer Mobilität und eingeschränkten Fähigkeiten der Migration besonders starke Konsequenzen (SCBD 2003; MALCOLM et al. 2006). Dies spiegelt sich auch in dem weltweit beobachteten starken Rückgang von Amphibien wider, zu dessen wahrscheinlichen Hauptursachen Habitatfragmentierung und –zerstörung zählen und der ebenfalls bereits für die Mata Atlântica dokumentiert wurde. Alle in der brasilianischen Roten Liste als gefährdet eingestuften Amphibienarten sind Arten der Mata Atlântica. Schwerpunkte sind besonders die Bundesstaaten Rio de Janeiro und São Paulo (SILVANO und SEGALLA 2005). Bestehende detaillierte Untersuchungen zu neotropischen Amphibien beziehen sich häufig auf die Ökologie einzelner Arten, ohne jedoch den Einfluss von Habitatveränderungen mit einzubeziehen (z.B. ZIMMERMAN und SIMBERLOFF 1996) oder, wenn derartige Veränderungen berücksichtigt werden, auf die Zusammensetzung der Artgemeinschaft (z.B. BIERREGAARD et al. 1997; TOCHER et al. 1997). Aus dem Gebiet der Mata Atlântica liegen besonders wenige Informationen über die Auswirkungen von Habitatveränderungen auf die Ökologie von Amphibien vor. Untersuchungen zur Zusammensetzung der Artenvielfalt in fragmentierten Landschaften und Veränderungen in der Zusammensetzung der Artgemeinschaften zeigen allerdings ein uneinheitliches Bild der Reaktion von Amphibienarten (z.B. MARSH und PEARMAN 1997; GASCON et al. 1999; TORAL et al. 2002; PINEDA und HALFFTER 2004; DIXO 2005). Insbesondere die uneinheitlichen Reaktionen auf Faktoren wie Habitatgröße (VALLAN 2002; PINEDA und HALFFTER 2004; DIXO 2005) oder Habitatfragmentierung (MARSH und PEARMAN 1997) legen den Schluss nahe, dass nicht Amphibien an sich eine funktionell gleich reagierende Gruppe darstellen, sondern je nach biologischen Eigenschaften betrachtet werden müssen. Bei unterschiedlicher Spezialisierung ist demnach anzunehmen, dass mit den Veränderungen des Habitates durch dessen Fragmentierung auf Populationsebene unterschiedliche Prozesse ablaufen. Zum Verständnis der unterschiedlichen Reaktionen von Amphibienarten ist es daher notwendig, detaillierte Informationen zur Ökologie des jeweiligen funktionellen Typs zur Verfügung zu haben (HENLE et al. 2004a).

1.2 Ziele und Hypothesen

Amphibienarten reagieren häufig uneinheitlich auf Fragmentierung. Insbesondere Spezialisierungsgrad und Habitatpräferenzen von Arten sind Faktoren, die ihre Reaktion auf Habitatfragmentierung und –isolation bestimmen (HENLE et al. 2004a). Die vorliegende Arbeit hat zum Ziel, Fragmentierungseffekte auf populationsökologische und morphologische Parameter ausgewählter neotropischer bodenlebender Anurenarten in der hochgradig fragmentierten Landschaft der brasilianischen Mata Atlântica zu analysieren. Hauptaugenmerk der vorliegenden Studie liegt dabei auf der Einschätzung der Bedeutung kleinräumiger Waldfragmente für Arten unterschiedlicher Spezialisierung. Der präsentierten Arbeit liegen dabei zwei in alle Kapitel eingehende Ansätze zugrunde. Zum einen wird die Anpassung ausgewählter Arten auf Landschaftsstrukturparameter untersucht. Zum anderen wird das Maß der Anpassung auf diese Strukturparameter in Abhängigkeit des Spezialisierungsgrades der untersuchten Arten differenziert betrachtet.

Dementsprechend liegen dem präsentierten Projekt zwei Haupthypothesen zugrunde:

1. Der Grad der Anpassung von Amphibienarten nimmt mit dem Grad der Habitatveränderung zu.
2. Der Spezialisierungsgrad von Amphibienarten bestimmt das Maß der Anpassung an Habitatfragmentierung und –isolation.

Diese Haupthypothesen werden in den folgenden Kapiteln zum einen an populationsökologischen Parametern als auch an morphologischen Eigenschaften der untersuchten Arten getestet. Das auf populationsökologische Parameter fokussierte Kapitel 3 basiert dementsprechend auf den folgenden spezifischen Hypothesen:

1. Generalistenarten haben eine höhere Überlebenschance in kleinen Fragmenten als Spezialistenarten.
2. Biotische und abiotische Veränderungen in der fragmentierten Landschaft führen sowohl bei Spezialisten- als auch bei Generalistenarten zu einer höheren individuellen Mortalität als in unfragmentierten Habitaten.
3. Das Fehlen von Korridorstrukturen beeinflusst die Überlebensrate von Arten mit hoher Habitatspezialisierung negativ.
4. Bei einer matrixtoleranten Art sind lediglich geringe Schwankungen in der Populationsgröße zwischen unfragmentiertem und fragmentiertem Habitat zu erwarten.
5. Abundanz und Populationsgröße von spezialisierten, die Matrix meidenden Arten korrelieren positiv mit der Habitatgröße.

Das Kapitel 4 analysiert Änderungen morphologischer Parameter und basiert auf folgenden spezifischen Hypothesen:

1. Autochthone Waldarten weisen Änderungen der morphologischen Parameter Körpergröße und Kondition hinsichtlich geringerer Werte in der fragmentierten Landschaft auf.
2. Habitatgeneralisten und –spezialisten zeigen dabei einen unterschiedlichen Grad der Änderungen.

Die empirischen Untersuchungen leisten einen wichtigen Beitrag zu zwei herausragenden Problemen der Naturschutzforschung: dem globalen, noch immer weit-gehend ungeklärten Rückgang von Amphibienarten und dem immer noch geringen Wissensstand zur Ökologie südamerikanischer Amphibien. Ein weiteres Hauptanliegen der vorliegenden Arbeit ist der Beitrag zur Entwicklung und Verbesserung effektiver Schutzstrategien für neotropische Amphibien. Dies zählt derzeit zu den höchsten Prioritäten im Naturschutz (BROOKS et al. 2002). Im Kapitel 5 werden daher die Ergebnisse der empirischen Untersuchungen unter dem Gesichtspunkt des Schutzes neotropischer Amphibien zusammengefasst.

1.3 Material und Methodik

Der vorliegenden Arbeit liegt ein vergleichender Ansatz zu Grunde. Kernansatz ist der Vergleich von Habitatgeneralisten und –spezialisten in einem unfragmentierten Gebiet und fragmentierten Gebieten unterschiedlichen Isolationsgrades. Im Gegensatz zu Fragmentierungsexperimenten, wie sie beispielsweise in Amazonien durchgeführt wurden (BIERREGAARD et al. 1992; DEBINSKI und HOLT 2000), verfolgt die vorliegende Arbeit einen deskriptiven Ansatz. Eine Beeinflussung der Ergebnisse durch kurzfristige Veränderung der räumlichen Struktur einer Landschaft, welche häufig heftige Reaktionen betroffener Arten hervorruft, wird damit vermieden (WITH und CRIST 1995; BOWMAN et al. 2002). Der Fokus der Arbeit liegt daher eher auf den Langzeitauswirkungen von Habitatfragmentierung und –isolation auf Populationsparameter betroffener Arten.

1.3.1 Untersuchungsgebiet

Der atlantische Wald *sensu lato* besteht hauptsächlich aus zwei unterschiedlichen Typen atlantischen Regenwaldes: einem immergrünen Wald und einem teilweise durch saisonalen Laubabwurf gekennzeichneten Waldtyp. Während der immergrüne Teil sich entlang der Küste von Südbrasilien bis zum Nordosten des Landes erstreckt, ist der zweite Teil weiter im Landesinneren anzutreffen (MORELLATO und HADDAD 2000; OLIVEIRA und FONTES 2000). Die floristischen Unterschiede sind maßgeblich von Temperatur und Niederschlagsregime abhängig. Die Nord-Süd-Differenzierung ist hauptsächlich auf das nach Norden hin ansteigende Temperaturmittel zurückzuführen. Der Niederschlagsgradient in Verbindung mit der Höhe über N.N. ist Hauptursache für die Differenzierung in Richtung Küste-Landesinneres (OLIVEIRA und FONTES 2000). Nach der Region des amazonischen Regenwaldes stellt die Mata Atlântica das zweitgrößte tropische Feuchtwaldgebiet Südamerikas dar. Beide Bereiche sind sowohl geografisch als auch funktionell abgetrennt. Die geografischen Barrieren sind offene semiaride Formationen wie die "Caatingas", die "Cerrado" und das "Chaco" (OLIVEIRA und FONTES 2000).

Die vorliegende Arbeit wurde im Waldreservat "Morro Grande" und einer fragmentierten Landschaft bei "Caucaia do Alto", ca. 40 km südwestlich von São Paulo, Brasilien, durchgeführt (Abb. 1.1). Die Untersuchungsgebiete befinden sich in den Verwaltungsgebieten der Gemeinden "Cotia" und "Ibiúna" in Höhenlagen zwischen 870 und 1030m über N.N. Das Relief der Region ist als hügelig zu bezeichnen und weitgehend durch Denudation gekennzeichnet. Die konvexen Hügel weisen Hangneigungen von mehr als 15% auf (ROSS und MOROZ 1997).

Das Klima ist als feucht-heiß klassifiziert mit einer mittleren Maximaltemperatur von 27°C und einer mittleren Minimaltemperatur von 11°C (IAC und CIIAGRO 2006). In den Jahren 2003 und 2004 wurde ein jährliches Mittel von 19°C gemessen. Die Jahresniederschlagsmenge liegt zwischen 1300 und 1400mm mit saisonalen Schwankungen. April bis August sind die trockensten und kältesten Monate.

Der natürliche Waldtyp der Region ist klassifiziert als niederer Bergregenwald, der den Übergang von atlantischem Küstenregenwald zu dem teilweise laubabwerfenden atlantischen Wald des Landesinneren darstellt (OLIVEIRA und FONTES 2000).

Die erste menschliche Besiedlung erfolgte in dem Gebiet vor über 8000 Jahren. Mit Entdeckung und Besiedlung der Mata Atlântica durch die Europäer im 16. Jahrhundert begannen die intensive Nutzung der Ressourcen und die fortschreitende Zerstörung der Wälder, die mit der Gewinnung und dem Export des so genannten "pau-brasil", einem roten und sehr harten Farbholz, das namensgebend für das Land Brasilien war, ihren Anfang fand (DEAN 1995; MORELLATO und HADDAD 2000; OLIVEIRA und FONTES 2000). Weitere Hauptursachen für die Zerstörung waren in der Folge die fortschreitende Besiedlung der Küstengebiete Brasiliens und der ansteigende Holzverbrauch während des Gold- und Diamantrausches. Flächenbedarf durch Viehzucht und Kaffeeplantagen stellen darüber hinaus wichtige Gründe für die Zerstörung und Fragmentierung dar (DEAN 1995). Aufgrund der weitgehenden wirtschaftlichen Abhängigkeit Brasiliens von Überseeexporten waren die Hauptregionen der voranschreitenden Entwicklung und Industrialisierung küstennahe Gebiete, von denen wichtige Häfen wie Rio de Janeiro, Parati oder Santos nicht weit entfernt lagen. Die Hauptursachen für die Zerstörung der Wälder im Untersuchungsgebiet im Bundesstaat São Paulo waren intensive Landnutzung, beispielsweise durch Anbau von Kaffee, und eine steigende Nachfrage nach Holzkohle während der Industriellen Revolution (DEAN 1995; METZGER et al. 2006a). Teile der bewaldeten Gebiete wurden vollständig abgeholzt, andere Teile intensiv genutzt und anschließend, vor ungefähr 50 bis 80 Jahren, aufgegeben. Seither sind die verbliebenen Wälder der Region weitgehend unverändert (DIXO 2005; PARDINI et al. 2005). Das Studiengebiet ist heute in den bewaldeten Gebieten hinsichtlich Relief, Klima, Waldtyp und Regenerationsstatus eine homogene Region. Die verbliebenen bewaldeten Regionen sind in der heutigen Zeit hauptsächlich durch die enorme Bevölkerungsdichte und dem damit einhergehenden Ressourcenverbrauch bedroht.

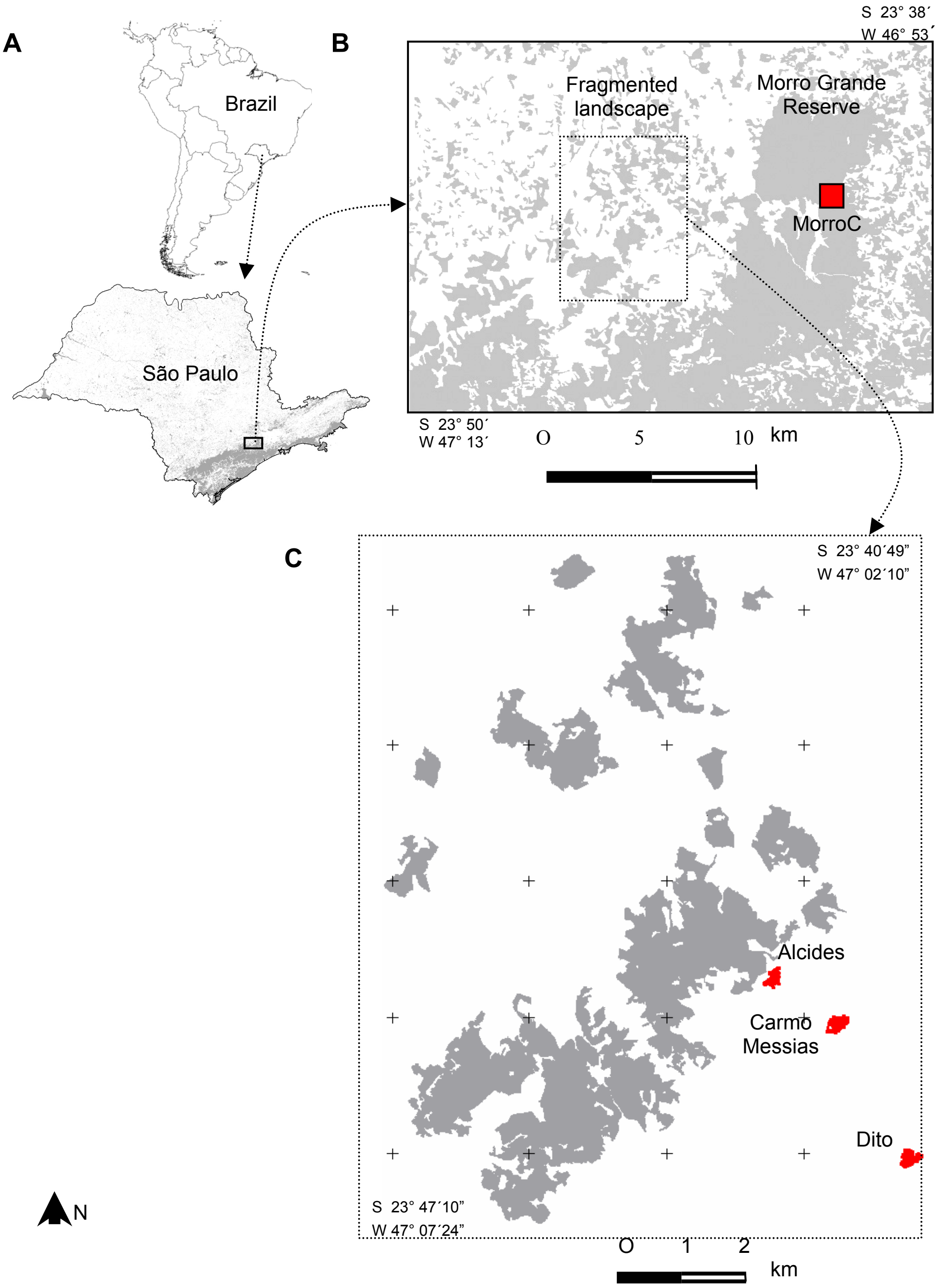

Abbildung 1.1: Geografische Lage des Untersuchungsgebietes in Brasilien bzw. im Bundesstaat São Paulo (A), Übersicht über das Untersuchungsgebiet (B) und detaillierte Darstellung des fragmentierten Gebietes auf dem Ibiúna-Plateau (C). Verbliebener Waldanteil der Region ist grau dargestellt, Untersuchungsgebiete sind rot markiert. Verändert nach (Dixo 2005).

Figure 1.1: Geographic overview of the study area and the state of São Paulo, Brasil (A). Overview of the study area (B) and detailed view on the fragmented landscape of the Ibiúna plateau (C). Remaining forest of the region is displayed in grey, study sites are indicated in red. Modified after (Dixo 2005).

Das "Morro Grande" Waldreservat umfasst ein insgesamt knapp 10.000 ha durchgängig mit heimischen Gehölzen bewaldetes Gebiet. Unterschiede zwischen dem nördlichen und dem südlichen Bereich bestehen hinsichtlich des Sukzessionsstadiums. Während der südliche Teil hauptsächlich durch alten Wald in einem fortgeschrittenen Stadium der Sukzession geprägt ist, besteht der nördliche Teil eher aus jungem, im Sukzessionsstadium den Waldfragmenten der umgebenden Region vergleichbarem Sekundärwald. Über weitere größere Waldbrücken ist das Reservat mit den Wäldern der "Serra do Mar" verbunden (METZGER et al. 2006a; METZGER et al. 2006b). Die fragmentierten Bereiche des Untersuchungsgebietes liegen südwestlich des Waldreservates. 31% des Untersuchungsgebietes sind mit weitgehend fragmentiertem, heimischem Wald bedeckt. Pinus- und Eukalyptus-Plantagen bedecken ca. 7% des Gebietes. Insgesamt 58% der untersuchten Region sind geprägt durch städtische Siedlungen, ländliche Gebäude, offene landwirtschaftlich genutzte Bereiche und Brachen, die junge Sukzessionsstadien heimischer Vegetation aufweisen. Durch ihre landwirtschaftlich intensiv genutzten Flächen zählt die Region zu den wichtigsten Versorgern des Großraums São Paulo mit seinen über 15 Millionen Einwohnern (IBGE 2001). Hauptsächlich wird Gemüse wie Kartoffeln, Zwiebeln, Tomaten und Salat in der Region angepflanzt. Neben der Nahrungsmittelproduktion werden hier auch Blumen und andere gartenbauliche Erzeugnisse gezüchtet. Der Waldtyp der verbliebenen Fragmente ist als Sekundärwald zu klassifizieren, der sich in einem vergleichbaren Regenerationsgrad wie der Wald des nördlichen Teils des "Morro Grande" Reservats befindet. Alle Waldfragmente des Gebietes sind in Privatbesitz. Das Waldreservat "Morro Grande" ist in staatlichem Besitz.

Alle Untersuchungsgebiete befinden sich in Sekundärwäldern. Die Waldfragmente wurden nach Größe in große (>50ha), mittlere (10-50ha) und kleine Fragmente (≤5ha) eingeteilt. Eine weitere Einteilung erfolgte über das Fehlen bzw. Vorhandensein von Waldkorridoren. Als Korridore wurden heimische Gehölzstreifen mit einer Breite zwischen 25 und 100m ausgewählt, welche eine verbindende Funktion zwischen zwei Waldfragmenten aufweisen. Aus diesem Pool klassifizierter Waldfragmente wurden für die vorliegende Studie vier kleinräumige Fragmente ausgesucht. Da vorhergehende Untersuchungen nur geringe Unterschiede in der Zusammensetzung der Amphibienartengemeinschaft zwischen unfragmentierten Wäldern und großen bzw. mittleren

Waldfragmenten ergaben, beschränkt sich die präsentierte Arbeit auf kleine Fragmente (DIXO 2005). Die vier ausgewählten Fragmente repräsentieren zwei isolierte ("Carmo Messias" 23°45'01" S 47°03’22” W, 5,5ha, 930m ü. N.N. und "Dito" 23°46’07” S 47°02’45” W, 5,0ha, 945m ü. N.N.) und zwei über Korridore mit größeren Fragmenten verbundene Waldhabitate (“Alcides” 23°44’41” S 47°03’54” W, 4,8ha, 960m ü. N.N. und “Luiza Osmal” 23°44’27” S 47°03’31” W, 3,6ha, 950m ü. N.N.). Aufgrund auftretender Probleme mit dem Besitzer des Fragmentes "Luiza Osmal" mussten die Freilandarbeiten kurz nach Beginn abgebrochen werden. Ein vergleichbares Gebiet stand nicht zur Verfügung. Im unfragmentierten Waldreservat "Morro Grande" wurde zur Sicherstellung gleicher Habitatqualität ein Kontrollgebiet im Sekundärwald des nördlichen Teils ausgewählt (“Plot C” 23°42’49” S 46°56’46” W, 9400ha, 940m ü. N.N.) (METZGER et al. 2006b). Unterschiede in Arealgröße und Höhenlage der Fragmente bestehen kaum. Die minimale Distanz zwischen dem Waldrand des Reservats und den untersuchten Fragmenten beträgt vier Kilometer. Die Entfernung zum Kontrollpunkt im Reservat beträgt 12km.

In allen Untersuchungsgebieten wurden drei parallele und abhängig von den jeweiligen Bedingungen lineare Fangtransekte mit jeweils 100m Länge eingerichtet. Der Abstand zwischen den Transekten wurde mit zehn Metern festgelegt. In jedem Untersuchungsgebiet wurden die Transekte mit A, B und C gekennzeichnet und alle zehn Meter markiert. Demnach erhielt jedes Untersuchungsgebiet insgesamt 33 individuelle Fangpunkte (Abb. 1.2).

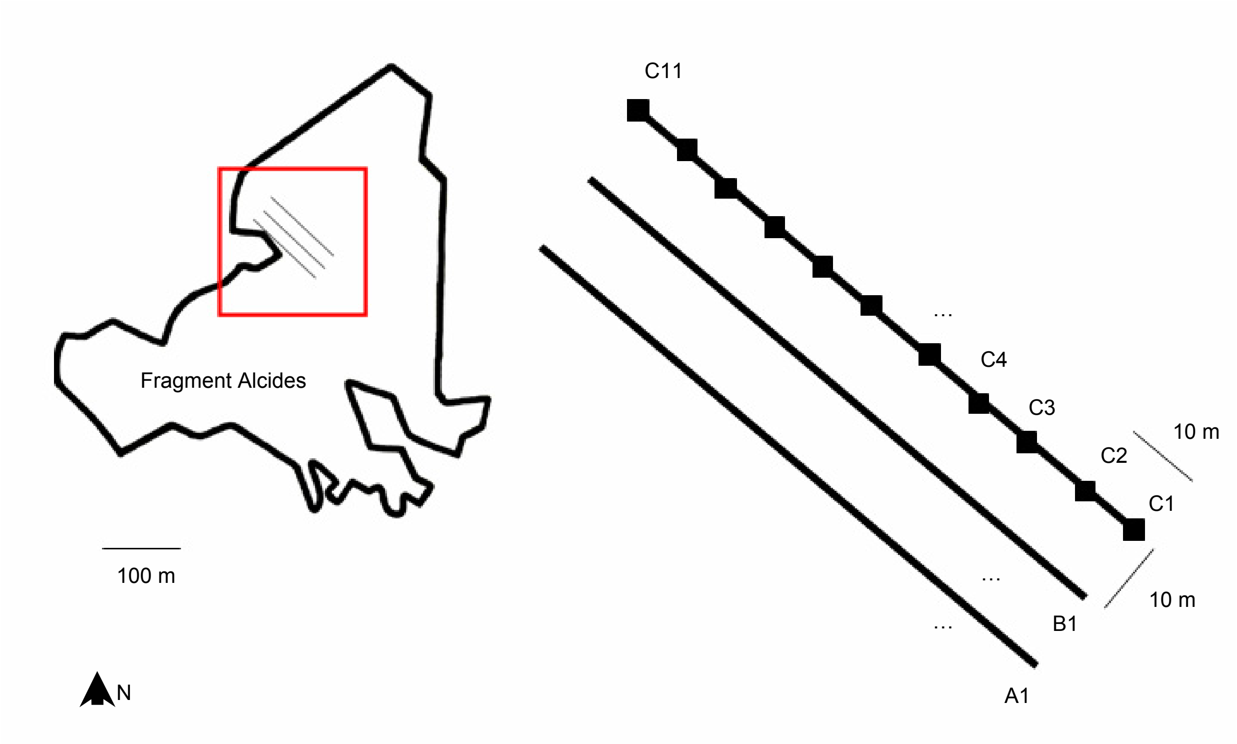

Abbildung 1.2: Schematische Darstellung der Fangtransekte im Fragment "Alcides".

Figure 1.2: Schematical illustration of capture transects in the fragment "Alcides".

1.3.2 Untersuchte Arten

Die Auswertung insbesondere von Fang-Wiederfang-Untersuchungen setzt einen großen Pool von Daten voraus. Bei der Auswahl der zu untersuchenden Arten spielte demnach eine relativ hohe Abundanz eine wichtige Rolle. Für die Auswahl der zu untersuchenden Arten wurden jedoch nicht nur Abundanzdaten herangezogen, auch Informationen zum Spezialisierungsgrad der Arten wurden berücksichtigt. Die Klassifizierung der Arten in Generalisten und Spezialisten erfolgte mit Hilfe von Ergebnissen vorhergehender Studien (DIXO 2005) zu räumlicher Verteilung und Abundanzen der vorkommenden Arten. Die für die vorliegende Arbeit ausgewählten Arten repräsentieren eine Generalistenart, welche sowohl in offenen Bereichen der die Wälder umgebenden Matrix vorkommt, als auch innerhalb von Waldhabitaten anzutreffen ist; eine Semi-Spezialistenart, welche eine geringe Toleranz gegenüber offenen Bereichen aufweist, jedoch in unterschiedlichen Waldhabitaten weit verbreitet ist sowie eine Spezialistenart, welche nur innerhalb von Waldhabitaten vorzufinden ist. Das natürliche Habitat aller drei Arten sind die Wälder der Mata Atlântica São Paulos. Die Klassifizierung in Generalist, Semi-Spezialist und Spezialist erfolgte ausschließlich aufgrund ihrer Habitatpräferenzen. Auch die Generalistenart ist demnach eine autochthone Waldart mit ausgeprägter Toleranz gegenüber offenen und veränderten Habitaten.

Die Nomenklatur der untersuchten Arten richtet sich trotz anhaltender Debatten und neuerer Umbenennungen nach dem "Amphibian tree of life" (FROST et al. 2006).

Kurzsteckbriefe der Arten:

Die Generalistenart *Chaunus ornatus* (SPIX, 1824) (Abb. 1.3), ist eine Krötenart mittlerer Größe. Die mittlere Kopf-Rumpf-Länge beträgt 70mm (Männchen) bzw. 90mm (Weibchen). Parotiddrüsen sind ausgeprägt; das Tympanum ist sichtbar mit einem Durchmesser von ca. 2/3 des Augendurchmessers. Die Färbung der Adulti ist sehr variabel. Grundfarbe ist hellbraun oder ocker mit dunkelbraunen Flecken und/oder schwarzen Punkten; häufig ist ein hellbrauner Dorsalstreifen mit schwarzen Rändern vorhanden. Der Bauch ist meist weiß oder hellgrau mit grauen Punkten. Die Art ist vorwiegend nachtaktiv. Während der gegen Ende der Trockenzeit (Juli-August) beginnenden Reproduktionsphase wandern adulte Individuen zu Laichgewässern in der Umgebung, um dort Laichschnüre zu platzieren. Über Laichmenge, Verweildauer am Laichgewässer oder zurückgelegte Strecken sind keine verlässlichen Informationen verfügbar. Die Reproduktion erfolgt über ein Kaulquappenstadium in temporären oder dauerhaften stehenden bis leicht fließenden Gewässern. Nach Abschluss der Metamorphose wandern die Jungtiere von den Gewässern in das umliegende Waldhabitat. Das Hauptverbreitungsgebiet liegt in der Mata Atlântica der Bundesstaaten São Paulo und Rio de Janeiro. *C. ornatus* ist in bewaldeten Gebieten wie auch offenen Bereichen, beispielsweise Weideland anzutreffen. Zur Reproduktion werden sowohl im Wald gelegene als auch im Offenland gelegene Gewässer genutzt.

Quellen: HEYER et al. 1990; IZECKSOHN und DE CARVALHO-E-SILVA 2001; KWET 2001; BALDISSERA JÚNIOR et al. 2004; DIXO 2005; HADDAD und PRADO 2005; RIBEIRO et al. 2005; FROST et al. 2006; IUCN et al. 2006.

Abbildung 1.3: *Chaunus ornatus*. Pärchen im Amplexus.

Figure 1.3: *Chaunus ornatus*. Couple in amplexus.

Die Art mittlerer Habitatspezialisierung, *Eleutherodactylus guentheri* (STEINDACHNER, 1864) (Abb. 1.4), ist ein kleiner bis mittlerer Vertreter der Brachycephaliden. Die mittlere Kopf-Rumpflänge beträgt 25mm (Männchen) bzw. 36mm (Weibchen). Die Länge der Tibia übersteigt die Länge des Oberschenkels deutlich. Sie weist ausgeprägte Haftscheiben auf; Schwimmhäute fehlen. Das Tympanum ist sichtbar; Durchmesser ca. ½ des Augendurchmessers. Färbung ist sehr variabel; meist in verschiedenen Brauntönen, selten Grüntönen. Dorsal sind häufig eine x-artige Markierung und laterale Streifen zu beobachten. Der Bauch ist meist einfarbig hellgelb, weiß oder durchscheinend. Diurnale Art mit verstärkter nächtlicher Aktivität. Die Reproduktion erfolgt während der Hauptregenzeit von Oktober bis Februar. Aus ca. 20 bis 30 im Boden unter Steinen oder

Totholz abgelegten Eiern entwickeln sich kleine, aber vollständig ausgebildete Juvenes. Die Entwicklung erfolgt ohne Kaulquappenstadium. *E. guentheri* zeichnet sich durch große Ortstreue und geringe Mobilität aus, bewohnt Waldhabitate, ist jedoch auch häufig in der Nähe von Waldrändern in umgebender Vegetation anzutreffen. Verbreitung über weite Teile der Mata Atlântica von Espírito Santo im Norden bis Rio Grande do Sul im Süden. Das Verbreitungsgebiet bedarf aufgrund aktueller bioakustischer Untersuchungen wahrscheinlich einer Revision.

Quellen: HEYER et al. 1990; KWET und DI-BERNARDO 1999; IZECKSOHN und DE CARVALHO-E-SILVA 2001; KWET 2001; RAMOS und GASPARINI 2004; HADDAD und PRADO 2005; KWET und SOLÉ 2005; RIBEIRO et al. 2005; FROST et al. 2006; IUCN et al. 2006.

Abbildung 1.4: *Eleutherodactylus guentheri*. Pärchen im Amplexus.

Figure 1.4: *Eleutherodactylus guentheri*. Couple in amplexus.

Die Spezialistenart *Eleutherodactylus parvus* (GIRARD, 1853) (Abb. 1.5) ist ein kleiner Vertreter der Brachycephaliden. Die mittlere Kopf-Rumpf-Länge beträgt 14mm (Männchen) bzw. 20mm (Weibchen). Tibia und Oberschenkel weisen die gleiche Länge auf. Die Fingerspitzen sind verdickt, Schwimmhäute fehlen. Das Tympanum ist nicht sichtbar. Die Färbung ist braun, beige oder cremefarben mit schwarzen Flecken. Das Dorsum weist ähnlich *E. guentheri* häufig eine x-förmige schwarze Markierung auf. Die Kehle ist meist gelblich oder weiß gefärbt. Der Bauch ist sehr variabel in der Färbung von grünlich, grau, weiß bis bronze- oder cremefarben mit dunkelbraunen Flecken. Diurnale Art mit verstärkter nächtlicher Aktivität. Ortstreue Art mit geringer Mobilität. Wie bei den anderen Arten der Gattung *Eleutherodactylus* erfolgt auch bei *E. parvus* die Entwicklung direkt ohne Kaulquappenstadium. Die Reproduktion erfolgt ähnlich wie bei *E. guentheri* in der Hauptregenzeit über am Boden abgelegte Eipakete. *E. parvus* kommt im Südosten der Mata Atlântica vor und ist ausschließlich in Waldhabitaten anzutreffen.
Quellen: HEYER et al. 1990; IZECKSOHN und DE CARVALHO-E-SILVA 2001; DIXO 2005; HADDAD und PRADO 2005; FROST et al. 2006; IUCN et al. 2006.

Abbildung 1.5: *Eleutherodactylus parvus*. Adultes Männchen.

Figure 1.5: *Eleutherodactylus parvus*. Adult male.

2 General introduction

Biological diversity or just biodiversity is simply the variety of life on earth (WILSON 1997). Not until the term "biodiversity" was introduced, but since the beginning of systematical research, biologists focus on the inventory of species. Calculations for eukaryote species showed that already about 300 thousand plant species, 45 thousand vertebrate species and more than 3 million invertebrate species are being described today. The total number of extant species is uncertain. Conservatively, there are about seven million eukaryote species in the world (MAY 1997). Most of these are animals and around 85% are terrestrial (PIMM and RAVEN 2000). Tropical regions contain about two-thirds of the known species. Recently, MYERS et al. (2000) identified 25 hotspots of biodiversity in the world, which contain 44% of all known vascular plants and 35% of all known mammals, reptiles, amphibians, and birds of the world, but only cover a land surface of 1.4%. From all 25 hotspots, 19 are located in tropical regions.

An important part of this extreme diversity is the group of amphibians. Amphibians are a very diverse species group. Today, more than 6000 amphibian species are being described (FROST 2006). Thus, more amphibian species than mammal species are known in the world (GLAW and KÖHLER 1998). Tropical regions and especially the Neotropics are distribution hotspots of amphibians (DUELLMANN and HEATWOLE 1999). Two thirds of all newly described amphibian species of the last years are species from the Neotropics, but likely many remain undescribed (GLAW and KÖHLER 1998). However, amphibians are seriously threatened. Due to their reproductive modes, life history, and morphology, amphibians are usually more exposed and more sensitive to pollution or habitat changes than other taxa and are thus often used as indicators for environmental changes (MYERS 1993; BLAUSTEIN et al. 1994; TYLER 1994; ALFORD and RICHARDS 1999; PINEDA and HALFFTER 2004). As observed in the last decades, this sensitivity to outer influences led to a global amphibian decline (ALFORD and RICHARDS 1999; HOULAHAN et al. 2000; HOULAHAN et al. 2001; STUART et al. 2004), which has put one third of all described amphibian species of the world to threat (MENDELSON et al. 2006). The process of global amphibian decline is part as well as indicator of a global loss of biological diversity (MYERS 1993).

Especially tropical regions are strongly affected by the overall loss of biodiversity (PIMM and RAVEN 2000). This loss is exceptionally fatal as tropical regions contain the majority of the hotspots of biodiversity (MYERS et al. 2000). One of the immensely affected hotspots is the Brazilian Atlantic Forest or "Mata Atlântica".

Mata Atlântica is a collective term for all different forest types within an area of 8° to 28° south latitude and from coast to inland from 100 km in the north to 500km in the south (DEAN 1995). The Brazilian Atlantic Forest is a biome, which originally covered 1.3 million km^2. With 1.1 million km^2, it is mostly distributed over Brazilian territory. Only small parts enter Argentina and Paraguay (MORELLATO and HADDAD 2000; OLIVEIRA and FONTES 2000). The whole biome presents high endemism rates for vertebrate species: about 30% for bird, mammal, and reptile species, and about 90% for amphibian species (MYERS et al. 2000). Today, about 60% of the Brazilian population, which is about 110 million people, lives in the original distribution area of the Mata Atlântica (IBGE 2001). The original area of the Mata Atlântica today is one of the most developed and industrialised regions in South America. This development led to an extreme loss of forest area and to the fragmentation of remnants. Today, only 7.6% of its original distribution area is still covered with native forests (SOS MATA ATLÂNTICA and INPE 2002). These remnants are mainly small-sized and disturbed forest fragments or distributed over steep mountain slopes (OLIVEIRA and FONTES 2000). Remnants of the Mata Atlântica and its fauna nowadays are mainly threatened by harvesting of firewood and illegal logging as well as hunting, plant collecting, and the invasion of alien species (TABARELLI et al. 2005).

Habitat destruction and fragmentation are among the most important processes in species extinction (HENLE and STREIT 1990; SARRE et al. 1996; PIMM and RAVEN 2000; SALA et al. 2000; YOUNG et al. 2001; HENLE et al. 2004b; ETEROVICK et al. 2005). The progressing land use change has led to a steady loss of habitat and the increasing isolation of remnants (HENLE et al. 2004a). The destruction and fragmentation of habitats leads to numerous changes in environmental parameters. Main factors influencing species richness or species community are 1) landscape spatial structure, as e.g. habitat size or connectivity, 2) habitat characteristics or habitat quality, and 3) biological characteristics of concerning species (WITH and CRIST 1995; HENLE et al. 2004a). However, not all species are affected in the same extent by habitat destruction and fragmentation (HENLE et al. 2004a). Biological characteristics as dispersal power, reproductive potential, or habitat preferences play a main role in determining species sensitivity to habitat fragmentation (HENLE et al. 2004a). A better understanding of these differential sensitivities is an essential contribution to the enhancement of ecological theories and the interpretation of evolutionary history, as well as for the setting of priorities and the identification of target species in applied conservation biology (HENLE et al. 2004a). For the understanding of extinction processes and for the development of effective conservation strategies, a detailed knowledge of fragmentation-driven changes in the ecology of concerned species or populations is fundamental (HENLE et al. 2004a). But there is still a great lack of knowledge of species living in the tropics (YOUNG et al. 2001). The key priority for the research in fragmented tropical ecosystems therefore is the study of natural history of species (BIERREGAARD et al. 1997).

In particular, little is known about the ecology of tropical amphibians in fragmented landscapes. But the loss of habitat poses a threat especially to species with low migration rates such as amphibians or reptiles (SCBD 2003; MALCOLM et al. 2006). This special threat to amphibians is reflected in the global amphibian decline. An evident decline of amphibians was also documented for the Mata Atlântica (SILVANO and SEGALLA 2005). All of the threatened amphibians listed in the Brazilian Red List are distributed in the Atlantic Forest. Especially the states of São Paulo and Rio de Janeiro are hotspots of threat (SILVANO and SEGALLA 2005). Recent studies on Neotropical amphibians mainly focus on the ecology of selected species, not taking into account the influence of habitat changes (e.g. ZIMMERMAN and SIMBERLOFF 1996), or if such changes are considered, studies are focussed on species communities (e.g. TOCHER et al. 1997). From the area of the Mata Atlântica very little is known about the impact of habitat changes on the ecology of amphibian species. Nevertheless, studies on species richness and community changes in fragmented landscapes show inconsistent response of amphibian species (e.g. MARSH and PEARMAN 1997; GASCON et al. 1999; TORAL et al. 2002; PINEDA and HALFFTER 2004; DIXO 2005). Especially the inconsistent response to factors as habitat size (VALLAN 2002; PINEDA and HALFFTER 2004; DIXO 2005) or habitat fragmentation (MARSH and PEARMAN 1997) imply that amphibians per se do not act as a group of functional similar responding species. It is therefore most likely that fragmentation-driven adaptational processes at population level depend on e.g. the degree of species specialisation. Depending on biological characteristics, different processes may thus occur at population level. Consequently, for the understanding of processes which lead to different response of amphibian species to habitat fragmentation, more information about the ecology of species representing particular functional types is necessary (HENLE et al. 2004a).

2.1 Aims and hypotheses

Amphibian species often respond inconsistently to habitat fragmentation. Among other factors, the degree of specialisation and habitat preferences are main factors that determine this response of species to habitat fragmentation and isolation (HENLE et al. 2004a). The presented study intends to analyse fragmentation effects on parameters of population ecology and morphology of selected Neotropical leaf-litter frogs in a highly fragmented area of the Brazilian Atlantic Forest. The study emphasizes on the evaluation of small forest patches for amphibian species in relation to differences in the degree of specialisation. Consequently, the presented study and all chapters follow two main approaches: 1) the adaptation of selected species on landscape spatial structure and 2) the differentiation of the degree of adaptation in relation to the degree of specialisation of species.

Accordingly, the presented project is based on two main hypotheses:

1. The degree of adaptation of amphibians increases with the degree of habitat alteration.
2. The degree of specialisation determines the strength of adaptation of amphibian species on habitat fragmentation and isolation.

In the following chapters these main hypotheses are tested on parameters of population ecology as well as on morphological characteristics of selected species. Chapter 3, which is focussed on population ecology, is thus based on following specific hypotheses:

1. Generalist species are more likely to survive in small fragments than specialist species.
2. Biotical and abiotical changes in the fragmented landscape lead to higher individual mortality of specialist as well as of generalist species than in the continuous forest habitat.
3. Absence of corridors negatively influences survival of species with high habitat specialisation.
4. A species with matrix tolerance does not show major changes in population size within continuous forest in comparison to a fragmented landscape.
5. Specialised species with matrix aversion show an increase of abundance and population size with the increase of habitat area.

Chapter 4 analyses morphological shifts and is based on following specific hypotheses:

1. Native forest species of amphibians show shifts in body size and body condition towards smaller size and lower condition following habitat fragmentation.
2. Habitat specialist and generalist species show different degrees in morphological shifts.

The empiric parts of the presented study contribute to conservation research on two major problems: the enigmatic amphibian decline in the world and the lack of knowledge on the natural history of amphibian species in South America. Another main aim of the presented project is the contribution to the development and enhancement of effective conservation strategies for Neotropical amphibians. The development of such strategies is of the top priority in nature conservation (BROOKS et al. 2002). Chapter 5 therefore gives a synthesis of results of the empiric parts and focuses on conclusions for the conservation of Neotropical amphibians.

2.2 *Material and methods*

The presented project is based on a comparative approach. It thus compares habitat specialist and habitat generalist species in a continuous habitat and fragmented habitats with different degrees of isolation. In contrast to fragmentation experiments (BIERREGAARD et al. 1992; DEBINSKI and HOLT 2000), the presented study has a descriptive approach. It thus avoids bias through changes in spatial patterns of the landscape, which often results in strong response of affected species (WITH and CRIST 1995; BOWMAN et al. 2002). For this reason, the study focuses more on long-term effects of habitat fragmentation and isolation on the population level of affected species.

2.2.1 Study area

The Atlantic Forest sensu lato mainly consists of two vegetation types: Atlantic Rain Forest and Atlantic Semi-deciduous forest. Whereas the rain forest is mostly distributed along the coastline from southern to north-eastern Brazil, the semi-deciduous forest extends into the interior of Brazil (MORELLATO and HADDAD 2000; OLIVEIRA and FONTES 2000). The floristic differentiation mainly depends on rainfall regime and temperature. One of the most important factors determining the north-south floristic differentiation is the mean temperature, which increases northwards. Temperature and rainfall combined with altitude causes most of the internal variation within the two forest types (OLIVEIRA and FONTES 2000). After the Amazonian domain, the Atlantic Forest is the second largest tropical moist forest area of South America. Both biomes, Amazonia and the Mata Atlântica, are separated by the open formations of the semiarid Caatingas, the Cerrado and the Chaco (OLIVEIRA and FONTES 2000).

The presented study was carried out in the continuous forest of the Morro Grande Reserve and a fragmented landscape surrounding Caucaia do Alto, located 40km south-west of São Paulo in the municipalities of Cotia and Ibiúna, Brazil (Fig 1.1). The relief is characterised by denudation, convex hills and inclinations of more than 15% and presents altitudes between 870 and 1030m (ROSS and MOROZ 1997).

The climate is characterised as humid and hot (IAC and CIIAGRO 2006) with a mean maximum temperature of 27°C and a mean minimum temperature of 11°C. The years 2003 and 2004 presented a mean annual temperature of 19°C. Annual rainfall is about 1300 to 1400mm with seasonal variation. Driest and coldest months are between April and August.

The original forest of the study region is classified as lower montane rainforest and forms a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest (OLIVEIRA and FONTES 2000).

First human settlement of the area was dated at more than 8000 years ago. With the European invasion in the 16th century, the intensive use of the resources and the ongoing destruction of the forests of the Mata Atlântica began (DEAN 1995; MORELLATO and HADDAD 2000; OLIVEIRA and FONTES 2000). One of the first threats had been the export of the "pau-brasil", a red and very hard dyewood, which actually was the eponym of the country. Other threats were intense settlement with increasing need of wood during the following gold and diamond rush, cattle grazing, and coffee farming, which mostly took place in the southern part of the Mata Atlântica (DEAN 1995). Depending on overseas exports, the Brazilian industrial development mainly went on in the southern coastal region where harbours like Rio de Janeiro, Santos, or Parati were accessible. The main reasons of the destruction of the forest in the state of São Paulo, which occurred mainly since 1850, were intensive land use of plantations, such as coffee, and the increased needs of charcoal with the ongoing industrial revolution (DEAN 1995; METZGER et al. 2006a). Some parts of the forest have been cut entirely; others were abandoned after intensive use. Since that time, the forest mainly remained unchanged for about 50 to 80 years (DIXO 2005; PARDINI et al. 2005). Today, the study region represents a homogeneous area concerning relief, climate, forest type, and forest regeneration stage. Recently, the major threats for forest remnants are the population density within the area of the Atlantic Forest and the resource consumption of this population (MORELLATO and HADDAD 2000).

The Morro Grande Reserve consists of about 10,000 ha of native continuous forest. Mature forest is present only in the southern part. The northern part of the reserve represents continuous secondary forest. Over other large forested areas in the south it is connected to the Serra do Mar (METZGER et al. 2006a; METZGER et al. 2006b). The fragmented landscape is located south westwards of the Reserve. About 31% of this landscape are covered by native forest. Pine and eucalyptus plantations cover about 7% of the area. The other parts with a total percentage of 58% of the region are covered by urban areas, rural buildings, open areas with agricultural fields, and areas with native vegetation in early stages of regeneration. The agricultural area is one of the most important providers of vegetables for the city of São Paulo and the surrounding area, which hosts more than 19 million inhabitants (IBGE 2001). The main vegetables are potatoes, onions, tomatoes, lettuce, but also flowers and horticultural crop are cultivated. The forest type of the fragmented landscape is secondary forest of the same regeneration stage as it is found in the northern part of the Morro Grande Reserve. While the forest reserve is federal property, all forest fragments are in private ownership.

2.2.2 Study sites

All study sites are located in native secondary forest. Fragments were classified according to size in large (>50ha), medium-sized (10-50ha) and small forest patches (≤5ha). Fragments were also categorised by presence or absence of corridors. As corridors, native forest stripes with a width of 25 to 100 metres connecting forest fragments were selected. From all classified forest fragments, four small sized fragments were selected for the study (Fig. 1.1). Only small fragments had been selected while the data of (DIXO 2005) implied that only few differences in the community structure between the unfragmented forest and large and medium forest fragments exist. The four selected small fragments represented two isolated patches ("Carmo Messias" at 23°45'01" S 47°03'22" W, 5.5ha, 930m altitude and "Dito" at 23°46'07" S 47°02'45" W, 5.0ha, 945m altitude) and two patches connected with larger fragments ("Alcides" at 23°44'41" S 47°03'54" W, 4.8ha, 960m altitude and "Luiza Osmal" at 23°44'27" S 47°03'31" W, 3.6ha, 950m altitude). Due to problems with the owner of the fragment "Luiza Osmal", this fragment had to be abandoned afterwards. A comparable fragment was not available. In the continuous forest we selected one control site in the secondary forest of the northern part of the reserve ("Plot C" 23°42'49" S 46°56'46" W, 9400ha, 940m altitude) to maintain a similar habitat quality while all fragments represent secondary forest (METZGER et al. 2006b). All selected fragments slightly differed in area and altitude. The minimum linear distance between the border of the forest reserve and the studied fragments was four kilometres. The distance to the control point inside the reserve was 12km.

In all study sites, three linear and parallel and, depending on local conditions, more or less straight capture transects with a length of 100m each were established. In every site, transects were named A, B, and C and marked every ten metres, receiving a grid of 33 points. Distance between transects was ten metres (Fig. 1.2).

2.2.3 Studied species

Especially capture-recapture studies, as presented in chapter three, demand a selection of few species with relatively high abundance to achieve a large data pool. In consideration of abundance data for the study area and the degree of habitat specialisation, three species had been selected. For the classification of specialist or generalist species, data on spatial distribution and abundance patterns provided by former studies (DIXO 2005) were used. The selected species represent a generalist species occurring in matrix and forest habitats, a semi specialist species with little matrix tolerance but mainly living in forest habitats, and a specialist species only occurring in forest habitats. Native habitats of all species are the forests of the Mata Atlântica including the region of São Paulo. The classification in generalist, semi-specialist, and specialist was exclusively based on habitat preferences. Also the generalist species thus is an autochthonous forest species with a high tolerance to open and modified habitats.

Although there is an ongoing debate on the taxonomy of the studied species, the nomenclature used in this thesis follows "The amphibian tree of life" (FROST et al. 2006).

The generalist species, *Chaunus ornatus* (SPIX, 1824) (Fig. 1.3), is a medium sized bufonid species with a mean body length of 70mm (males) and 90mm (females). *C. ornatus* shows distinct parotid glands and a large and distinct tympanum with a diameter of about $^{2}/_{3}$ of eye diameter. It has a brown dorsum in various shades, dark-stained with brown or black spots and a light brown mid-dorsal stripe, edged with black. Chest and belly are white with grey spots. Activity is predominantly nocturnal. During reproduction, starting at the end of the dry season (July to August), adult individuals migrate to surrounding ponds and deposit egg-strings. Information on amount of spawn, resting

time at spawning ponds, or migration distances is not available. *C. ornatus* shows aquatic reproduction with tadpoles in temporary or permanent bodies of stagnant or slowly running water. After metamorphosis, juveniles migrate from ponds into surrounding forest habitats. *C. ornatus* is mainly distributed over the Mata Atlântica of São Paulo and Rio de Janeiro. In general, it occurs and reproduces in forest habitats but can also be found in open areas and pasture and also uses open area ponds for reproduction.
References: HEYER et al. 1990; IZECKSOHN and DE CARVALHO-E-SILVA 2001; KWET 2001; BALDISSERA JÚNIOR et al. 2004; DIXO 2005; HADDAD and PRADO 2005; RIBEIRO et al. 2005; FROST et al. 2006; IUCN et al. 2006.

The semi-specialist species, *Eleutherodactylus guentheri* (STEINDACHNER, 1864) (Fig. 1.4), is a small to medium sized brachycephalid species with a mean snout-vent-length of 25mm (males) and 36mm (females). The tibia length exceeds femoral length. *E. guentheri* shows distinct toe discs but lacks toe webbing. Tympanum is usually distinct with a diameter ½ of eye diameter. Body colouration is very variable – usually brown in various shades, but sometimes also green. The dorsum often shows an x-wise marking and lateral stripes. Belly and chest are usually light yellow or translucent. The species is diurnal with increased nocturnal activity. During reproduction, which mainly occurs during the main raining season from October to February, the female deposits an egg clutch of 20 to 30 eggs terrestrially, hidden below trunks and stones. Because the species is a direct developer, hatchlings are small, but completely developed frogs. *E. guentheri* is a species with low mobility and inhabits forest habitats but can also be encountered near the forest edge in surrounding vegetation. It is widely distributed over the Mata Atlântica. Records reach from the state of Espírito Santo in the north to Rio Grande do Sul in the south. Regarding recent studies on bioacustics, the distribution area of this species likely needs a revision.
References: HEYER et al. 1990; KWET and DI-BERNARDO 1999; IZECKSOHN and DE CARVALHO-E-SILVA 2001; KWET 2001; RAMOS and GASPARINI 2004; DIXO 2005; HADDAD and PRADO 2005; KWET and SOLÉ 2005; RIBEIRO et al. 2005; FROST et al. 2006; IUCN et al. 2006.

The specialist species, *Eleutherodactylus parvus* (GIRARD, 1853) (Fig. 1.5), is a small brachycephalid species with a mean snout-vent-length of 14 mm (males) and 20 mm (females). Tibia and femoral are equal in length. *E. parvus* has pointed toe tips, but lacks toe webbing as *E. guentheri*. The tympanum is hidden with a diameter ½ of eye diameter or less. Body colouration is brown, beige, or creamy, with black markings and usually a typical dark x-wise dorsal marking. Chin and throat are yellow or white. The belly shows a high variety of colours with greenish grey, white, pearl, bronze, or cream with dark brown markings. The species is diurnal with increased nocturnal activity. As likely all members of the genus *Eleutherodactylus*, *E. parvus* has direct development with terrestrial egg clutches. It is a species with low mobility and restricted to forest habitats. *E. parvus* occurs in the southeast of the Brazilian Mata Atlântica.

References: HEYER et al. 1990; IZECKSOHN and DE CARVALHO-E-SILVA 2001; DIXO 2005; HADDAD and PRADO 2005; FROST et al. 2006; IUCN et al. 2006.

3 Life history traits of three leaf-litter frogs in Neotropical forest patches

3.1 *Introduction*

The world's biodiversity is currently experiencing a phase of mass extinction (MYERS 1993; PIMM and RAVEN 2000). Due to human activities, one third to a half of the world's biodiversity is threatened with extinction (MYERS 1993; BROOKS et al. 2002; STOCKWELL et al. 2003). The most likely major causes of the loss of terrestrial biodiversity are the destruction and the fragmentation of habitats (SAUNDERS et al. 1991; PIMM and RAVEN 2000; LAURANCE and COCHRANE 2001; HENLE et al. 2004a). The fragmentation of a landscape being defined as a process during which a continuous habitat is converted into a number of smaller remnants of smaller total area separated by a matrix of converted habitats unlike the original (FAHRIG 2003).

Although the most obvious and problematic consequence of fragmentation is the disappearance of habitat, the process of habitat fragmentation also results in other effects: an increase in the number of patches, a decrease in patch size, an increase in isolation, and an increase in edges (LOVEJOY et al. 1986; LAURANCE 2000; FAHRIG 2003;). Habitat loss reduces trophic chain length, the number of specialist large-bodied species, but also changes species interactions and animal behaviour, and can negatively affect breeding and dispersal success (FAHRIG 2003). Fragmentation per se may not have such consistently negative effects on ecosystems and species compared to habitat loss (FAHRIG 2003; YAACOBI et al. 2007), but it does however result in changes in habitat geometry and thus directly influences habitat quality parameters. This in turn can influence the extinction risk of populations and the composition of communities within patches (SAUNDERS et al. 1991; HOKIT and BRANCH 2003; EWERS et al. 2007). In particular, an increase of edges in relation to patch area results in numerous changes to abiotic and biotic parameters within remnants (LAURANCE 2000). Edge effects include microclimatic changes, such as an increase in solar radiation, desiccation, and temperature variability near forest edges

(SAUNDERS et al. 1991; LAURANCE 2000). Furthermore, increased wind effects may cause alterations to forest structure (LAURANCE 2000), and are also known to affect the nutrient cycle (WEATHERS et al. 2001). Nevertheless, an increase of forest edges can also directly influence species communities within forests, because it facilitates the influx of generalist open area species (DIDHAM 1997), which in turn can influence the extinction risk of populations near edges (LAURANCE 2000; HOKIT and BRANCH 2003). Hence, in a fragmented landscape changes to biogeographic parameters as well as changes to parameters of the physical environment occur (SAUNDERS et al. 1991).

Consequences for species living in a fragmented landscape are complex and result from a combination of described effects of habitat loss on the one hand and effects of fragmentation per se on the other hand (FAHRIG 2003). Whether a species in a fragmented habitat is vulnerable to extinction or not however depends not only on the spatial configuration of the landscape, but also on individual demographic parameters and ecological traits (WITH and CRIST 1995; HENLE et al. 2004a). Empirical and theoretical evidence shows that not all species decline following fragmentation. Among the most important predictors of species sensitivity to fragmentation are population size, population fluctuation, dispersal power, reproductive potential, body size, trophic position, and ecological specialisation (HENLE et al. 2004a). Population size and fluctuation determine whether species are able to maintain stable populations, are prone to stochastic extinction (SARRE et al. 1996), and have direct influence on genetic diversity within populations (HENLE et al. 2004a). Dispersal power in principle determines the extinction risk of spatially-structured populations (HENLE et al. 2004a; OVASKAINEN and HANSKI 2004). Nevertheless, it does not automatically correlate with species sensitivity to fragmentation, as other factors, such as the size of individual home ranges and the extinction rate within subpopulations that may negate any beneficial effects of dispersal power (HENLE et al. 2004a). Reproductive potential and further life-history traits have a complex influence on how prone a species is to extinction. A high reproductive potential may positively influence other traits, especially colonisation success, but implies on the other hand low annual survival rates, which, in contrast, makes species more extinction prone to extinction than species with a low reproductive potential (HENLE et al. 2004a).

Body size and trophic position are very closely related ecological traits. Large-bodied species, which are often species at a high trophic level often presenting lower population densities, are usually at greater risk of extinction than small-bodied species (HENLE et al. 2004a). The loss of top-predators and direct fragmentation effects (e.g. edge effects) are likely to lead to increased population sizes of medium-sized generalist predators and lead in consequence to the demise of predation-sensitive species (TERBORGH 1974; HENLE et al. 2004a). HENLE and others (2004) conclude that "predator sensitive species with traits rendering them insensitive to habitat fragmentation should survive better in smaller than in medium-sized remnants because predators should be absent in small fragments". Nevertheless, this facilitation between species in small fragments is only likely without predators that are broad habitat generalists (HENLE et al. 2004a). Usually, generalist species are regarded as less fragmentation-sensitive than habitat specialists. Ecologically-specialised species are likely to show a variable and patchy distribution (WITH and CRIST 1995; GASCON et al. 1999) and are therefore prone to extinction in fragmented landscapes (HENLE et al. 2004a). HENLE and others (2004) assume that specialists have a higher extinction risk as the chance that their niche is represented in remnants of a fragmented landscape is smaller than for generalist species. Furthermore, population size within patches is usually smaller for specialists than for generalists (SARRE et al. 1996; HENLE et al. 2004a).

Studies on island biogeography and population viability analysis (PVA) have shown that small areas usually harbour only a fraction of the species that can be maintained in larger areas (MAC ARTHUR and WILSON 1967; TERBORGH 1976; DIAMOND and MAY 1980; BURKEY 1995; DRECHSLER and BURGMAN 2004; ARPONEN et al. 2007). Regarding the equilibrium theory of island biogeography (ETIB) the main predictors of species numbers are island size and isolation (MAC ARTHUR and WILSON 1967). In consequence, the ETIB often serves as a key component of concepts in the conservation of fragmented landscapes (TERBORGH 1976; BURKEY 1995; HOKIT and BRANCH 2003). Nevertheless, the application of the ETIB to conservation biology has been discussed controversially (DIAMOND 1976; SIMBERLOFF and ABELE 1976a; SIMBERLOFF and ABELE 1976b; TERBORGH 1976; DIAMOND and MAY 1980) because it does not take into account species identity, characteristics, and requirements (WATLING and DONNELLY 2007). When applied to relatively small species with limited mobility and less area requirements (i.e. insects or small vertebrates) the ETIB may lack relevance (ZIMMERMAN and BIERREGAARD 1986; TSCHARNTKE et al. 2002). In addition to species size and mobility, reproductive output plays an important role regarding the minimum area requirements of species. Even very small habitats may be sufficient to maintain stable populations if the reproduction rate is high in relation to mortality (FAHRIG 2002). Beyond these conceptional difficulties however, the application of the ETIB to applied conservation biology is also limited due to practical reasons. Human-dominated areas in particular, where single large remnants hardly exist anymore or areas such as hotspots of biodiversity, which present high endemism rates, sometimes regardless of remnant size, require more complex approaches. Small patches can therefore prove to be important within networks for the conservation of small species with limited mobility (GUTIERREZ 2005).

The tropical hotspots of biodiversity are disproportionately affected by habitat destruction and fragmentation (PIMM and RAVEN 2000; ACHARD et al. 2002; BROOKS et al. 2002; BAWA et al. 2004). The most important consequences of the destruction and fragmentation of the hotspots are the threat and extinction of endemic species. Today about 60% of all threatened terrestrial vertebrates are hotspot endemics (BROOKS et al. 2002). One of the hotspots immensely affected by habitat destruction and fragmentation is the Brazilian Atlantic Forest or Mata Atlântica. Less than eight percent of its original area remain wooded with native, mainly highly fragmented, and disturbed forests (OLIVEIRA and FONTES 2000; SOS MATA ATLÂNTICA and INPE 2002). Some areas are characterised by tiny and widely separated fragments, but still contain a high number of endemic species (TABARELLI et al. 2005). Among all endemic taxa of the Mata Atlântica amphibian species represent an outstanding rate of endemism (>90%) (MYERS et al. 2000).

With regards to amphibians in particular, comparably little is known about area requirements. In the case of temperate wetlands there is evidence that small isolated habitat patches can have great value for sustaining amphibian diversity (SEMLITSCH and BODIE 1998) and studies on Neotropical forests have highlighted the importance of factors such as habitat quality for breeding or the matrix tolerance of species (ZIMMERMAN and BIERREGAARD 1986; WATLING and DONNELLY 2007). However, the knowledge about the value of small patches for the conservation of small vertebrates with limited mobility in tropical forest areas is scarce. Amphibians are a suitable group to address this issue. Amphibian species represent a number of special characteristics (e.g. reproductive modes, life history, morphology), which makes this group more sensitive to environmental changes than other species groups, deeming it a frequently used indicator for such changes (WEYGOLDT 1989; MYERS 1993; BLAUSTEIN et al. 1994; POUNDS and CRUMP 1994; TYLER 1994; ALFORD and RICHARDS 1999; PINEDA and HALFFTER 2004; POUNDS et al. 2006). Because of this high sensitivity to changes in their environment, amphibians are currently experiencing a massive global decline (ALFORD and RICHARDS 1999; HOULAHAN et al. 2000; HOULAHAN et al. 2001; MENDELSON et al. 2006), which even exceeds the decline rates of birds or mammals for example (STUART et al. 2004). Amphibians are however an important component of forest ecosystems, in particular Neotropical ones, which are a distribution hotspot for amphibians (MAY 1997; DUELLMANN and HEATWOLE 1999).

Little is known about the effects of habitat fragmentation of tropical forests for amphibian species. Studies using amphibians as indicators are often limited to the community level (e.g. TOCHER et al. 1997; PINEDA and HALFFTER 2004; DIXO 2005; BELL and DONNELLY 2006). However, existing studies have revealed differences among amphibian taxa in response to habitat fragmentation, finding that ground-living species (PINEDA and HALFFTER 2004), naturally rare species, and species with a high habitat specialisation are more affected than others (GASCON et al. 1999; WATLING and DONNELLY 2007). Although changes in abundance in relation to patch size have been observed (MARSH and PEARMAN 1997) and inbreeding depression is known to affect amphibian survival (HALVERSON et al. 2006), the loss of area per se usually assumed to be less important for amphibian species than the change of microhabitat diversity and quality (ZIMMERMAN and BIERREGAARD 1986; PINEDA and HALFFTER 2004). High species diversity can therefore also be found in small fragments (BELL and DONNELLY 2006). Species presence does not however automatically equate to habitat quality (CUSHMAN 2006). The high impact of edges in small fragments can lead to severe changes in amphibian communities near forest borders (LEHTINEN et al. 2003). An increase in solar radiation and temperatures near edges, for example, leads to an increased drying-out of leaf litter and can thus affect the reproduction succes of species with terrestrial egg clutches (STEWART 1995). Amphibian community composition and population persistence in small fragments are therefore also influenced by the reproductive mode of species. However, the most important indicators for population persistence are population size and survival rates. In particular knowledge on such demographic factors of populations in fragmented landscapes is scarce however (BIERREGAARD et al. 1997). Since many species show differences in critical thresholds of response to fragmentation (WITH and CRIST 1995), the effective remnant size providing sufficient resources for target species, is important information for applied conservation (FAHRIG 2002).

In this chapter the importance of small fragments for the conservation of Neotropical leaf litter frogs is analysed. The chapter follows the main hypothesis that generalist species are more likely to survive in small fragments than specialist species. Nevertheless, biotical and abiotical changes in the fragmented landscape are expected to lead to a higher individual mortality of specialist as well as generalist species than in continuous forest habitat. Furthermore, the isolation of forests is hypothesised to negatively influence the survival of species with high habitat specialisation. In addition it is assumed that a species with matrix tolerance does not show major changes in population size between continuous forest and fragmented landscape. Specialised species with matrix aversion are expected to show a strong increase in abundance and population size with an increase in habitat area.

3.2 Material and methods

Study area and species:

The study was carried out on four sites on the Atlantic Plateau of São Paulo. Sites included two isolated forest fragments ("Carmo" and "Dito"), one forest fragment ("Alcides") connected by a forest corridor to a large forest area, and a control site within the continuous forest ("MorroC"). Forest fragments covered an area of five hectares and contained no water bodies within the forest area. The continuous forest was about 10,000 hectares. There was no water body present at the control site within a radius of 200 metres. All study sites, including the control site were characterised by secondary forest and remained mainly undisturbed for at least 50 years. A detailed description is given in the general methods (Chapters 2.2.1 and 2.2.2) (Fig. 1.1).

Three amphibian leaf-litter species with different degrees of habitat specialisation have been studied: a generalist, a species of intermediate habitat specialisation and a specialist species. All species are leaf-litter forest species, native to the Mata Atlântica of São Paulo.

Chaunus ornatus, a bufonid species, was selected as a habitat generalist due to its high tolerance to matrix habitats (Fig. 1.3). This species is mainly distributed throughout the Atlantic Forest in the states of São Paulo and Rio de Janeiro (IUCN et al. 2006) and can be found in continuous forest areas as well as in disturbed habitats (HEYER et al. 1990). *C. ornatus* is a pond-breeding species (HADDAD and PRADO 2005). Individuals migrate over the reproduction period to temporary and permanent ponds within forests and open areas (IZECKSOHN and DE CARVALHO-E-SILVA 2001). Reproduction starts at the end of the dry season from late July to the beginning of August (DIXO 2005).

The species with intermediate habitat specialisation, *Eleutherodactylus guentheri* (Fig. 1.4), is distributed throughout large areas of the Mata Atlântica (IUCN et al. 2006). *E. guentheri* occurs within forest habitats but can sometimes also be encountered in vegetation near the forest edge (HEYER et al. 1990). During reproduction, the females deposit egg clutches terrestrially, hidden below trunks and stones (KWET and DI-BERNARDO 1999; IZECKSOHN and DE CARVALHO-E-SILVA 2001). The species is a direct developing frog; hatchlings are small, but completely developed frogs (HEYER et al. 1990; IZECKSOHN and DE CARVALHO-E-SILVA 2001).

As a specialist species *Eleutherodactylus parvus* (Fig. 1.5) was selected. This species is distributed throughout the southeast of the Mata Atlântica in the states of Espírito Santo, Rio de Janeiro, Minas Gerais, and São Paulo and restricted to forest habitats (HEYER et al. 1990; IUCN et al. 2006). Reproduction is similar to *E. guentheri* with direct development (HEYER et al. 1990; IZECKSOHN and DE CARVALHO-E-SILVA 2001; HADDAD and PRADO 2005). Both, *E. guentheri* and *E. parvus* are supposed to be territorial species that do not migrate over long distances. Nevertheless, data on individual behaviour is scarce.

A detailed description of species is given in the general methods (Chapter 2.2.3).

Data collection:

Animals were sampled at all four study sites along three transects per site (Fig. 1.2). With a mean investigation diameter of five metres, the investigation area along one transect covered a total of 525 m^2 resulting in a total investigation area of 1575 m^2 per study site.

Capture periods were undertaken during the rainy seasons 2003/2004 (from November 2003 until April 2004) and 2004/2005 (from October 2004 until April 2005). For each transect a robust mark-recapture design was used, as this design allows data analysis for short-term studies using closed population models. (POLLOCK 1982; POLLOCK et al. 1990). The time distance between primary periods differed from 2.4 to 8.7 weeks. Each primary period consisted of five consecutive nights. At all study sites at least five primary capture sessions were undertaken. In one fragment however a sixth capture session took place, resulting in a total of 105 capture nights. A sixth capture session was cancelled in all other fragments on security grounds. Each transect was surveyed only once per night. Animals were caught by hand between 21:00 hours and at least midnight. Transects were surveyed simultaneously by different persons searching the leaf-litter intensively with spotlights. A grid was placed across each transect enabling identification of the capture sites for each animal.

All individuals of the three species studied, *Eleutherodactylus guentheri*, *E. parvus*, and *C. ornatus* were measured and weighed, sex determined if possible and the individual classified as being a juvenile or adult based on its measurements. Snout-vent length was measured using a calliper. If animals measured less than 80% of the minimum snout-vent length for adults described by HEYER (1990), then animals were classified as juveniles.

For individual identification, photos were taken of all body sides of all captured animals using a digital camera with a macro lens and a flash bulb (Olympus E-20, macro converter lens MCON-35, flash Olympus FL-40). Because tissue samples were collected from *Eleutherodactylus guentheri* and *Chaunus ornatus* for accompanying genetic studies, additional toe-clipping was applied to individuals of these species. After taking all information, measurements, photos, and tissue samples, animals were released at their point of capture.

Data analysis:

The mark recapture data were analysed following the robust design, which allows the combination of closed population models with open population models (POLLOCK 1982). Population size was estimated with data from the secondary periods using the closed population models from the programme CAPTURE (OTIS et al. 1978). The programme CAPTURE enables the consideration of differences in capture probability presenting three possible variations: i) individual heterogeneity (Model M_h), ii) behavioural response to capture (Model M_b), or iii) temporal variation (Model M_t). It therefore avoids the problem of the often unrealistic assumption of an equal capture probability over the whole study period (Model M_0). The programme CAPTURE also provides estimators for all possible combinations of these sources of variability except for the Model M_{thb}. Model selection is provided by CAPTURE.

Survival probabilities were calculated using the standard Cormack-Jolly-Seber model implemented in the programme MARK (WHITE and BURNHAM 1999). This Cormack-Jolly-Seber model is an open population model for survival estimates and was used to estimate survival probabilities between primary capture periods.

The calculation of daily survival rates resulted in computational problems with MARK. The time distance between primary capture periods was therefore transformed from days into weeks to calculate the weekly survival rate.

For the selection of estimation models in most cases the model selection routine of MARK, based on the corrected Akaike information criterion (AIC_c) was used (cp. HURVICH and TSAI 1989). If ΔAIC_c was less or equal to 4.0 then the model representing time-independend survival probability was selected for better comparability.

To determine whether survival probabilities differed significantly between study sites, log-based 85% confidence intervals were calculated and checked for overlap. If 85% confidence intervals did not overlap, then the difference between the corresponding estimates was considered to be significant at the 5% level ($\alpha \leq 0.05$) (BUCKLAND et al. 1993).

3.3 Results

3.3.1 Database

In total 632 individuals of the three focal species were captured at least once, representing 383 individuals of *E. guentheri*, 133 individuals of *E. parvus*, and 116 individuals of *C. ornatus*.

3.3.2 Number of captures

The species of intermediate habitat specialisation, *E. guentheri*, was the species most often captured at all study sites (Table 3.1). The forest specialist *E. parvus* was only captured only in isolated small forest patches, mainly in the most isolated fragment "Dito". The generalist species *Chaunus ornatus* was encountered comparatively frequently in the fragment "Carmo Messias" and in low numbers on the remaining sites.

Capture numbers did not differ significantly between years (*E. guentheri:* $\chi^2=8.63$, DF=7, p=0.28, *E. parvus:* $\chi^2=3.94$, DF=7, p=0.27, *C. ornatus:* $\chi^2=12.15$, DF=7, p=0.09).

The number of captures per primary period of *E. guentheri* tended to be higher in isolated fragments than at the control site "MorroC" (Fig. 3.1A). However, none of the comparisons between the control site and the three fragments was statistically significant (Wilcoxon test, with Bonferroni correction: $\alpha>0.05$).

The number of captures per primary period for *C. ornatus* showed the same tendencies as *E. guentheri* (Fig. 3.1B). However, none of the comparisons between the control site and the three fragments was statistically significant either (Wilcoxon test, with Bonferroni correction: $\alpha>0.05$). Only a comparison of the fragment "Carmo Messias" with the control site "Morro C" yielded a nearly significant result (Wilcoxon test, with Bonferroni correction: $\alpha=0.07$).

Table 3.1: Number of captures of *Eleutherodactylus guentheri*, *E. parvus* and *Chaunus ornatus* in the study areas.

	Total abundance	Median of primary period abundance	Mean of primary period abundance
Morro C			
Eleutherodactylus guentheri	19	2	3.6
Eleutherodactylus parvus	0	0	0
Chaunus ornatus	9	2	1.8
Alcides			
Eleutherodactylus guentheri	63	8	11.2
Eleutherodactylus parvus	0	0	0
Chaunus ornatus	13	1	2.6
Carmo Messias			
Eleutherodactylus guentheri	136	16	22
Eleutherodactylus parvus	4	0	0.8
Chaunus ornatus	73	17	14.8
Dito			
Eleutherodactylus guentheri	165	26	21.8
Eleutherodactylus parvus	129	33	26.2
Chaunus ornatus	21	5	4.2

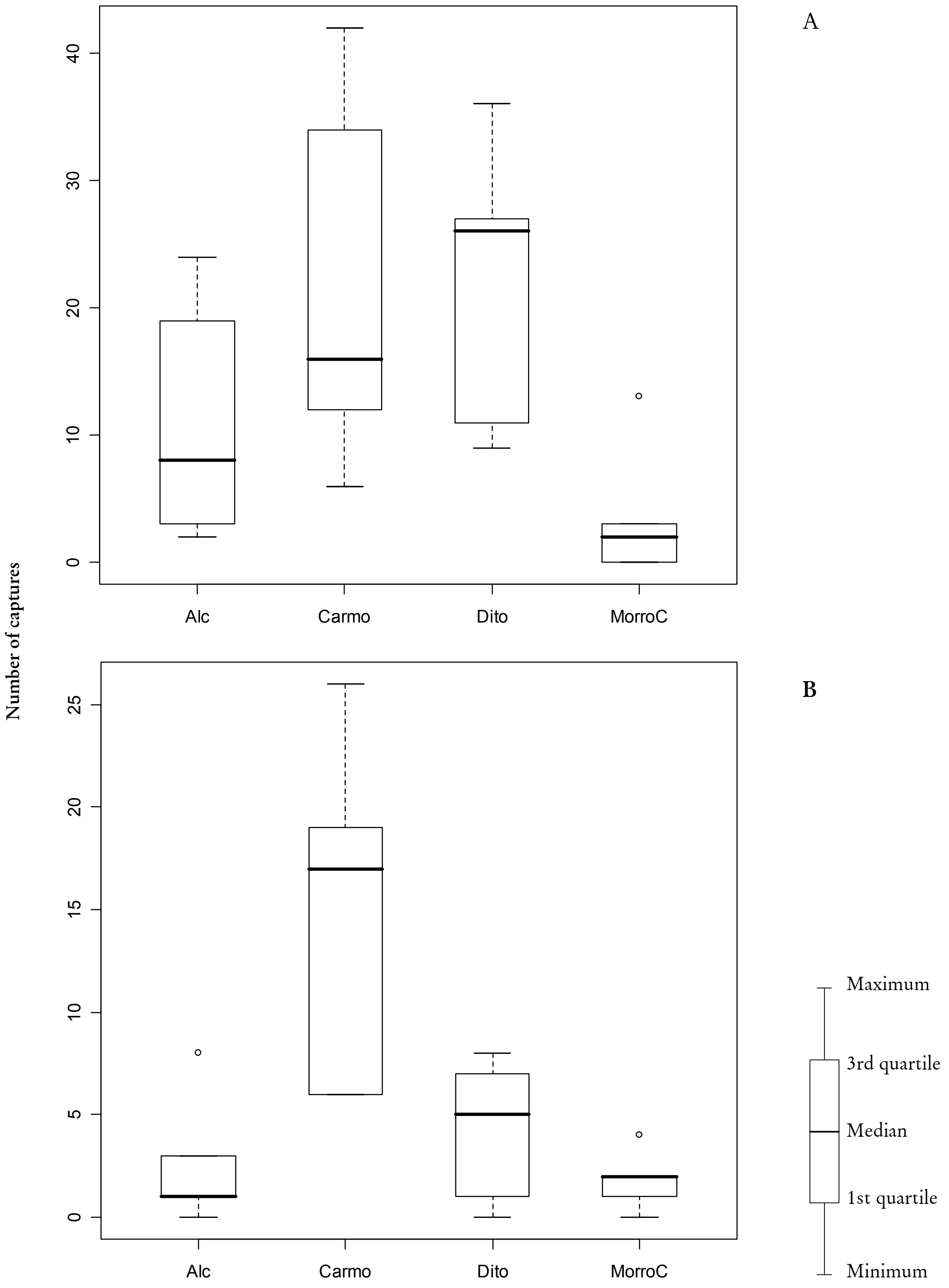

Figure 3.1: Comparison of the number of captures in the study sites: (A) *E. guentheri* and (B) *C. ornatus*. The median, first and third quartile, minimum–maximum range, and outliers of capture rates are indicated. Abbreviations: MorroC = control site, Alc = connected fragment Alcides, CarmoM = isolated fragment Carmo Messias.

3.3.3 Population size:

The results of the population size estimate are presented in Table 3.2. In most cases, for which sufficient data were available, the model selection routine of CAPTURE suggested Model M_0. Population size was only estimated for secondary capture periods, which provided sufficient data. In two cases for the fragment Dito, primary periods three for *E. guentheri* and two for *E. parvus*, respectively, CAPTURE selected model M_{tbh}, for which CAPTURE has no estimator available. Therefore, the second most appropriate model was selected. To estimate population size for periods without recaptures, a linear calibration function to convert capture numbers into population size was determined by a linear regression of the estimated population sizes on capture numbers through the origin (Fig. 3.2).

For *E. guentheri* the estimated population sizes tended to be higher in the fragments compared to the control site for all primary periods, for which estimates were available for the control site (Fig. 3.3), but none of the differences was significant.

E. parvus only provided sufficient data for a population estimate for the fragment "Dito" (Table 3.2) and it was neither captured in the fragment "Alcides" nor the control site "MorroC" (Table 3.1). Although *C. ornatus* was captured on all study sites, recaptures were insufficient for a population size estimate except for two primary periods in the fragment "Carmo Messias" and one in the fragment "Dito".

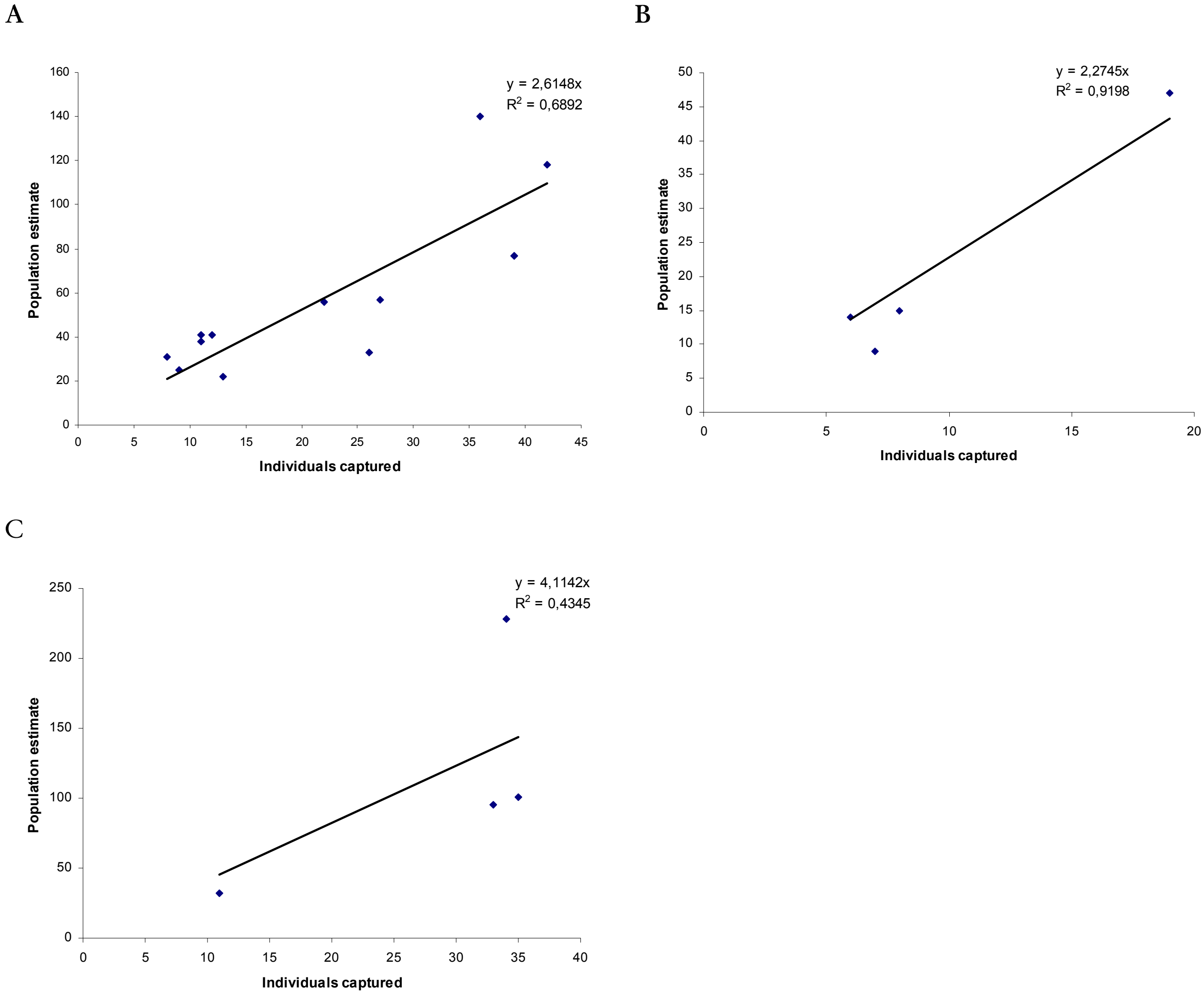

Figure 3.2: Calibration functions of A) *E. guentheri*, B) *C. ornatus*, and C) *E. parvus* for the prediction of population size during capture sessions with insufficient recapture data.

Table 3.2: Models selected and estimated population sizes (N) for *E. guentheri*, *E. parvus*, and *C. ornatus* on the study sites. *: estimates based on the calibration functions of Figure 3.2. A missing "Estimate N" indicates no individuals captured for this species at the corresponding session number.

Site	Species	Session number	Selected model	Estimate N	Standard error	95% Confidence interval	
						lower	upper
Alcides	*E. guentheri*	1	M_t	56	20.632	35	125
		2*	-	8	-	-	-
		3*	-	50	-	-	-
		4	M_o	38	31.813	15	176
		5*	-	5	-	-	-
	C. ornatus	1	M_o	15	7.191	10	45
		2*	-	-	-	-	-
		3*	-	7	-	-	-
		4*	-	2	-	-	-
		5*	-	2	-	-	-
Carmo Messias	*E. guentheri*	1	M_o	118	37.348	73	230
		2*	-	16	-	-	-
		3	M_o	77	18.984	54	133
		4	M_o	41	19.030	23	110
		5*	-	21	-	-	-
		6	M_o	31	13.264	19	79
	C. ornatus	1*	-	59	-	-	-
		2	M_o	47	18.273	29	109
		3	M_o	14	10.136	8	60
		4*	-	39	-	-	-
		5*	-	9	-	-	-
		6*	-	5	-	-	-
Dito	*E. guentheri*	1	M_o	57	16.311	38	108
		2	M_o	41	34.593	16	190
		3	M_t	140	72.050	67	391
		4	M_b	33	3.595	31	48
		5	M_o	25	10.514	16	64
	E. parvus	1	M_o	228	148.117	86	766
		2	M_h	95	13.879	74	128
		3*	-	74	-	-	-
		4	M_o	101	14.316	79	135
		5	M_o	32	7.414	24	56

Continued on next page.

Continuation of Table 3.2.

Site	Species	Session number	Selected model	Estimate N	Standard error	95% Confidence interval	
						lower	upper
Dito	*C. ornatus*	1	M_o	9	2.978	8	23
		2*	-	-	-	-	-
		3*	-	2	-	-	-
		4*	-	18	-	-	-
		5*	-	11	-	-	-
MorroC	*E. guentheri*	1	M_o	22	16.474	11	95
		2*	-	5	-	-	-
		3*	-	-	-	-	-
		4*	-	8	-	-	-
		5*	-	-	-	-	-

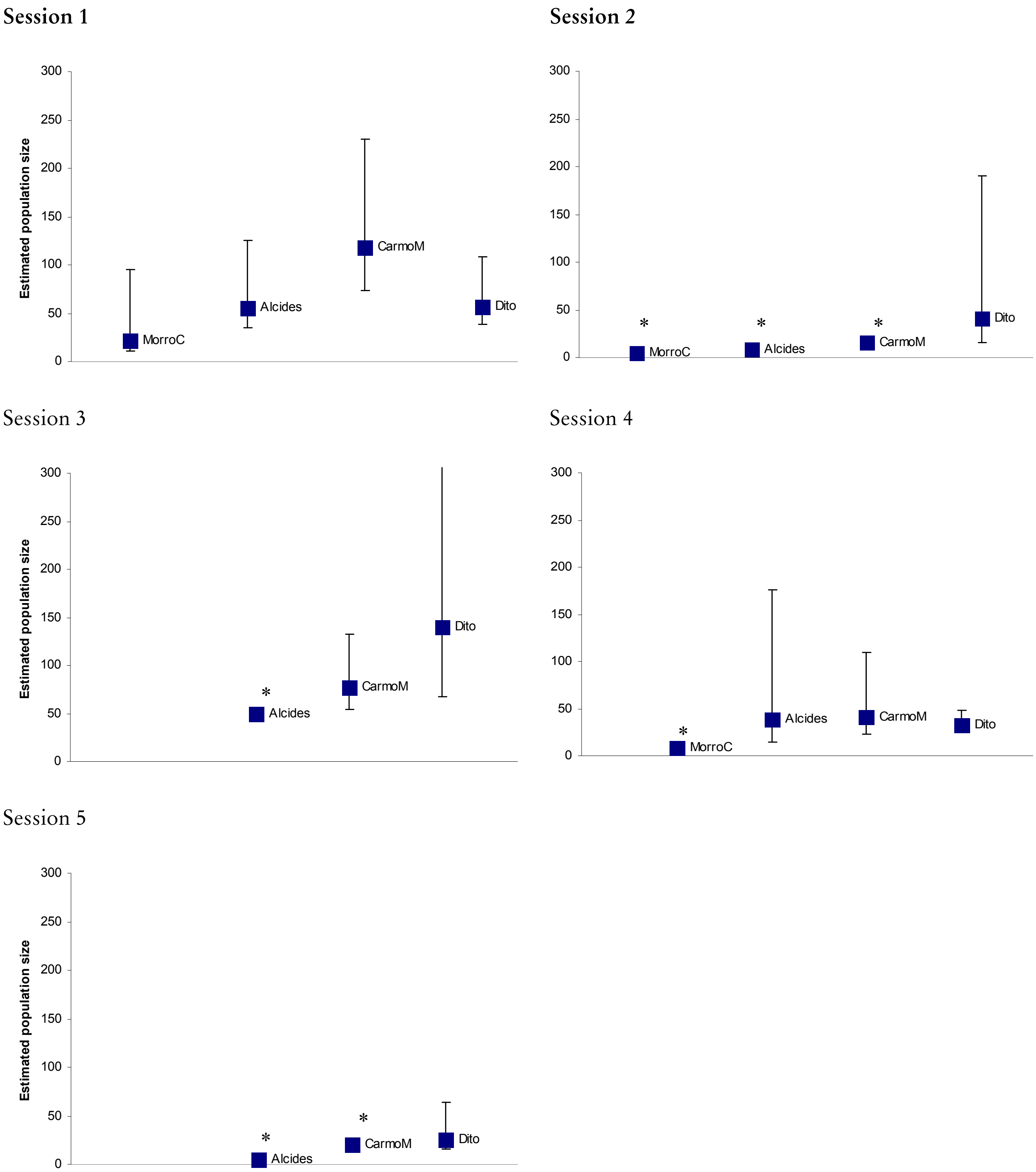

Figure 3.3: Comparison of estimated population sizes and their 95% confidence intervals for *E. guentheri* on the study sites. *: values calculated with calibration function.

3.3.4 Survival probability:

Survival probability ϕ was calculated for *E. guentheri* at all study sites. Capture-recapture data of *E. parvus* were only sufficient for the calculation of ϕ for the fragment "Dito". Survival probabilities of *C. ornatus* were calculated for all sites except for the fragment "Alcides", where sufficient data could not be collected. In all but two cases, that is for *E. guentheri* in the fragment "Carmo Messias" and for *C. ornatus* at the control site "Morro C", time-independent models achieved the lowest AIC_c or rendered an ΔAIC_c within the threshold (Table 3.3) and were therefore used for parameter estimation. Nevertheless, because of high confidence intervals of time-dependent models due to seasonally poor recapture rates in these two cases, models providing time-independent survival probability were also preferentially selected for parameter estimation (Table 3.3).

The results show a significantly higher survival probability for *E. guentheri* in the fragmented habitats "Alcides", "Dito", and "Carmo Messias" compared to the control site "MorroC" with a significantly highest value in "Carmo Messias" (Table 3.4, Fig. 3.4). The estimated survival probabilities of *C. ornatus* were high for the isolated patch "Carmo Messias" (ϕ = 99 %) and the control site "MorroC" (ϕ = 94 %), but relatively low for the isolated patch "Dito" (ϕ = 68 %). However the estimates showed broad confidence intervals that did not enable a meaningful statistical comparison (Fig. 3.4). The specialist species *E. parvus* proved to have a very high survival probability in the isolated patch "Dito". In this fragment, *E. parvus* was the species with the highest survival probability from all of the studied species.

Table 3.3: Overview of the results of model selection based on the corrected Akaike Information Criterion (AIC_c) for estimating survival probability (ϕ) estimation. Model parameters: ϕ (.) = time-independent survival probability; ϕ (t) = time-dependent survival probability; p(.) = time-independent capture probability; p(t) = time-dependent capture probability.

	Model tested	AIC_c	ΔAIC_c	AIC_c weight	Parameters
Alcides	*E. guentheri*				
	ϕ (.) p(t)	35.455	0.000	0.846	5
	ϕ (.) p(.)	40.068	4.614	0.084	2
	ϕ (t) p(t)	41.250	5.795	0.047	8
	ϕ (t) p(.)	42.695	7.240	0.023	5
Carmo Messias	*E. guentheri*				
	ϕ (t) p(t)	145.685	0.000	0.607	9
	ϕ (t) p(.)	146.589	0.904	0.386	6
	ϕ (.) p(.)	154.716	9.031	0.007	2
	ϕ (.) p(t)	161.432	15.747	0.000	6
	C. ornatus				
	ϕ (.) p(.)	45.443	0.000	0.890	2
	ϕ (.) p(t)	50.137	4.694	0.085	6
	ϕ (t) p(.)	53.303	7.860	0.020	6
	ϕ (t) p(t)	55.103	9.660	0.007	9
Dito	*E. guentheri*				
	ϕ (.) p(t)	70.224	0.000	0.699	5
	ϕ (.) p(.)	73.019	2.795	0.173	2
	ϕ (t) p(t)	73.927	3.702	0.110	7
	ϕ (t) p(.)	77.454	7.230	0.019	5
	E. parvus				
	ϕ (t) p(.)	97.256	0.000	0.466	5
	ϕ (t) p(t)	98.058	0.802	0.312	7
	ϕ (.) p(t)	98.823	1.567	0.213	5
	ϕ (.) p(.)	105.087	7.830	0.009	2
	C. ornatus				
	ϕ (.) p(.)	10.624	0.000	0.528	2
	ϕ (t) p(.)	12.345	1.721	0.223	3
	ϕ (t) p(t)	12.345	1.721	0.223	3
	ϕ (.) p(t)	16.649	6.024	0.026	4

Continued on next page.

Continuation of Table 3.3.

	Model tested	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Parameters
MorroC	*E. guentheri*				
	ϕ (t) p(t)	18.569	0.000	0.560	2
	ϕ (.) p(.)	19.829	1.261	0.298	2
	ϕ (t) p(.)	21.363	2.794	0.138	3
	ϕ (.) p(t)	28.657	10.089	0.004	5
	C. ornatus				
	ϕ (t) p(t)	5.439	0.000	0.851	1
	ϕ (t) p(.)	9.173	3.733	0.132	2
	ϕ (.) p(.)	13.234	7.795	0.017	2
	ϕ (.) p(t)	43.479	38.040	0.000	5

Table 3.4: Summary of the results of survival estimates. Model description as in Table 3.3.

Species	Selected model	Survival estimate	Standard error	95% (85%) Confidence interval	
				lower	upper
Alcides					
E. guentheri	ϕ (.) p(t)	0.933	0.015	0.898 (0.909)	0.957 (0.951)
C. ornatus		data not sufficient for calculation			
Carmo Messias					
E. guentheri	ϕ (.) p(.)	0.979	0.010	0.947 (0.959)	0.992 (0.990)
C. ornatus	ϕ (.) p(.)	0.992	0.023	0.289 (0.649)	0.999 (0.999)
Dito					
E. guentheri	ϕ (.) p(t)	0.927	0.012	0.901 (0.908)	0.947 (0.943)
E. parvus	ϕ (.) p(t)	0.974	0.013	0.931 (0.946)	0.991 (0.988)
C. ornatus	ϕ (.) p(.)	0.676	0.121	0.415 (0.485)	0.860 (0.822)
MorroC					
E. guentheri	ϕ (.) p(.)	0.726	0.132	0.418 (0.504)	0.907 (0.874)
C. ornatus	ϕ (.) p(.)	0.938	0.117	0.228 (0.455)	0.998 (0.996)

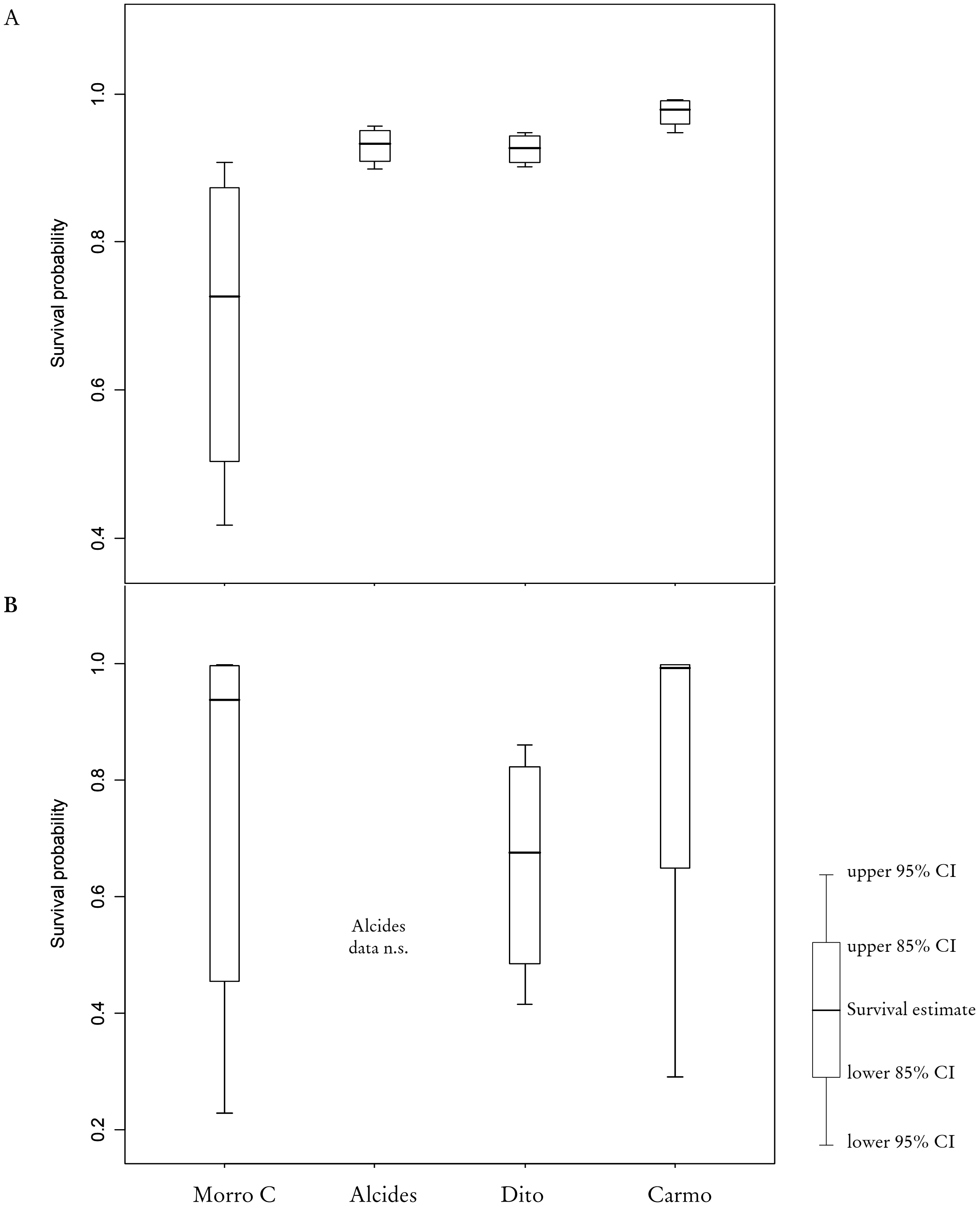

Figure 3.4: Comparison of weekly survival probability estimates φ of (A) *E. guentheri* and (B) *C. ornatus* at the study sites. 95% confidence intervals are indicated. Abbreviations: MorroC = control site, CarmoM = Carmo Messias, data n.s. = data not sufficient for calculation.

3.4 Discussion

Forest fragmentation reduces the size of available habitat, increases edge effects, and the isolation of remnants (SAUNDERS et al. 1991; LAURANCE 2000; FAHRIG 2003). Edge effects are known to lead to a decrease in habitat quality especially for forest specialist species (LAURANCE 2000). A reduced size and quality of habitats combined generally negatively affect the abundance and survival rates of populations (MARSH and PEARMAN 1997; HOKIT and BRANCH 2003; HENLE et al. 2004a; HENLE et al. 2004c). The isolation of remnants can lead to the isolation of populations and consequently negatively survival rates (HALVERSON et al. 2006; WATLING and DONNELLY 2007). Habitat specialists with a high matrix aversion are expected to be more strongly affected by these processes than generalists (WITH and CRIST 1995; DAVIES et al. 2004; HENLE et al. 2004a; WATLING and DONNELLY 2007).

Reduced habitat size and quality are expected to increase mortality and diminish the abundance of species in the fragmented landscape. Habitat loss causes changes in trophic chains and species communities inside forests (HENLE et al. 2004a). Furthermore, open area species invade forest edges and can, depending on the niche overlap of native and immigrating species, lead to increased interspecific competition (DIDHAM et al. 2007). The reduction of habitat leads to a reduction of possible niches for specialists rather than for generalist species (SARRE et al. 1996; HENLE et al. 2004a). Besides habitat reduction, an increase in edges is one of the most important consequences of habitat fragmentation. Edge effects are known to cause changes in microhabitat quality inside forests (SAUNDERS et al. 1991). Increased solar radiation leads to higher temperatures near forest edges and is likely to lead to increased drying of the leaf litter and upper soil layers (SAUNDERS et al. 1991), which should consequently pose a threat to the direct developers with terrestrial egg clutches, i.e. *E. guentheri* and *E. parvus*, that require high humidity (HÖDL 1990; STEWART 1995). The *Eleutherodactylus* species were therefore expected to have a lower abundance and higher mortality rate in the fragments compared to the control area and the more specialised species of the two, *E. parvus*, should be most affected.

The observed results did not match the expectations well. The abundance of *E. guentheri* did not show significant changes in the fragmented landscape compared to the continuous forest. However, contrary to the hypotheses, the continuous forest presented the lowest capture numbers for this species. The abundance of the generalist, *C. ornatus*, was nearly significantly higher in the isolated fragment "Carmo Messias" than at the control site. Adverse to the expectations, the abundance of *C. ornatus* was very low in the continuous forest, intermediate in the connected fragment "Alcides" and high in the isolated fragments. As far as a more apparent effect on specialist versus generalist species is concerned, the habitat generalist *C. ornatus* showed a more apparent difference in abundance between control sites and fragments than the more specialised *E. guentheri*, but as expected the greatest difference was observed for the forest specialist species *E. parvus*. Surprisingly, this species could neither be found in the continuous control site nor in the connected fragment. Individuals were only caught in the isolated forest fragments. In the most isolated forest, i.e. the fragment "Dito", *E. parvus* was the second most abundant species.

Survival probabilities of *E. guentheri* were, contrary to the hypothesis, significantly higher in the fragmented landscape than in the continuous forest of the control site. The capture data of *E. parvus* only provided an estimate of survival probabilities for the isolated fragment "Dito", where survival probability was unexpectedly very high. For the generalist species, *C. ornatus*, significant changes could not be derived. The low recapture rates of *C. ornatus* in the connected fragment "Alcides" did not provide sufficient data for robust survival estimates. For the remaining sites, the generalist presented an inconsistent result with an apparently high survival rate (i.e survival within the study plots) on the control site and in the isolated fragment "Carmo Messias" and a low survival rate in the isolated fragment "Dito".

Habitat reduction did not have the hypothesised extremely negative effect on the abundance and survival of specialists. The changes in habitat size however apparently even caused a positive response of *E. guentheri* and *C. ornatus* and therefore did not lead to the hypothesised negative changes in habitat quality for this species. The abundance and survival data of *E. guentheri* indicated that the small forest fragments did provide sufficient habitat size and quality and consequently host stable populations. For the remaining species insufficient data were available to draw any robust conclusions.

The positive generalist response was not expected. For generalist species habitat fragmentation leads to a reduction of the preferred habitat (With and Crist 1995). For pond-breeding species habitat fragmentation can lead to changes in breeding habitat availability and quality. In the Mata Atlântica forest remnants are usually small and distributed over steep mountain slopes (Oliveira and Fontes 2000). Breeding ponds therefore are more likely to be situated in depressions outside of forests. A matrix-tolerant pond-breeding species like *C. ornatus* is consequently forced to leave its preferred forest habitat for reproduction. As studies on other species indicate, open areas in particular increase the predation risk of migrating species (Fahrig and Merriam 1994; Gruber and Henle 2004). Because other fragmentation consequences like edge or isolation effects do not play a major role for matrix-tolerant species, *C. ornatus* was hypothesised to show negative but only slight changes in abundance and survival in the fragments compared to the control area. Nevertheless, no such effect could be observed for *C. ornatus*. The loss and fragmentation of habitat therefore did not lead to the hypothesised negative change in habitat quality for the generalist species.

The effects of patch isolation were expected to be stronger for the specialists than for the generalist species, because the matrix acts as a stronger barrier for the former rather than the latter (Hanski 1991; Fahrig and Merriam 1994; Gascon et al. 1999). An exchange of individuals among fragments contributes to the maintenance of genetic diversity (Clobert et al. 2004; Whitlock 2004). With increasing isolation, the exchange of individuals decreases (Saunders et al. 1991; Rosenberg et al. 1997). This in turn should increase the rate of inbreeding (Lacy and Lindenmayer 1995; Madsen et al. 1996; Srikwan and Woodruff 2000). In most organisms (Lacy and Lindenmayer 1995; Dudash and Fenster 2000; Gaggiotti and Hanski 2004), including amphibians (Halverson et al. 2006), survival decreases with the rate of inbreeding (Brook et al. 2002). Therefore, survival and abundance should be lower in the isolated compared to the connected fragment.

Habitat isolation revealed no significant response from any of the studied species. Population size and therefore a sufficient remnant size may also be the most likely reason for the lack of response to isolation. Genetic variability in particular depends more on population size than on the exchange of individuals between populations (MADSEN et al. 2000). However, the number of captures was consistently lower in the connected fragment "Alcides" for *E. guentheri*, but surprisingly also for the generalist *C. ornatus*. The most specialised species, *E. parvus*, was interestingly only captured in isolated forest fragments. It is possible, that populations of *E. parvus* remained for whatever reasons only in few forest patches and vanished from others. However, no captures does not automatically mean the absence of a species. Abundance and therefore detection probability may have been too low for captures on the other study sites. This result is completely contrary to the expected response to habitat fragmentation and isolation and also stands in contrast to results of the former study on community composition using the same study plots (DIXO 2005). During this study, in general very few individuals of *E. parvus* were encountered. Except for one individual found in a medium-sized fragment (~19ha), all individuals were captured in the continuous forest reserve only. With regard to these results, *E. parvus* was assumed to be one of the species most sensitive to habitat fragmentation, disappearing from fragmented habitats (DIXO 2005). This is obviously not the case in the presented research. The most likely reason for these contrasting results are methodological differences. Capture using pitfalls, as used by DIXO (2005) seems to lead to an under-representation of *E. parvus* in capture results.

An increased abundance of species in fragments compared to controls has been observed before in fragmentation studies. Previous studies have analysed experimentally fragmented forest (TOCHER et al. 1997). They observed a crowding of individuals inside forest fragments after clear-cutting the surrounding area, followed by an easing of population sizes in subsequent years (DEBINSKI and HOLT 2000; BOWMAN et al. 2002). This explanation is unlikely for the studied landscape, because fragmentation occurred about 50 years ago and no major changes occurred over recent years, i.e., a time span much longer than that observed for an easing of population sizes in fragmentation studies.

A higher abundance or (local) survival rates of leaf-litter amphibians in fragments compared to control areas show, that other factors apart from habitat fragmentation or isolation per se are important for sustaining amphibian populations in fragmented forest landscapes. The studied leaf-litter frogs seem to be more robust to changes in landscape spatial structure than predicted. The most likely reasons for the observed response are positive changes to habitat quality for the studied species. Such an increase in quality is most likely derived from a decrease in predation risk and/or an increase in available resources. Studies from the Amazon have shown an increase in the abundance of some leaf-litter invertebrate species in small fragments compared to controls. Such species are potentially important prey for leaf-litter amphibians (e.g. WHITFIELD and DONNELLY 2006) and their increase could be an explanation for the higher abundance of *C. ornatus* in the fragments (DIDHAM 1997; DIDHAM et al. 1998). Higher resource availability also may have resulted from a replacement of species more sensitive to fragmentation with overlapping niches. Nevertheless, knowledge about niche occupancy and fragmentation vulnerability of syntopic amphibians is scarce and such effects can therefore only be speculated. A higher abundance of prey might be one factor influencing amphibian abundance although this has low relevance for changes in survival rates. Furthermore, the temporal variability of abundance changes in leaf-litter invertebrates remains unclear.

Changes in predation risk are likely relevant causes of the observed response. The disappearance of predators sensitive to fragmentation can lead to a higher survival probability of species less sensitive to fragmentation (HENLE et al. 2004a). Knowledge about predators of the studied species is scarce. Nevertheless, ants, spiders, snakes, and mainly understorey birds (obligatory ant-followers) are supposed to be the main predators of the studied generalist and specialist species (MCCORMICK 1982; VILLARD and PAVIS 1998; POULIN et al. 2001; GRAY et al. 2002; PRADO and BORGO 2003; TOLEDO 2003; TOLEDO et al. 2007). These groups are known to be sensitive to the fragmentation of tropical forests (STOUFFER and BIERREGAARD 1995; PARTRIDGE et al. 1996; BIERREGAARD and STOUFFER 1997; BOSWELL et al. 1998; HARRISON and BRUNA 1999; GIBB and HOCHULI 2002; SEKERCIOGLU et al. 2002; BRÜHL et al. 2003; VASCONCELOS et al. 2006) and consequently the meso-predator release hypothesis (TERBORGH 1974) could explain a higher survival and abundance of amphibian populations in fragments.

The fact that forest specialist species still occur in a landscape of secondary forest which was fragmented at least 50 years ago is an indication of their lower sensitivity to fragmentation itself and on further effects of the fragmentation process. It shows that even small forest fragments can have important conservation value, especially for taxonomic groups with limited spatial requirements that benefit from the absence of predators. Similar conclusions were reached by TSCHARNTKE et al. (2002) for herbivore insects and by (OGLE 1987) for endemic carnivorous snails in New Zealand forest. Notwithstanding, this should not distract from the fact that large tracts of continuous forest have overriding conservation importance.

4 Morphological shifts in populations of generalist and specialist amphibians in response to the fragmented landscape of the Mata Atlântica of São Paulo

4.1 Introduction

Changes of morphological factors, such as body size, body condition, and leg length are important indicators of fundamental changes in life history or habitat quality (PALKOVACS 2003; BUCKLEY et al. 2005; LOWE et al. 2006). Environmental parameters are main drivers of adaptational shifts in morphology (WADE 2004). Habitat loss and fragmentation lead to changes in the abiotic and biotic environment and therefore to changes in habitat quality (SAUNDERS et al. 1991) and furthermore leading to changing selective pressures on morphology (THOMAS et al. 1998; EWERS and DIDHAM 2006). The strongest impact of habitat fragmentation can be observed in naturally homogeneous landscapes such as the vast forests of tropical regions (BAWA et al. 2004), where numerous biotic and abiotic factors are affected (LOVEJOY et al. 1986; TABARELLI et al. 1999; TABARELLI et al. 2004). This change in habitat quality affects life within fragments at all levels, from the community to the individual.

Important environmental factors known to influence the phenotype are resource availability as well as predation risk. Both factors co-vary with maximum body size (BALL and BAKER 1996; JESSOP et al. 2006) and can also influence body condition (DU 2006). An increase of resource availability can lead to better body condition and larger body size (DU 2006; JESSOP et al. 2006; WU et al. 2006). An increase in the presence of predators can additionally lead to a smaller size at emergence, and lower growth and developmental rates, due to the cost of anti-predator behaviour (BALL and BAKER 1996).

Current debates on insular shifts in morphological parameters are based on two ideas: a) a direct influence of environmental parameters on morphological traits and b) adaptation as a result of life history changes (ROUGHGARDEN 1995; PALKOVACS 2003; LOMOLINO 2005; READING 2007). Whereas the direct influence hypothesis mainly explains insular shifts in morphological traits with changes in competition, predation, or resource availability, the second approach follows long-term effects caused by evolutionary shifts of life history traits or genetic drift. In any case, for habitat remnants in fragmented landscapes this adaptation process should depend on the degree of fragmentation, time since the fragmentation, and insularisation, as well as on species characteristics, including species specific thresholds of fragmentation (WITH and CRIST 1995).

Insular size trends have been studied in detail for vertebrate groups, including mammals and reptiles, showing inconsistent results of adaptations to island habitats, mainly depending on the trophic niche of the species concerned (e.g. CASE and SCHWANER 1993; ADLER 1996; MICHAUX et al. 2002; PALKOVACS 2003; ROBINSON-WOLRATH and OWENS 2003; LOMOLINO 2005). Only few studies examined such a trend among populations of single species and even less studied morphological shifts in amphibians. Those existing studies found inconsistent results (WU et al. 2006; GVOŽDÍK and MORAVEC n.d.). V. GVOŽDÍK (pers. comm.) found significantly smaller individuals of *Hyla savignyi* in Cypriote populations compared to mainland populations. In contrast, WU et al. (2006) found a significant increase in the body size of Chinese rice frogs (*Rana limnocharis*) in island habitats compared to mainland populations and explained this result by higher resource availability on islands. An increase in resource availability for leaf-litter amphibians can also be observed in tropical forest fragments compared to continuous forests, because matrix species of leaf litter invertebrates invade forest edges (DIDHAM 1997; LAURANCE et al. 2002). Nevertheless, such results of island-mainland comparisons are difficult to transfer to fragmented landscapes because island populations are most likely separated for a longer period of time than remnant populations in a fragmented habitat, unless they are naturally fragmented. Morphological changes on islands are based on long term evolutionary effects (PALKOVACS 2003) and are therefore expected to be stronger compared to fragmented habitats. A second important reason for a cautious interpretation of such results is an essential difference in habitat configuration, because habitat fragments are surrounded by a matrix of modified, yet not necessarily completely inhospitable habitat. This may lead to interactions between species in remnants and invading matrix species, and in extremely unlikely cases lead to an insularisation of remnants (GASCON et al. 1999; FAHRIG 2003). In contrast to real islands, species in a fragmented landscape present individual traits rendering them more or less sensitive to habitat fragmentation (WITH and CRIST 1995; HENLE et al. 2004a).

Morphological changes of vertebrate species following habitat fragmentation have been examined in very few studies (DIAZ et al. 1999; NECKEL-OLIVEIRA and GASCON 2006). In particular, knowledge on morphological changes of anuran amphibian species following habitat fragmentation is scarce. In an existing study NECKEL-OLIVEIRA and GASCON (2006) showed body size shifts of a habitat generalist (*Phyllomedusa tarsius*) in fragments, regrowing forest, and pasture compared to continuous forest, with larger individuals in the latter and explained these shifts with changes in habitat quality. Therefore, similar changes in body size in fragments compared to non-fragmented habitats of the Mata Atlântica can be predicted. Moreover, habitat specialists are particularly more sensitive to changes of microhabitat quality in fragmented habitats, and are consequently more prone to extinction in the fragmented landscape than generalists (MARGULES 1996; HENLE et al. 2004a), and are therefore also assumed to show a stronger response regarding morphological shifts.

In this chapter, the hypothesis is tested that species in fragments should show shifts in body size and body condition to a smaller size or lower condition, respectively. Furthermore, it is examined, whether generalists and specialists show different degrees of shifts in body size.

4.2 Material and methods

Study area:

The study was carried out at four sites on the Atlantic Plateau of São Paulo: two isolated small forest fragments ("Carmo" and "Dito"), one small forest fragment ("Alcides") connected by a forest corridor to a larger forest area, and a control site within the continuous forest ("MorroC"). Forest fragments covered an area of five hectares and contained no water bodies within the forest area. The continuous forest was about 10,000ha. There was no water body present at the control site within a radius of 200m. All study sites, including the control site were characterised by secondary forest and remained undisturbed for at least 50 years. A detailed description is provided in the general methods (Chapters 2.2.1 and 2.2.2) (Fig. 1.1).

Studied species:

Two leaf-litter dwelling forest species were chosen for comparison.

Chaunus ornatus, a bufonid species, was selected as a habitat generalist due to its high tolerance to matrix habitats (Fig. 1.3). This species is distributed throughout the Atlantic Forest in the states of São Paulo and Rio de Janeiro (IUCN et al. 2006) and can be found in undisturbed continuous forest areas as well as in disturbed forest fragments (HEYER et al. 1990; own obs.). *C. ornatus* breeds in temporary and permanent ponds within forests and open areas (IZECKSOHN and DE CARVALHO-E-SILVA 2001; HADDAD and PRADO 2005). Reproduction starts at the end of the dry season in late July, beginning of August (DIXO 2005).

Eleutherodactylus guentheri was selected as a specialist species. It is distributed over large parts of the Mata Atlântica (IUCN et al. 2006). *E. guentheri* occurs within forest habitats but can sometimes also be encountered in vegetation near the forest edge (HEYER et al. 1990). Females deposit egg clutches terrestrially, hidden below tree trunks and stones (KWET and DI-BERNARDO 1999; IZECKSOHN and DE CARVALHO-E-SILVA 2001). Frogs undergo direct development within the egg capsule (HEYER et al. 1990; IZECKSOHN and DE CARVALHO-E-SILVA 2001).

A detailed description of both species is given in the general methods (Chapter 2.2.3).

Data collection:

During the capture-recapture study described in chapter three, individuals of *C. ornatus* and *E. guentheri* were captured by hand at night (21:00 – 01:00) (cp. Chapter 3.2). Animals were captured during the rainy seasons 2003/2004 and 2004/2005 over a total period of at least 25 nights per study site. Only at one site capture took place exceptionally for a total of 30 nights.

Measurements of snout-vent-length (SVL) and tibia length (TL), as indicator of locomotor performance (BUCKLEY et al. 2005), of all individuals were taken using a calliper with an accuracy of 0.1mm. Tibia length has been taken constantly from the left body side. Individuals were weighed using a digital balance with an accuracy of 0.1g (Kern CM 250-1).

During the 105 capture nights a total of 499 individuals of the selected species were captured, representing 116 individuals of *C. ornatus* and 383 individuals of *E. guentheri*. As juveniles were seldom captured, only the data from adult individuals were considered in the analysis. Individuals that could not be classified with certainty as adults and recaptures were also excluded from the analysis. Thus, for *C. ornatus* a total of 54 individuals and for *E. guentheri*, a total of 376 individuals was used in the analysis (Table 4.1).

Data analysis:

Males and females were combined in the analysis because usually sex differentiation is not possible for both of these two species. A body condition index (BCI) was calculated from snout-vent-length (SVL) and body mass by regressing body mass on the ln–transformed 3rd power of SVL of all individuals from all study sites. Logarithmic transformation of body mass data was used to improve the linearity of the relationship between the variable and the normality of its distribution. The residual index (JAKOB et al. 1996) was used as the BCI. All variables did not deviate from a normal distribution (Kolmogorov-Smirnov-Test: $D=0.5–0.7$, $\alpha>0.05$), therefore data was analysed using ANOVA. For significant results, a pairwise t-test with Bonferroni correction was used to assess differences among individual sites.

ANCOVA was used to analyse differences in the body condition index between study sites, with tibia length as a covariate. The BCI was preferred for further analysis rather than snout-vent-length and body mass because a higher occurrence of sub-adult animals can result in biased morphological comparisons. A clear determination as to whether an individual was adult or sub-adult was not always possible and differences in the population structure therefore have biased results. For significant results of ANCOVA the multivariate redundancy analysis (RDA) was used in the following (VAN DEN WOLLENBERG 1977; LEGENDRE and ANDERSON 1999; MCARDLE and ANDERSON 2001). Analyses were performed using the programme "R" (R FOUNDATION 2007).

4.3 Results

The maximum body length found for the specialist species *E. guentheri* in the fragmented landscape did exceed the maximum body length in the unfragmented control by about 36% (ranging from 34 to 39%). Furthermore, the maximum tibia length of this species in the fragmented landscape also exceeded the maximum tibia length in the unfragmented control by about 38% (32 to 43%) (Table 4.1). Snout-vent-length, tibia length, and body mass of *E. guentheri* did not differ significantly among sites (ANOVA F=1.35, α=0.26, F=1.79, α=0.15, and F=2.36, α=0.07) (Table 4.2). Only the BCI of this species showed significant differences between sites (ANOVA F=2.67, $\alpha<0.05$) (Table 4.2). Nevertheless, pairwise t-tests could not reveal any significant differences between two of the study sites (Table 4.3).

For *C. ornatus* the comparison of maximum body length and maximum tibia length of the generalist species showed higher results in the unfragmented control site. The largest individuals of *C. ornatus* in the fragmented study area showed a snout-vent-length of about 28% (i.e. 21 to 35%) shorter than those in the control, whereas the maximum tibia length was about 19% (i.e. 15 to 24%) shorter than in the control (Table 4.1). Snout-vent-length, tibia length, and body mass differed significantly among sites (ANOVA F=5.03, $\alpha<0.01$, F=5.02, $\alpha<0.01$, and F=3.30, α=0.03) (Table 4.2). Pairwise t-tests showed that these differences were due to significantly lower values of these parameters in the isolated fragment "Carmo Messias" compared to the control site "MorroC" (SVL $\alpha<0.01$, TL $\alpha<0.01$, body mass α=0.04) (Table 4.4). Furthermore, pairwise t-tests revealed that tibia length was nearly significantly smaller in the isolated fragment "Dito" compared to the control site ($\alpha<0.10$) (Table 4.4).

Table 4.1: Overview of the number of captures per study site and morphological traits of the studied species. SVL = snout-vent-length, TL = tibia length, BCI = body condition index, max = maximum value, SD = standard deviation. Control = MorroC, connected fragment =Alcides, isolated fragments = Carmo and Dito.

	Captures	**SVL**			**TL**			**BCI**	
		max	mean	SD	max	mean	SD	mean	SD
E. guentheri									
MorroC	18	24.7	19.9	2.4	17.1	13.8	1.5	0.08	0.12
Alcides	60	33.0	21.4	4.4	22.5	15.0	3.1	0.04	0.21
Carmo	136	33.4	20.2	5.1	24.4	14.0	4.0	-0.05	0.31
Dito	162	34.4	19.6	7.0	23.9	13.4	5.5	0.02	0.30
C. ornatus									
MorroC	9	89.9	57.8	22.2	37.0	26.5	9.2	-0.37	2.16
Alcides	6	64.6	51.2	12.5	30.4	23.9	6.3	-0.21	1.45
Carmo	26	58.6	39.4	8.5	28.2	18.3	4.0	0.09	0.82
Dito	13	71.2	44.4	12.2	31.6	20.1	6.2	0.16	1.81

Table 4.2: ANOVA models of the generalist species *C. ornatus* and the specialist species *E. guentheri* for measurements and body condition. The α-value explains the difference of the model considering differences between study sites to the Null-model. Significant results are in bold.

	DF	**Deviance**	**Residual DF**	**Residual Deviance**	**F**	**α -value**
C. ornatus						
snout-vent-length	3	2514.60	50	8324.10	5.03	**0.004**
tibia length	3	520.67	50	1728.98	5.02	**0.004**
ln (body mass)	3	7.24	50	36.52	3.30	**0.028**
BCI	3	0.05	50	1.82	0.42	0.738
E. guentheri						
snout-vent-length	3	138.20	372	12671.80	1.35	0.257
tibia length	3	108.40	369	7443.00	1.79	0.149
ln (body mass)	3	6.52	368	338.34	2.36	0.071
BCI	3	0.67	368	30.97	2.67	**0.048**

Table 4.3: α-values of significance from the pairwise t-tests for site differences in the BCI of *E. guentheri* in the fragments and at the control site. Control = MorroC, connected fragment =Alcides, isolated fragments = Carmo Messias and Dito.

	Alcides	**Carmo Messias**	**Dito**
Carmo Messias	0.290	-	-
Dito	1.000	0.120	-
MorroC	1.000	0.470	1.000

Table 4.4: α-values of significance from the pairwise t-tests for site differences in snout-vent-length (SVL), tibia length (TL), and body mass (mass) of *C. ornatus* in the fragments and at the control site. Significant results are in bold. Control = MorroC, connected fragment =Alcides, isolated fragments = Carmo Messias and Dito.

	Alcides			**Carmo Messias**			**Dito**		
	SVL	TL	mass	SVL	TL	mass	SVL	TL	mass
Carmo Messias	0.292	0.245	0.388	-	-	-	-	-	-
Dito	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-
MorroC	1.000	1.000	1.000	**0.004**	**0.004**	**0.037**	0.124	0.095	0.401

Whereas ANOVA already yielded significant differences in the BCI for *E. guentheri*, the consideration of tibia length as a covariate improved the model significantly (ANOVA $F_{1,367}=7.26$, $\alpha<0.01$) resulting in highly significant differences among sites (ANCOVA $r^2=0.02$, $F_{2,367}=4.38$, $\alpha=0.01$). The data analysis of *C. ornatus* did not reveal such a significant influence on tibia length data for the analysis of differences among sites (ANCOVA $r^2=0.00$, $F_{2,51}=0.94$, $\alpha=0.40$).

In the following multivariate analysis of body condition index and tibia length data of *E. guentheri*, RDA1 almost entirely explained the constrained variance (Table 4.5). RDA1 separates the connected fragment "Alcides" from the remaining sites (Figure 4.1). The RDA1 distance of the variables of the fragment "Alcides" to the other study sites therefore accounts for the significant differences found in ANCOVA.

Table 4.5: Redundancy analysis inter-set correlations of study sites against the canonical axes for tibia length and body condition index data of *E. guentheri* (centroid loadings). The table further shows Eigenvalues and the cumulative percentage of constrained variance explained by axes RDA1 and RDA2.

	RDA 1	**RDA 2**
MorroC	0.138	-0.992
Alcides	-0.953	-0.497
Carmo	-0.122	0.601
Dito	0.441	-0.224
Eigenvalue	0.304	0.002
% variance	99.670	0.330

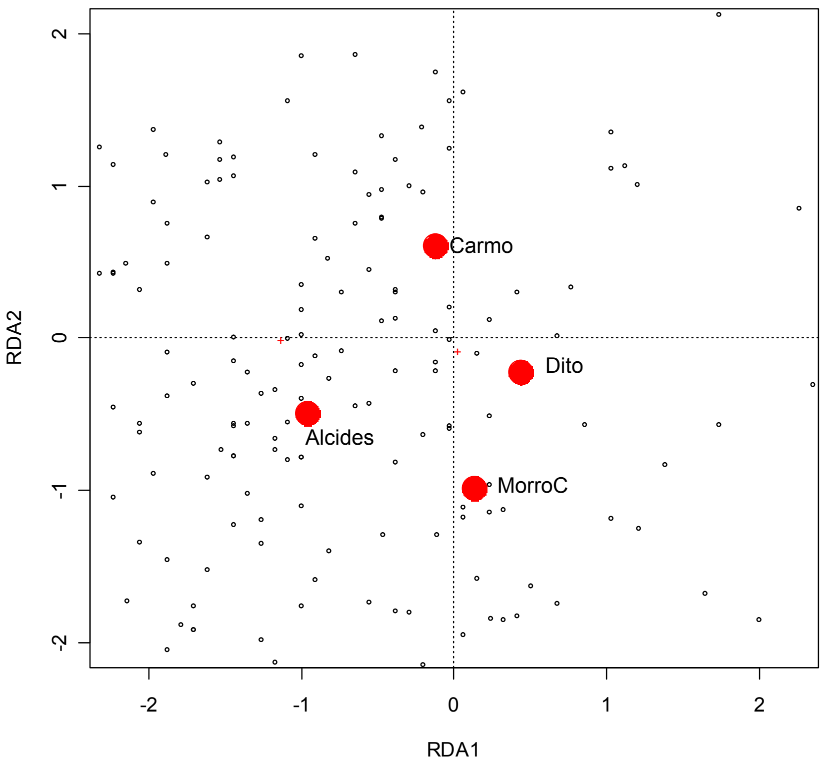

Figure 4.1: Redundancy analysis biplot of inter-set correlations (red dots) of study sites against the canonical axes for tibia length and body condition index of *E. guentheri*. Abbreviation: Carmo = Carmo Messias. Control = MorroC, connected fragment =Alcides, isolated fragments = Carmo Messias and Dito.

4.4 Discussion

The studied species showed contrasting results in the analysis. The expected fragmentation effect was only observed in maximum values of snout-vent-length and tibia-length of *C. ornatus*. Encountered individuals of *C. ornatus* were smaller in forest fragments compared to the control, whereas for *E. guentheri* the opposite applied. Although these results are an indicator for shifts, the explanatory power is limited as they are yielded from a simple comparison of maximum values, which is highly dependent on sample size. For the studied specialist, *E. guentheri*, ANOVA only revealed significant differences among sites for the body condition index. The studied generalist, *C. ornatus*, differed significantly in all other parameters except for the BCI. Nevertheless, significant differences between individual study sites were only revealed for *C. ornatus*. Individuals of this species were significantly smaller, proved to have shorter legs, and were lighter in the isolated fragment "Carmo Messias" than in the control site. A similar, yet not significant tendency compared to the control site was found in the other isolated fragment "Dito". The combination of BCI and tibia length in the analysis of covariance and the multivariate analysis only revealed significant differences among study sites for the specialist *E. guentheri*. In contrast to the hypothesis, not the control site but the connected fragment "Alcides" accounted mostly for this difference, where mean tibia length was higher than in all other study sites and body condition was higher than in the isolated fragments but lower than in the control.

The observed results partly meet the hypotheses. In general, a different pattern of morphological shifts were found for the generalist and the specialist species. The results of the generalist species *C. ornatus* partly conform with the predictions for smaller individuals in the fragmented landscape compared to the unfragmented forest. The most evident changes in body length and tibia length, in this case becoming smaller, were found in the isolated fragment "Carmo Messias". Although not significant at the five percent level, the same tendencies were observed for tibia length in the isolated fragment "Dito" compared to the control. Similar results were found for a generalist species (*Phyllomedusa tarsius*) in Amazonia, with larger individuals in continuous forest compared to fragmented and otherwise disturbed habitats (NECKEL-OLIVEIRA and GASCON 2006). The most likely explanation for the observed pattern of morphological shifts in *C. ornatus* is a decrease in the area of the preferred habitat and changes in breeding habitat quality. Changes in microhabitat quality following fragmentation within the forest habitat were assumed to be of minor relevance because generalist species show a high tolerance to edge effects for example (HENLE et al. 2004a). Nevertheless, a reduction of the preferred habitat (in this case forest) is likely to lead to the increasing isolation of breeding ponds and to changes in breeding habitat quality for *C. ornatus*. In the Mata Atlântica, forest remnants often distributed over steep mountain slopes (OLIVEIRA and FONTES 2000) and breeding ponds are therefore more likely to be found in hollows and depressions outside of forests. The increased isolation of breeding ponds causes an increase in migration time (MARSH et al. 1999) in the matrix habitat, which in turn can increase predation risk (FAHRIG and MERRIAM 1994; GRUBER and HENLE 2004). However, ponds outside of forest possibly also show changes in physical conditions. BEACHY (1995) showed that breeding pond temperature and resource availability can have a strong effect on larval growth and the time of metamorphosis. Whereas little is known about resource availability and the changes in larval competition following fragmentation, a temperature increase in matrix ponds compared to forest ponds is very likely. This in turn would lead to an earlier metamorphosis, resulting in a smaller size at metamorphosis and probably a smaller size at maturity and adult size (SMITH 1987; SEMLITSCH et al. 1988; BEACHY 1995; STÅHLBERG et al. 2001). These conditions together with a possible increase in anti-predator behaviour and changes in resource availability and/or quality therefore affect the morphological parameters of larvae and adults (SMITH 1987; SEMLITSCH et al. 1988; BEACHY 1995; STÅHLBERG et al. 2001), but apparently not adult body condition. Genetic drift probably does not play a major role for *C. ornatus* (SMITH and GREEN 2005). As studies on other pond-breeding species have shown, low breeding pond fidelity of individuals leads to a high genetic exchange among populations, even in fragmented landscapes (SINSCH 1992). The results of the genetic studies in the study area support this theory. DIXO (2005) did not find a relationship between genetic distance and geographic distribution for *C. ornatus* in the fragmented landscape. Nevertheless, because this study also showed a decrease in genetic diversity with a decrease in forest cover, long-term genetic effects may play a more important role in the future.

The results of *C. ornatus* have to be interpreted cautiously because differences between isolated study sites and the control were not found in body condition. This suggests that significant differences found in snout-vent-length, tibia length, and body mass for *C. ornatus* might have been caused by differences in the population structure in the isolated fragment "Carmo Messias" compared to the other sites. An increased occurrence of sub-adult individuals in this fragment could have made the results biased. Nevertheless, it remains unclear as to whether this increased occurrence of sub-adult individuals results from fragmentation effects or from site-specific characteristics. Detailed information however on the age structure of populations (e.g. age at maturity) and the migration behaviour of sub-adults are scarce and such an effect therefore has to be investigated in further studies.

In contrast to the hypothesis, the specialist species, *E. guentheri*, showed a less clear pattern. Although the mean body condition was highest for the control site and ANOVA revealed significant differences between sites, the pairwise t-test comparison did not differentiate individual sites significantly. The RDA also did not help in reaching some form of clarification because it separated the connected fragment "Alcides" from all other sites. In contrast to the hypothesis, the specialist species *E. guentheri* therefore did not apparently show any clear morphological adaptations due to habitat fragmentation and isolation. Although slight differences in habitat quality between the study sites cannot be excluded, the inconclusive pattern in the response of *E. guentheri* suggests that changes in habitat quality, which probably account mainly for the observed shifts of *C. ornatus*, were apparently less important for *E. guentheri*. The inconsistent observations are more likely to be a result of genetic drift due to limited exchange between populations of *E. guentheri*, rather than shifts resulting from changes in habitat quality following habitat fragmentation. Genetic differences among island populations (SEPPÄ and LAURILA 1999) and the effect of landscape structure on population genetics (DRISCOLL 1998; FUNK et al. 2005) have previously for amphibians. Studies on other vertebrates, including mammals (GERLACH and MUSOLF 2000) and reptiles (CUNNINGHAM and MORITZ 1998; TEMPLETON et al. 2001), showed that habitat fragmentation can also cause such an effect as observed on islands or with other geographical barriers. The high capture numbers, which suggest a high population size and the short time since separation are probably main reasons for the weak response (GIBBS 1998). Further investigations for sound conclusions are required because detailed knowledge on the genetic variability of *E. guentheri* remains scarce.

According to the literature and theory, a higher species specialisation leads to higher fragmentation sensitivity and higher extinction risk in the fragmented landscape (WITH and CRIST 1995; FAHRIG 2002; FAHRIG 2003; HENLE et al. 2004a). Because more specialised species are more greatly influenced by changes in the quality of microhabitat following habitat fragmentation, selective pressures and also morphological changes should be greater than for generalist species. The observed morphological shifts imply the contrary however. Nevertheless, the observed results may have been influenced by species-specific characteristics. Whereas the habitat specialist *E. guentheri* is a direct developer, restricted to forest habitats, the generalist *C. ornatus* is a pond-breeding species. The presence of *E. guentheri* at forest edges and high capture numbers in small fragments suggest that this species is more robust to changes in habitat quality within forest fragments than hypothesised. In fact, it is likely that habitat fragmentation led to greater changes in the availability and quality of breeding habitat for the pond-breeding species *C. ornatus* compared to *E. guenteri*. In conclusion, the two studied species seem to be affected by different processes driving morphological shifts. As a result of species-specific characteristics *E. guentheri* is apparently more affected by long-term processes due to life history changes and genetic drift, whereas *C. ornatus* shows shifts that suggest a direct influence from changes in habitat quality following fragmentation.

Although most studies usually assume that habitat quality deteriorates for forest-dependent species after fragmentation (e.g. SAUNDERS et al. 1991; FAHRIG 2003; HENLE et al. 2004a), this study showed that specialised leaf-litter frogs may also be unaffected from altered conditions in fragmented landscapes. The studied species also showed positive responses regarding demographic variables (Chapter 3), with both species being more abundant and with *E. guentheri* displaying lower mortality in small isolated fragments than for the control site. Although populations in small isolated fragments are frequently most at risk from extinction, this is not invariably the case (HENLE et al.

2004a). A better understanding of these differences and the conditions under which fragments can provide favourable conditions for the survival of species, could considerably improve the effectiveness of local conservation plans.

5 Implications for the conservation of amphibians in fragmented landscapes of the Mata Atlântica: A synthesis

5.1 Introduction

Fragmentation and the destruction of habitats are among the main causes for the global loss of biodiversity, including amphibians (HENLE et al. 2004b; ETEROVICK et al. 2005). Global hotspots of biodiversity, and the Mata Atlântica in particular are extremely affected by habitat loss and fragmentation (BROOKS et al. 2002; GALINDO-LEAL et al. 2003; MALCOLM et al. 2006). At present the Brazilian part of the Mata Atlântica has been reduced from 1.1 million km^2 to less than 8% of its original distribution area (SOS MATA ATLÂNTICA and INPE 2002), but still presents very high endemism rates with about 30% for birds, mammals, and reptiles, and more than 90% for amphibians (MYERS et al. 2000). The reduction of habitat poses a threat to extinction, especially to highly endemic species. Amphibian population declines have been reported from the Mata Atlântica. Overall, 30 species have been reported as having either declined or already disappeared (SILVANO and SEGALLA 2005), mainly in two geographic regions of the Atlantic Forest in Southeastern Brazil: the "Serra do Mar" and the "Serra da Mantiqueira" (HEYER et al. 1988; ETEROVICK et al. 2005; SILVANO and SEGALLA 2005). Numerous studies have investigated the impact of habitat fragmentation on amphibian communities (e.g. TOCHER et al. 1997; GASCON et al. 1999; LAURANCE et al. 2002; DIXO 2005; FARIA et al. 2007). Nevertheless, little is known about the processes within populations or population characteristics following habitat fragmentation. The presented study therefore focused on the comparison of life history traits and morphological parameters of populations of generalist and specialist species in forest fragments and an unfragmented area. The results of the preceding chapters allow a detailed insight into the response of leaf-litter frog species with different habitat specialisation but native to the forests of the Mata Atlântica to habitat fragmentation.

5.2 Summary of results

The study on abundance, population size, fluctuations, and mortality (Chapter 3) showed the hypothesised high response of species with high habitat specialisation (i.e. matrix aversion). In contrast to the initial hypothesis, species with high specialisation showed an apparently positive response to fragmentation and the isolation of forest habitats. The generalist however showed inconsistent results. Such coherent patterns were not found in the study on morphological shifts of populations of the generalist and one specialist species in forest fragments compared to the unfragmented control (Chapter 4). In fact, hypothesised shifts were found only for the generalist species.

The most specialised species, *Eleutherodactylus parvus*, showed the greatest response to habitat fragmentation. Contrary to expectations this species was found only in small isolated forest fragments and not in the control. Survival probability was very high in the only isolated fragment, where estimation was possible. Because it was captured only in isolated fragments *E. parvus* did not provide sufficient data for comparison and was therefore excluded from the further analysis of morphological traits.

The species of intermediate habitat specialisation, *E. guentheri*, showed consistently higher capture rates, higher population estimates, and significantly higher survival probability in forest fragments compared to the control. Abundance and population size estimates were highest in isolated forest fragments. In fact, populations in isolated forest fragments were largest and presented a high individual survival rate. Morphological shifts of *E. guentheri* did not show such coherent patterns. Body length, leg length, and body mass did not differ among study sites. Nevertheless, analysis revealed significant differences in body condition among the sites, which could mainly be accounted for by differences within the fragmented landscape.

The matrix-tolerant generalist, *Chaunus ornatus*, showed inconsistent life history trait patterns in response to habitat fragmentation. Although capture rates of this species were relatively low on all study sites, an increased abundance was found in isolated forest fragments. Survival estimates were affected by low capture and recapture rates that could not provide a reliable estimate for the connected fragment. Nevertheless, high survival probability was found in the control as well as in one isolated fragment, whereas the other isolated fragment showed a much lower estimate. Morphological shifts of *C. ornatus* did partly conform to the hypothesised shifts and showed changes in snout-vent-length, leg length, and body mass towards smaller values in isolated fragments with the greatest changes in one isolated fragment. Such patterns were not observed for body condition.

5.3 Implications for the conservation of leaf-litter amphibians

With regard to ecological theory specialist species are generally assumed to be most affected by habitat loss and fragmentation because they are most sensitive to changes in habitat quality following fragmentation (SAUNDERS et al. 1991; HENLE et al. 2004a). The results of the presented study suggest that the population dynamics of specialist leaf-litter amphibians are not invariably affected by these habitat quality changes. The changes in morphological shifts unexpectedly imply that habitat generalists may be more affected in their individual traits by changes to their environment than habitat specialists (Chapter 4), because highly specialised species with a corresponding matrix aversion disappear from inferior habitat (i.e. matrix) whereas habitat generalists, on the other hand, would sometimes even reproduce in it. This was also the case in the study area. Changes in the larval habitat quality most likely lead to the observed changes. The results of Chapter 4 corroborate the findings of NECKEL-OLIVEIRA and GASCON (2006) in the Amazon and therefore suggest the high importance of the quality of breeding habitats.

Life history traits of the two species with high matrix aversion (*E. guentheri* and *E. parvus*) suggest that large populations and high survival rates of specialist amphibian species do not necessarily depend on habitat size or isolation. Comparable studies on the dynamics of populations in fragmented landscapes are scarce. Nevertheless, a high population size and high individual survival rates are important indicators for the persistence of populations and indicate that small forest fragments can host stable populations of even specialist species. Studies on community composition corroborate these findings and highlight the value of fragmented landscapes for species diversity. In the same study area

DIXO (2005) found most species regardless of specialisation in both, forest fragments and unfragmented forest habitats. Other studies confirm that the species-area relation from the theory of island biogeography is not always relevant for the conservation of amphibian communities (ZIMMERMAN and BIERREGAARD 1986) and depending on habitat quality, small patches can be of high importance in maintaining local amphibian diversity (SEMLITSCH and BODIE 1998).

Habitat connectivity is an important factor for the maintenance of metapopulations (OVASKAINEN and HANSKI 2004). Isolation effects usually have a greater influence on specialist compared to generalist species because the matrix acts as a stronger barrier for the former rather than the latter (HANSKI 1991; FAHRIG and MERRIAM 1994; GASCON et al. 1999). However, the study on population dynamics did not reveal a coherent pattern in the response to habitat isolation. The inconsistent morphological shifts on the other hand, could partly be a result of genetic drift. Nevertheless, for sound conclusions regarding isolation effects detailed studies on genetic characteristics would be required.

Small habitat patches have been suggested as being important for the maintenance of amphibian species diversity (ZIMMERMAN and BIERREGAARD 1986; SEMLITSCH and BODIE 1998; PINEDA and HALFFTER 2004). Corresponding results have been found for bird species of the Mata Atlântica, which showed that a high habitat specialisation is not necessarily a good indicator of fragmentation sensitivity (DOS ANJOS 2006). Furthermore, studies on small mammals of the Mata Atlântica revealed the high importance of both forest fragments and continuous forest for species diversity (PARDINI 2004; PARDINI et al. 2005). Knowledge of individual traits and dynamics of populations directly affected by fragmentation however was scarce. The results show that in addition to contributing to species diversity, small patches can host large populations of leaf-litter amphibians with high survival rates, even if species are specialised. Although the presented study has to be interpreted as a case study and replicates are required for generalisation, it suggests that small habitat patches can play an important role for the regional persistence of those species in particular with limited mobility and limited spatial requirements. Such results have been found for other vertebrate and invertebrate groups before (OGLE 1987;

TSCHARNTKE et al. 2002; GUTIERREZ 2005; DOS ANJOS 2006). Nevertheless, community studies on amphibians and small mammals highlighted the importance of habitat quality for the maintenance of species richness (GARDNER et al. 2007; UMETSU and PARDINI 2007). As the results of the morphological parameter analysis and other studies suggest (NECKEL-OLIVEIRA and GASCON 2006), the availability and quality of breeding habitat is of high importance, even for generalist species. This suggests that habitat quality and not only patch size can therefore considerably improve local conservation plans. Recommendations usually made for conservation should be complemented with strategies targeting leaf-litter amphibians and other species with limited mobility. Although large tracts of continuous forest are of overriding importance for conservation, small habitat patches can play an important role for the conservation of amphibian species.

6 Summary

6.1 *Background and approach*

Habitat destruction, fragmentation, and the isolation of habitat remnants are among the most important reasons for the global loss of biodiversity (HENLE and STREIT 1990; SARRE et al. 1996; PIMM and RAVEN 2000; SALA et al. 2000; YOUNG et al. 2001; VALLAN 2002; ETEROVICK et al. 2005). Fragmentation of landscapes causes vast environmental changes and leads to biogeographical shifts (SAUNDERS et al. 1991). Although tropical forests are partly still huge in extent, they are highly affected by habitat destruction and fragmentation (PIMM and RAVEN 2000; ACHARD et al. 2002; BAWA et al. 2004). The Brazilian Atlantic Forest or Mata Atlântica is an outstanding example because it is extremely fragmented. Huge destructions reduced the original distribution area of 1.1 million km^2 to less than 8% (MORELLATO and HADDAD 2000; SOS MATA ATLÂNTICA and INPE 2002).

Habitat fragmentation generally modifies the spatial configuration of landscapes. Fragmentation mainly causes the increase in the number of habitat remnants, the decrease of remnant size, and the increase of remnant habitat isolation (FAHRIG 2003). Habitat loss, in most cases an inextricably occurring process additionally decreases the area of the original habitat (FAHRIG 2003). Fragmented landscapes therefore consist of remnants of natural vegetation surrounded by a modified, usually agricultural used matrix (SAUNDERS et al. 1991; FAHRIG 2003). As described by the theory of biogeography, a decrease of habitat size leads in turn to a decrease of the number of species hosted by that habitat (MAC ARTHUR and WILSON 1967). Studies on invertebrate species with limited mobility however showed that the species-area relationship of the equilibrium theory of the theory of biogeography is not always relevant (OGLE 1987; TSCHARNTKE et al. 2002). Similar results found for amphibian communities lead to the conclusion that depending on habitat quality such findings may be valid for other species with limited mobility, too (ZIMMERMAN and BIERREGAARD 1986; SEMLITSCH and BODIE 1998; DIXO 2005). Nevertheless, habitat fragmentation and destruction lead to changes of abiotic characteristics of habitat remnants: in particular, changes in fluxes of radiation, water, and wind (SAUNDERS et al. 1991; LAURANCE 2000). As a consequence of changes in spatial and microclimatic characteristics, the species community in fragmented landscapes also changes. Therefore destruction and fragmentation of habitats result in principle in the loss of biodiversity. Although the diversity of habitats and species often increases locally, an impoverishment of the autochthonous species community can be observed on regional scale (FAHRIG 2003; DIDHAM et al. 2007). In particular in regions with high endemism rates like the Mata Atlântica such species loss following habitat fragmentation and destruction result in according consequences for biodiversity on global scale (MYERS et al. 2000).

Whether species respond to changes to their habitat and to which intensity does not only depend on the extent of such changes, but is also determined by the degree of specialisation of concerned species (WITH and CRIST 1995; DIAZ et al. 1999; HENLE et al. 2004a). Extensive studies on species communities of different species groups in fragmented forests shows that among other factors a high habitat specialisation leads to disappearance of species in fragmented landscapes (BIERREGAARD and STOUFFER 1997; DIDHAM 1997; GASCON et al. 1999; DEBINSKI and HOLT 2000; EWERS and DIDHAM 2006).

Knowledge on processes at population level of species remaining in fragmented landscapes is scarce. It has to be assumed that changes of biotic and abiotic factors following habitat fragmentation do not only lead to the disappearance of species at an individual threshold, but also affect population dynamics and other individual parameters before reaching that threshold (HOKIT and BRANCH 2003). In particular factors like increase of competition within fragments by invading species, a decrease of habitat quality by changes of abiotic parameters, or isolation of populations likely result in a decrease of survival probability of autochthonous populations and different selective pressures on morphological characteristics of concerned populations (STEWART 1995; WHITLOCK 2004; EWERS and DIDHAM 2006; HALVERSON et al. 2006). Therefore individual survival probability, size and fluctuation of populations and changes of morphological characteristics in fragmented landscapes are important indicators for the extinction proneness and fragmentation sensitivity of species.

To address the question of the response of amphibian populations on habitat fragmentation and isolation, the presented case study compares individual life-history traits of populations of leaf-litter frog species with different degrees of habitat specialisation in fragmented and unfragmented habitats. The study compares main parameters of population dynamics and morphology of populations of autochthonous amphibian species within fragments with different degree of isolation and populations within an unfragmented habitat. Based on the assumption that the degree of habitat specialisation mainly determines the species sensitivity to habitat changes, a comparison of generalist with specialist species is used. Differences in the habitat specialisation are therefore expected to be reflected in population dynamics and morphological parameters of populations. Fragmentation effects are generally assumed as negative and to be stronger for forest-dwelling species compared to species which also occur in the modified surrounding matrix.

6.2 Life history traits of three leaf-litter frogs in Neotropical forest patches

In Chapter 3 populations of three leaf-litter frog species with different degree of habitat specialisation are studied: *Eleutherodactylus parvus* as forest specialist species, *E. guentheri* as forest specialist species with edge tolerance, and *Chaunus ornatus* as generalist species. The focus of the chapter is to test the hypothesis that habitat fragmentation generally causes a negative response of populations but mostly affects population sizes and survival probabilities of species with highest habitat specialisation. A negative influence of habitat isolation is hypothesised only for the forest-dwelling species *E. parvus* and *E. guentheri*. In a capture-mark-recapture study populations of two isolated and one connected fragment are compared with populations in a study plot in an unfragmented forest area. Abundance, population size estimates, and individual survival rates are tested for differences.

According to the hypothesis, strongest response on habitat fragmentation and isolation is observed for the most specialised species *E. parvus*. The response itself however stands in contrast to the expectations. *E. parvus*, the most specialised forest-dwelling species, was found only in isolated forest fragments but not at the other study sites. The survival probability was very high ("Dito" $\phi > 97\%$) in the only isolated fragment were a calculation was possible. *E. guentheri*, the specialist species with edge tolerance, was captured at all study sites, but shows highest abundance and highest population and survival estimates in the fragmented landscape. In contrast to the expectations capture rates of the generalist species, *C. ornatus* are in general very low. Highest abundances are found for this species in the fragmented landscape. Survival probability estimation for *C. ornatus* was limited due to partly poor recapture rates, therefore results of the survival probability estimation show an inconsistence with high estimates in the unfragmented control and one isolated fragment and a low estimate for the other isolated fragment.

The results imply that populations of specialist species in particular, are in contrast to the hypothesis not negatively affected by habitat fragmentation and isolation or even benefit from these processes. Therefore the change of microclimates seems not to have the assumed high influence on population size and mortality within populations of the studied species. Possible explanations of the partly positive response can be diverse. Most likely reasons are an increase of resource availability and a decrease of predation risk following fragmentation. An increase in the abundance of generalist invertebrates, a potentially important food resource for the studied species (DIDHAM 1997; DIDHAM et al. 1998; WHITFIELD and DONNELLY 2006), and a decrease or disappearance of competing species with higher fragmentation sensitivity than the studied species may have led to higher resource availability. The disappearance of species with higher fragmentation sensitivity than the studied species further may have led to the disappearance of predator species, which in turn could have affected positively the survival probability of remaining species (TERBORGH 1974; HENLE et al. 2004a). On the other hand, the high population size is a very likely explanation for the missing response of specialist species populations on habitat isolation. Large populations are in particular mainly insensitive to inbreeding and the inbreeding linked decrease of individual survival (MADSEN et al. 2000; HALVERSON et al. 2006).

6.3 Morphological shifts in populations of generalist and specialist amphibians in response to the fragmented landscape of the Mata Atlântica of São Paulo

Chapter 4 focuses on morphological shifts among populations of two leaf-litter frog species in the fragmented and unfragmented habitats described in Chapter 3. Selected species for the comparison are *E. guentheri* as forest specialist and *C. ornatus* as generalist species. The main task is to test whether the specialist species underlies due to narrow habitat requirements higher selective pressure in the fragmented landscape than the habitat generalist. Accordingly, greater differences in morphological characteristics as snout-vent length, tibia length, body mass, and body condition are expected for populations of the specialist than the generalist. Shifts of morphological characteristics are generally assumed as negative in the fragmented landscape.

Results show the hypothesised shifts only for the generalist *C. ornatus*. Snout-vent length, tibia length, and body mass showed significant differences among the study sites with significant lower values in one isolated fragment compared to the unfragmented control and the same tendency in the other isolated fragment compared to the control. In body condition index no significant difference among study sites can be observed. *E. guentheri*, the specialist species, on the other hand, shows significant differences among sites only for the body condition index. Significant differences between individual sites were not found however. Nevertheless, the multivariate analysis of body condition index and tibia length revealed that these differences could mainly be accounted for by differences within the fragmented landscape.

Differences between the studied species can only partly be interpreted by species specialisation and are further likely a result of specific differences in reproductive modes of the studied species. The results found for the generalist species confirm results of morphological differences of generalist species in fragmented and otherwise disturbed habitats compared with unfragmented primary forest habitats in the Amazon (NECKEL-OLIVEIRA and GASCON 2006). Most likely reason for smaller individuals with less body mass and shorter legs in the fragmented landscape is the extreme change of the quality of the breeding habitat. In the study area this can be mainly found in the matrix for the pond breeding species *C. ornatus*. Changed abiotic parameters, changes in larval competition, and higher predation risk in the breeding habitat are known to influence the morphology of juveniles and in the following of adult individuals (SMITH 1987; SEMLITSCH et al. 1988; BEACHY 1995; STÅHLBERG et al. 2001). Genetic drift is likely not a reason for the observed shifts (DIXO 2005). *E. guentheri* is in contrast to *C. ornatus* a direct developing species, which does not need ponds for reproduction. Because this species does not have to leave the forest habitat for reproduction it is likely much less affected by breeding habitat quality changes. Although differences in habitat quality between the study sites can not be excluded, such changes are likely only partly a reason for the observed slight morphological shifts. On the other hand, the missing strong response can be an indicator for an unexpected robustness of this species against fragmentation effects. Detailed genetic studies are required to clearify whether genetic drift or other population genetic characteristics influenced the observed results.

6.4 Implications for the conservation of amphibians in fragmented landscapes of the Mata Atlântica: A synthesis

Chapter 5 summarises the results of the population dynamic and the morphological studies and focuses on the interpretation of these results for the conservation of amphibians in fragmented forests of the Mata Atlântica.

The observed findings of the population dynamics show that small and isolated forest fragments can host large populations with high individual survival probability even of high specialised forest-dwelling leaf-litter frog species. Results found for invertebrate species with limited mobility therefore seem to be transferable to amphibian species with limited mobility in tropical forest fragments and are reflected at population level (Chapter 3). Beside species composition of amphibians (ZIMMERMAN and BIERREGAARD 1986) also individual population parameter of amphibian species with limited mobility seem to be mainly unaffected by habitat size. Although it is usually assumed that habitat fragmentation deteriorates habitat quality in particular for specialist species (SAUNDERS et al. 1991; FAHRIG 2003; HENLE et al. 2004a), the morphological shifts imply that specialist amphibian species can also be mainly unaffected by these changes (Chapter 4). The observed morphological shifts of the generalist species, *C. ornatus*, are probably an indicator for the importance of breeding habitat quality, in particular for migrating species (Chapter 4). Other studies on morphological shifts (NECKEL-OLIVEIRA and GASCON 2006) and species communities of amphibians and small mammals confirm these findings (GARDNER et al. 2007; UMETSU and PARDINI 2007).

Beside habitat size, detailed data on habitat quality should be considered in local conservation plans and conservation networks to improve the situation of amphibian populations within these networks. Although large tracts of continuous forest and large conservation areas are of overriding importance for the maintenance of large species communities, the presented results show in context with community studies that small forest patches can play an important role for the conservation of leaf-litter amphibians.

7 Zusammenfassung

7.1 *Hintergrund und Ansatz*

Zu den wichtigsten Ursachen des globalen Biodiversitätsverlustes gehören die Zerstörung und Fragmentierung von Habitaten und die Isolation verbliebener Habitatreste (HENLE and STREIT 1990; SARRE et al. 1996; PIMM and RAVEN 2000; SALA et al. 2000; YOUNG et al. 2001; VALLAN 2002; ETEROVICK et al. 2005). Die Fragmentierung einer Landschaft bewirkt starke Veränderungen der Umwelt und zieht biogeografische Verschiebungen nach sich (SAUNDERS et al. 1991). Gebiete der Erde, die besonders von Habitatzerstörung und -fragmentierung betroffen sind, sind die zum Teil noch immer großflächigen Wälder tropischer Ökosysteme (PIMM and RAVEN 2000; ACHARD et al. 2002; BAWA et al. 2004). Ein herausragendes Beispiel dafür ist der brasilianische atlantische Regenwald oder Mata Atlântica. Dieses Waldgebiet ist in besonderem Maße durch die Zerstörung und Fragmentierung des ursprünglichen Lebensraumes geprägt (MORELLATO and HADDAD 2000) und ist heute von ehemals ca. 1,1 Mio. km^2 durch Zerstörung und Fragmentierung auf weniger als 8 % geschrumpft (SOS MATA ATLÂNTICA and INPE 2002). Wie in anderen ursprünglich besonders dicht bewachsenen tropischen Regenwäldern (LAURANCE et al. 2002), resultieren die Zerstörung und die damit einhergehende Fragmentierung der Wälder auch in der Mata Atlântica in extremen Kontrasten zwischen ursprünglichem Habitat und veränderter Umgebung (Matrix).

Generell ändert sich durch die Fragmentierung eines Habitats die räumliche Konfiguration einer Landschaft. Dabei bewirkt der Prozess der Fragmentierung im Wesentlichen einen Anstieg der Anzahl von Resthabitaten, die Verringerung der Größe der Resthabitate und eine verstärkte Isolation dieser Reste (FAHRIG 2003). Habitatzerstörung, ein nahezu immer gleichzeitig auftretender Prozess, bewirkt zusätzlich die Verringerung der Gesamtgröße des ursprünglichen Habitats (FAHRIG 2003). Eine fragmentierte Landschaft besteht infolgedessen aus Überresten natürlicher Vegetation, die von einer veränderten, häufig landwirtschaftlich genutzten Matrix umgeben sind

(SAUNDERS et al. 1991; FAHRIG 2003). Wie bereits in der Theorie der Biogeografie beschrieben, verringert sich mit der Arealgröße eines Habitats auch die Anzahl der darin befindlichen Arten (MAC ARTHUR and WILSON 1967). Allerdings zeigten Ergebnisse von Untersuchungen an wenig mobilen wirbellosen Arten, dass der auf die Gleichgewichtshypothese der Theorie der Biogeografie zurückgehende Zusammenhang von Artenanzahl und Arealgröße nicht immer gültig ist (OGLE 1987; TSCHARNTKE et al. 2002). Untersuchungen an Amphibien lassen den Schluss zu, dass diese Erkenntnisse abhängig von der Habitatqualität auch für wenig mobile Wirbeltiere gültig sind (ZIMMERMAN and BIERREGAARD 1986; SEMLITSCH and BODIE 1998; DIXO 2005). Neben der Verringerung der Fläche des ursprünglichen Habitats bewirken Habitatfragmentierung und -zerstörung aber auch Veränderungen in abiotischen Eigenschaften, insbesondere der Energie- und Wasserbilanz und vorherrschender Windverhältnisse (SAUNDERS et al. 1991; LAURANCE 2000). Als Konsequenz der Veränderungen räumlicher und mikroklimatischer Parameter vollziehen sich Änderungen der Artengemeinschaft in einer fragmentierten Landschaft. Prinzipiell resultiert die Fragmentierung und Zerstörung von Habitaten damit im Verlust von Biodiversität. Zwar kann zunächst häufig ein lokaler Anstieg in der Vielfalt von Habitaten und Arten beobachtet werden, auf regionaler und überregionaler Ebene aber führen diese Prozesse zu einer Verarmung der autochthonen Artengemeinschaft (FAHRIG 2003; DIDHAM et al. 2007). Insbesondere in Schwerpunkten der globalen Artenvielfalt, die wie die Mata Atlântica extrem hohe Endemiegrade aufweisen, hat der aus der Zerstörung und Fragmentierung resultierende Artverlust entsprechende Konsequenzen für die Biodiversität auf globaler Skala (MYERS et al. 2000).

Ob und in welcher Intensität autochthone Arten auf Veränderungen ihres Habitates reagieren, hängt nicht nur von der Intensität der Habitatveränderungen an sich ab, sondern wird auch in besonderem Maße durch den Grad der Spezialisierung der betroffenen Arten determiniert (WITH and CRIST 1995; DIAZ et al. 1999; HENLE et al. 2004a). Umfangreiche Untersuchungen an Artengemeinschaften verschiedener Tiergruppen in fragmentierten Waldgebieten zeigten, dass neben anderen Faktoren insbesondere eine ausgeprägte Habitatspezialisierung von Arten zu deren Verschwinden in fragmentierten Landschaften führt (BIERREGAARD and STOUFFER 1997; DIDHAM 1997; GASCON et al. 1999; DEBINSKI and HOLT 2000; EWERS and DIDHAM 2006).

Wenig bis gar nichts ist bisher allerdings bekannt über die Prozesse, die sich innerhalb von Populationen von in fragmentierten Landschaften verbliebenen Arten abspielen. Es muss angenommen werden, dass die durch Fragmentierung verursachten Änderungen biotischer und abiotischer Faktoren im Ökosystem nicht nur ab einem bestimmten Schwellenwert zum Verschwinden einer Art führen und so Auswirkungen auf die Artengemeinschaft haben, sondern schon vor erreichen dieses Schwellenwertes auch die Dynamik und andere Faktoren lokaler Populationen beeinflussen (HOKIT and BRANCH 2003). Insbesondere Faktoren wie verstärkte Konkurrenz innerhalb der Fragmente durch einwandernde Offenlandarten, die Verschlechterung der lokalen Habitatqualität durch Änderungen abiotischer Parameter oder die Isolation von Populationen, führen wahrscheinlich zu einer Verminderung der Überlebenswahrscheinlichkeit autochthoner Populationen in Habitatfragmenten und zu unterschiedlichem selektiven Druck auf morphologische Merkmale betroffener Populationen (STEWART 1995; WHITLOCK 2004; EWERS and DIDHAM 2006; HALVERSON et al. 2006). Individuelle Überlebenswahrscheinlichkeit, Größe und Fluktuation von Populationen aber auch Veränderungen morphologischer Charakteristika in fragmentierten Habitaten sind demnach wichtige Anhaltspunkte, die Rückschlüsse auf das Extinktionsrisiko und die Sensibilität einer Art gegenüber Habitatfragmentierung zulassen.

Um die Frage der Reaktion von Amphibienarten auf Habitatfragmentierung und –isolation auf Populationsebene zu untersuchen, stellt die vorliegende Fallstudie individuelle Merkmale von Populationen unterschiedlich spezialisierter bodenlebender Amphibienarten in fragmentierten und unfragmentierten Habitaten gegenüber. Sie vergleicht die Hauptparameter der Populationsdynamik und morphologische Merkmale von Populationen autochthoner Amphibienarten unterschiedlicher Habitatspezialisierung und stellt dabei diese Parameter von Populationen in Fragmenten unterschiedlichen Isolationsgrades denen eines unfragmentierten Gebietes gegenüber. Der dieser Arbeit zugrunde liegende Vergleich von Generalisten- und Spezialistenarten in einer fragmentierten Landschaft basiert auf der zentralen Annahme, dass der Grad der Habitatspezialisierung die Sensibilität einer Art gegenüber Habitatveränderungen determiniert. Die Unterschiede in Habitatpräferenzen werden demnach auch in den Veränderungen populationsdynamischer und morphologischer Parameter von Populationen von Arten unterschiedlicher Habitatspezialisierung erwartet. Dabei werden die angenommenen negativen Effekte der Habitatfragmentierung bei strikten Waldarten tendenziell stärker ausgeprägt erwartet als bei Arten, die auch in der veränderten Matrix anzutreffen sind.

7.2 Populationsökologische Parameter von drei bodenlebenden Froscharten in neotropischen Waldfragmenten

Im Kapitel 3 werden Populationen von drei bodenlebende Amphibienarten unterschiedlicher Habitatspezialisierung untersucht: *Eleutherodactylus parvus* als Waldspezialist, *E. guentheri* als Waldspezialist mit Toleranz gegenüber Waldrändern und *Chaunus ornatus* als Generalist. Im Fokus des Kapitels stand der Test der Hypothese, dass Habitatfragmentierung sich zwar prinzipiell negativ auf alle drei Arten auswirkt, allerdings in verstärktem Maße Populationsgrößen und Überlebensraten von Arten mit höherer Habitatspezialisierung negativ beeinflusst. Ein negativer Einfluss von Isolationseffekten wurde nur für die Habitatspezialisten *E. parvus* und *E. guentheri* erwartet. In einer Fang-Wiederfang-Studie wurden zu diesem Zweck die Populationen in zwei isolierten Fragmenten, einem Fragment mit Korridorverbindung zu einem größeren Waldgebiet und einem Untersuchungsplot in einem unfragmentierten Waldgebiet auf Unterschiede in Abundanz, Populationsgröße und Überlebenswahrscheinlichkeit untersucht.

Die Ergebnisse zeigten gemäß der These die stärkste Reaktion auf Habitatfragmentierung und –isolation der am stärksten spezialisierten Art *E. parvus*. Die Art der Reaktion aller untersuchten Amphibienarten stand jedoch im Gegensatz zur Hypothese. Der strikte Waldspezialist *E. parvus* wurde ausschließlich in den isolierten Fragmenten, nicht aber in den anderen Untersuchungsgebieten nachgewiesen und wies in dem einzigen isolierten Fragment, für das eine Kalkulation möglich war eine hohe individuelle Überlebensrate innerhalb der Population (Dito ϕ>97%) auf. Der Waldspezialist mit Randtoleranz *E. guentheri* konnte in allen Untersuchungsplots nachgewiesen werden, wies aber im Vergleich zur unfragmentierten Kontrolle die höchste Abundanz, die größte Populationsgröße und eine signifikant höhere individuelle Überlebenswahrscheinlichkeit in der fragmentierten Landschaft auf. Fangraten der Generalistenart *C. ornatus* waren entgegen der ursprünglichen Erwartung generell niedrig. Analog zu *E. guentheri* wurden höchste Abundanzen in isolierten Fragmenten gemessen. Aufgrund geringer Wiederfänge war eine Schätzung der individuellen Überlebensrate innerhalb der Populationen der Generalistenart nur bedingt möglich. Entsprechend zeigten die Ergebnisse ein unklares Bild mit hohen Überlebensraten im Kontrollgebiet und in einem isolierten Fragment und niedriger Rate in dem verbliebenen isolierten Fragment.

Die gefundenen Ergebnisse implizieren, dass insbesondere die Populationen der untersuchten Spezialistenarten von der Fragmentierung ihres Habitates entgegen der Hypothese nicht negativ beeinflusst wurden, sondern sogar profitiert haben. Die Änderung der Mikroklimate scheint demnach nicht den vermuteten starken Effekt auf die Populationsgröße und Mortalität der Populationen der untersuchten Arten zu haben. Die möglichen Gründe für diese teilweise positive Reaktion der Populationen auf die Fragmentierung und Verinselung von Habitaten können vielfältig sein. Als wahrscheinlichste Erklärung für erhöhte Abundanz, größere Populationen und geringere Mortalitätsraten in Habitatfragmenten kommen eine Erhöhung der Ressourcenverfügbarkeit und eine Verringerung des Prädationsrisikos in Frage. Eine der Fragmentierung folgende Zunahme in der Abundanz von wirbellosen Generalistenarten, eine potentielle Nahrungsquelle für die untersuchten Arten (DIDHAM 1997; DIDHAM et al. 1998; WHITFIELD and DONNELLY 2006), und der Rückgang oder das Aussterben von fragmentierungssensibleren Arten in den Fragmenten, mit ähnlicher trophischer Nische wie die untersuchten Arten, könnten zu einer erhöhten Ressourcenverfügbarkeit geführt haben. Dieser Verlust von fragmentierungssensibleren Arten in den Fragmenten kann darüber hinaus zu einem Verlust von Prädatorarten geführt haben, welcher wiederum die Überlebenschancen der verbliebenen Arten begünstigt haben könnte und zu den beobachteten Populationsgrößen geführt hat (TERBORGH 1974; HENLE et al. 2004a). Die Größe der Populationen wiederum führt sehr wahrscheinlich zur fehlenden Reaktion der Waldspezialisten auf die Verinselung der Habitate. Insbesondere große Populationen sind auch bei bestehender Isolation gegenüber Inzuchtdepression und der damit verbundenen Verringerung der Überlebensrate eher unempfindlich (MADSEN et al. 2000; HALVERSON et al. 2006).

7.3 Morphologische Unterschiede von Spezialisten- und Generalistenpopulationen in der fragmentierten Landschaft von São Paulo

Das Kapitel 4 befasst sich mit morphologischen Unterschieden zwischen Populationen zweier bodenlebender Amphibienarten in fragmentierten und unfragmentierten Habitaten. Als Arten für den Vergleich wurden Populationen von *E. guentheri* als Waldspezialist und *C. ornatus* als Generalist in den in Kapitel 3 beschriebenen Untersuchungsgebieten ausgewählt. Durch den Vergleich von Kopf-Rumpf-Längen, Körpermasse, Tibialängen und der Kondition wurde die Hypothese getestet, dass die Spezialistenart aufgrund stärkerer Bindung an spezielle Habitatqualitätsparameter stärkerem selektiven Druck in fragmentierten Habitaten unterliegt als die Generalistenart. Entsprechend größere morphologische Unterschiede zwischen Populationen in unfragmentierten und fragmentierten bzw. isolierten Habitaten wurden für die Spezialistenart postuliert. Änderungen der Parameter wurden generell in negativer Tendenz in der fragmentierten Landschaft erwartet.

Die Ergebnisse zeigten die erwartete Veränderung der morphologischen Parameter lediglich für die Generalistenart *C. ornatus*. Kopf-Rumpf-Länge, Tibialänge und Körpermasse zeigten signifikante Unterschiede zwischen den Untersuchungsgebieten mit signifikant niedrigeren Werten in einem isolierten Fragment im Vergleich zum Kontrollgebiet und ähnlicher Tendenz in dem anderen isolierten Fragment. Der Konditionsindex zeigte keine signifikante Änderung. Die Spezialistenart *E. guentheri* zeigte hingegen signifikante Unterschiede zwischen den Untersuchungsgebieten ausschließlich für den Konditionsindex. Auch wenn die einzelnen Untersuchungsgebiete keine signifikanten Unterschiede zeigten, verdeutlichte die multivariate Analyse von Konditionsindex und Tibialänge, dass dieses Ergebnis auf Unterschiede zwischen den Fragmenten und nicht zwischen Fragmenten und Kontrollgebiet zurückzuführen ist.

Die Unterschiede zwischen den untersuchten Arten sind nur teilweise durch die Spezialisierung zu erklären und gehen vermutlich auch auf Unterschiede in der Fortpflanzungsstrategie der untersuchten Arten zurück. Die Ergebnisse der Generalistenart bestätigen Ergebnisse morphologischer Unterschiede von Generalistenpopulationen in fragmentierten und anderweitig gestörten Habitaten im Vergleich zu unfragmentierten

Primärwaldhabitaten aus Amazonien (NECKEL-OLIVEIRA and GASCON 2006). Hauptgrund für kleinere Tiere mit geringerer Körpermasse und kürzeren Extremitäten in fragmentierten Habitaten ist wahrscheinlich die starke Änderung der Habitatqualität im Laichhabitat für die in Tümpel ablaichende Art *C. ornatus*. Diese Tümpel befanden sich in den Untersuchungsgebieten in der umgebenden Matrix. Veränderte abiotische Parameter, Änderungen in der Larvalkonkurrenz und im Prädationsrisiko im Laichhabitat können den Entwicklungszyklus von Jungtieren und morphologische Parameter von Jungtieren wie adulten Individuen beeinflussen (SMITH 1987; SEMLITSCH et al. 1988; BEACHY 1995; STÅHLBERG et al. 2001). Genetische Drift kann für die Generalistenart ausgeschlossen werden (DIXO 2005). Die Spezialistenart *E. guentheri* ist im Gegensatz zur Generalistenart ein Direktentwickler, der zur Reproduktion das Habitat Wald nicht verlässt. Änderungen in der Qualität des Reproduktionshabitats sind für die gefundenen marginalen Unterschiede der untersuchten Populationen deshalb vermutlich nur teilweise verantwortlich. Habitatqualitätsunterschiede zwischen den einzelnen Untersuchungsgebieten sind jedoch nicht auszuschließen. Die weitgehend fehlende Reaktion dieser Art lässt auf eine unerwartete ausgeprägte Robustheit gegenüber Fragmentierungseffekten schließen. Inwieweit genetische Drift und andere populationsgenetische Parameter die gefundenen Ergebnisse beeinflussen, muss in detaillierten genetischen Untersuchungen geklärt werden.

7.4 Implikationen für den Amphibienschutz in fragmentierten Landschaften der Mata Atlântica: Eine Synthese

Kapitel 5 vereint die Ergebnisse der populationsdynamischen und morphologischen Untersuchungen und legt das Hauptaugenmerk auf die Interpretation dieser Ergebnisse vor dem Hintergrund des Schutzes von Amphibien in fragmentierten Wäldern der Mata Atlântica.

Die beobachteten Ergebnisse der Populationsdynamik zeigen, dass kleine und isolierte Waldfragmente große Populationen mit hohen individuellen Überlebensraten auch von stark auf das Habitat Wald spezialisierten bodenlebenden Amphibienarten beherbergen können. Ergebnisse, die für wenig mobile Invertebraten gefunden wurden, scheinen demnach auch auf wenig mobile Amphibien in tropischen Waldfragmenten übertragbar zu sein und spiegeln sich entsprechend auf Populationsebene wider (Kapitel 3). Neben der Zusammensetzung der Artgemeinschaft von Amphibien (ZIMMERMAN and BIERREGAARD 1986) scheinen also auch individuelle Parameter der Populationen wenig mobiler Amphibienarten weitgehend unbeeinflusst von der Größe des Habitates. Entgegen der häufigen Annahme, dass Habitatfragmentierung zu einer starken Veränderung der Habitatqualität insbesondere für Spezialistenarten führt (SAUNDERS et al. 1991; FAHRIG 2003; HENLE et al. 2004a), zeigen die morphologischen Untersuchungen, dass spezialisierte Amphibien auch weitgehend unbeeinflusst von diesen Änderungen bleiben können (Kapitel 4). Die morphologischen Unterschiede der Generalistenart *C. ornatus* sind allerdings ein Indikator dafür, dass die Qualität insbesondere des Reproduktionshabitates einen Einfluss auf die Populationen von migrierenden Amphibienarten haben kann (Kapitel 4). Andere morphologische Untersuchungen an Amphibien (NECKEL-OLIVEIRA and GASCON 2006) und Untersuchungen zur Artgemeinschaft von Amphibien- und Kleinsäugerarten bestätigen die Wichtigkeit der Habitatqualität (GARDNER et al. 2007; UMETSU and PARDINI 2007).

In lokalen Schutzgebietsplanungen und Schutzgebietsnetzwerken sollte nicht nur ausschließlich die Arealgröße, sondern auch eine detaillierte Betrachtung der Habitatqualität berücksichtigt werden um die Situation von Amphibienpopulationen innerhalb dieser Netzwerke zu verbessern. Obwohl große zusammenhängende Schutzgebiete von überragender Bedeutung für den Schutz bedrohter Ökosysteme sind, zeigen die vorgestellten Ergebnisse im Kontext mit Untersuchungen zur Artgemeinschaft, dass kleine Waldgebiete eine wichtige Rolle für den Schutz von Amphibien spielen können.

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Appendix I

Capture data and measurements

Site	Date	Code	Cap point	Species	Age	Sex	Recap	SVL	TL	Mass
MorroC	13.11.2003	MC13	A6	E. guentheri	ad	m	no	19,9	13,8	0,8
MorroC	13.11.2003	MC1	B2	E. guentheri	ad	m	yes			
MorroC	13.11.2003	MC3		E. guentheri	ad	m	yes			
MorroC	17.11.2003	MC5	A1	E. guentheri	ad	m	yes			
MorroC	17.11.2003	MC3		E. guentheri	ad	m	yes			
MorroC	17.11.2003	MC10	A7/8	E. guentheri	ad	m	yes			
Carmo	12.01.2004	CM1	A7/8	E. guentheri	ad		no	20,2	14,4	0,7
Carmo	12.01.2004	CM2	A7/8	E. guentheri	ad		no	18,3	13,0	0,4
Carmo	12.01.2004	CM3	A3/4	E. guentheri	ad		no	20,7	14,5	0,7
Carmo	12.01.2004	CM4	B7	E. guentheri	ad		no	19,7	13,9	0,6
Carmo	12.01.2004	CM7	C4	E. guentheri	ad		no	20,3	16,3	0,8
Carmo	12.01.2004	CM10	B8	E. guentheri	ad		no	21,4	15,0	0,8
Carmo	13.01.2004	CM11	B4/5	E. guentheri	ad	m	no	20,3	14,3	0,7
Carmo	13.01.2004	CM12	B7	E. guentheri	ad	m?	no	20,2	13,9	0,7
Carmo	13.01.2004	CM14	C10	E. guentheri	ad		no	19,4	14,4	0,7
Carmo	13.01.2004	CM15	A6	E. guentheri	ad	m	no	19,6	14,4	0,6
Carmo	13.01.2004	CM16	C8	E. guentheri	ad		no	21,3	15,0	0,8
Carmo	13.01.2004	CM17	C8	E. guentheri	ad		no	25,1	17,0	1,1
Carmo	13.01.2004	CM18	B4	E. guentheri	ad		no	21,3	14,3	0,8
Carmo	13.01.2004	CM19	C6	E. guentheri	ad		no	17,3	11,9	0,4
Carmo	13.01.2004	CM20	A3	E. guentheri	ad		no	22,7	17,1	1,2
Carmo	08.03.2004		A5	E. guentheri	juv		no	13,2	7,8	<0,1
Carmo	15.01.2004	CM40	A3/4	E. guentheri	ad		no	21,9	15,2	0,9
Carmo	15.01.2004	CM41	A7	E. guentheri	ad	m	no	21,5	14,3	0,9
Carmo	15.01.2004	CM44	B2/3	E. guentheri	ad		no	23,3	15,0	0,9
Carmo	15.01.2004	CM47	B6	E. guentheri	ad		no	22,0	15,8	1,1
Carmo	15.01.2004	CM49	A6	E. guentheri	ad		no	20,0	14,0	0,7
Carmo	15.01.2004	CM50	A9	E. guentheri	ad	m	no	21,6	15,7	0,9
Carmo	15.01.2004	CM52	A7/8	E. guentheri	ad		no	19,8	14,4	0,6
Carmo	15.01.2004	CM53	B11	E. guentheri	ad		no	20,9	14,9	0,7
Carmo	16.01.2004	CM18	B5	E. guentheri	ad		yes			
Carmo	16.01.2004	CM1	A9/10	E. guentheri	ad		yes			
Carmo	16.01.2004	CM55	A9/10	E. guentheri	ad		no	19,9	15,6	0,8
Carmo	16.01.2004	CM56	A9/10	E. guentheri	ad		no	21,6	15,0	0,9
Carmo	16.01.2004	CM12	B7	E. guentheri	ad		yes			
Carmo	16.01.2004	CM57	A9	E. guentheri	ad		no	23,1	14,7	1,0
Carmo	16.01.2004	CM58	A9	E. guentheri	ad		no	22,3	14,6	0,8
Carmo	16.01.2004	CM10	B8	E. guentheri	ad		yes			
Carmo	16.01.2004	CM59	B8	E. guentheri	ad		no	20,3	14,4	0,6
Carmo	16.01.2004	CM62	B8	E. guentheri	ad		no	20,1	15,0	0,7
Carmo	16.01.2004		C6	E. guentheri	juv		no	11,4		<0,1
Carmo	13.01.2004	CM22	C6	E. guentheri	ad	m	no	20,4	14,0	0,7
Carmo	13.01.2004	CM23	C6	E. guentheri	ad	f	no	29,0	21,8	2,9
Carmo	14.01.2004	CM24	A10	E. guentheri	ad	f	no	28,7	19,1	1,5
Carmo	14.01.2004	CM18	B5	E. guentheri	ad	m	yes			
Carmo	14.01.2004	CM31	A1/2	E. guentheri	ad	f	no	27,7	20,5	2,0
Carmo	14.01.2004	CM22	C6	E. guentheri			yes			

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Carmo	14.01.2004	CM32	C1	E. guentheri	ad	f	no	28,7	19,6	1,7
Carmo	14.01.2004	CM16	C8	E. guentheri			yes			
Carmo	15.01.2004	CM38	B7/8	E. guentheri	ad		no	22,1	17,2	1,2
Carmo	15.01.2004	CM39	B7/8	E. guentheri	ad		no	20,2	13,4	0,7
Carmo	09.03.2004		A5	E. guentheri	juv		no	11,4	7,2	<0,1
Carmo	10.03.2004		A6	E. guentheri	juv		no	13,0	8,6	<0,1
Carmo	10.03.2004		B1	E. guentheri	juv		no	14,3	9,0	<0,1
Carmo	10.03.2004	CM81	B1/2	E. guentheri	ad		no	21,9	16,5	0,5
Alcides	21.01.2004	A16	B5	E. guentheri	ad	m	no	23,8	15,6	1,0
Alcides	21.01.2004	A17	B5	E. guentheri	ad		no	21,0	15,3	0,8
Alcides	21.01.2004	A18	B5	E. guentheri	ad		no	22,2	14,3	0,7
Alcides	21.01.2004	A19	A7/8	E. guentheri	ad		no	22,0	13,6	0,9
Alcides	21.01.2004	A21	B6	E. guentheri	ad	f	no	33,0	21,4	3,1
Alcides	21.01.2004	A22	C6	E. guentheri	ad		no	23,0	15,5	1,0
Alcides	21.01.2004	A23	B9	E. guentheri	ad		no	27,2	19,7	1,7
Alcides	21.01.2004	A24	A10/11	E. guentheri	ad	m	no	21,1	15,8	1,0
Alcides	21.01.2004	A25	A10/11	E. guentheri	ad	m	no	20,7	13,9	0,8
Alcides	21.01.2004	A27	C8	E. guentheri	ad		no	22,8	16,1	0,9
Alcides	22.01.2004	A28	B2	E. guentheri	ad		no	20,0	14,0	0,6
Alcides	22.01.2004	A14	C1	E. guentheri	ad	f	yes			
Alcides	22.01.2004		C1	E. guentheri	juv		no	10,8	6,0	<0,1
Alcides	22.01.2004	A27	C8	E. guentheri	ad		yes			
Alcides	22.01.2004	A29	B8	E. guentheri	ad		no	19,8	14,0	0,5
Alcides	23.01.2004	A12	B1/2	E. guentheri	ad		yes			
Carmo	10.03.2004	CM82	B3	E. guentheri	ad		no	22,7	16,5	0,5
Carmo	10.03.2004	CM44	B3/4	E. guentheri	ad		yes			
Carmo	10.03.2004		C8	E. guentheri	ad		no	13,4	8,5	<0,1
Carmo	16.01.2004	CM63	B8/9	E. guentheri	ad		no	19,8	15,2	0,7
Carmo	16.01.2004	CM64	C5	E. guentheri	ad		no	21,7	15,2	0,9
Carmo	16.01.2004	CM65	C5	E. guentheri	ad		no	22,0	14,7	0,9
Carmo	16.01.2004	CM66	A4/5	E. guentheri	ad		no	20,0	14,3	0,7
Carmo	16.01.2004	CM67	A4/5	E. guentheri	ad		no	22,0	14,5	0,7
Carmo	16.01.2004	CM7	C4	E. guentheri	ad		yes			
Carmo	16.01.2004	CM68	C4	E. guentheri	ad		no	25,6	17,3	1,1
Carmo	16.01.2004		B4	E. guentheri	ad		no	18,0	13,6	0,6
Alcides	19.01.2004		B2	E. guentheri	juv		no	7,6	-	<0,1
Alcides	19.01.2004	A2	B3	E. guentheri	ad		no	21,0	13,9	0,7
Alcides	19.01.2004	A3	A4/5	E. guentheri	ad		no	20,8	15,2	0,9
Alcides	19.01.2004	A4	A4	E. guentheri	ad		no	22,6	15,7	0,9
Alcides	19.01.2004	A5	A4	E. guentheri	ad		no	20,8	14,6	0,7
Alcides	19.01.2004	A7	C10	E. guentheri	ad		no	21,9	15,7	0,8
Alcides	20.01.2004	A8	C2	E. guentheri	ad		no	23,0	17,0	1,2
Alcides	21.01.2004	A10	A2	E. guentheri	ad	m	no	22,6	14,1	0,9
Alcides	21.01.2004	A11	A2/3	E. guentheri	ad	m	no	24,0	16,1	1,0
Alcides	21.01.2004	A12	B2	E. guentheri	ad	m	no	24,2	16,4	1,1
Alcides	21.01.2004	A13	A4	E. guentheri	ad	f	no	25,3	19,3	1,4
Alcides	21.01.2004	A14	C2	E. guentheri	ad	f	no	26,2	20,1	1,8
Alcides	23.01.2004	A32	A5/6	E. guentheri	ad		no	-	-	-
Alcides	23.01.2004	A23	B8/9	E. guentheri	ad		yes			
Dito	25.01.2004	D1	A2	E. guentheri	ad	m	no	24,7	16,0	1,1
Dito	25.01.2004	D2	A2	E. guentheri	ad	f	no	32,7	21,6	3,9
Dito	25.01.2004	22-4/04	A2	E. parvus	ad	m	no	19,0	11,0	0,7

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Dito	25.01.2004	22-5/04	B3	E. parvus	ad		no			
Dito	25.01.2004	D4	B1	E. guentheri	ad	f?	no	27,0	21,3	1,9
Dito	25.01.2004	D5	C0	E. guentheri	ad		no	24,0	15,1	1,0
Dito	25.01.2004	D6	C6	E. guentheri	ad		no	23,3	17,0	1,3
Dito	25.01.2004	22-12/04	C3	E. parvus	ad		no	24,9	11,9	1,4
Dito	25.01.2004	D9	C8/9	E. guentheri	ad		no	25,7	16,9	1,2
Dito	25.01.2004	22-14/04	A8/9	E. parvus	ad	f	no	23,4	12,7	1,4
Dito	25.01.2004	22-15/04	B8	E. parvus	ad		no	19,0	10,1	0,5
Dito	25.01.2004	22-16/04	C2	E. parvus?	ad?		no	18,2	10,5	0,4
Dito	25.01.2004	23-1/04	B2	E. parvus	ad		no	21,3	12,6	0,8
Dito	25.01.2004	23-2/04	A6	E. parvus	ad		no	21,7	12,2	0,9
Dito	25.01.2004	23-3/04	C5	E. parvus	ad		no	17,7	10,0	0,4
Dito	25.01.2004	D10	C5	E. guentheri	ad	m	no	25,8	16,9	1,2
Dito	25.01.2004	23-5/04	A2	E. parvus	ad	f	no	23,0	13,2	1,0
Dito	25.01.2004	23-6/04	A2	E. parvus	ad	m?	no	19,2	10,0	0,4
Dito	26.01.2004	D1	A1/2	E. guentheri	ad	m	yes			
Dito	26.01.2004	D12	C0	E. guentheri	ad		no	25,2	18,0	0,9
Dito	26.01.2004	24-5/04	B2/3	E. parvus	ad	m?	no	18,8	10,5	0,6
Dito	26.01.2004	24-6/04	B2/3	E. parvus	ad	f?	no	24,0	12,3	1,1
Dito	26.01.2004	D13	B4	E. guentheri	ad	f	no	34,4	21,8	3,1
Dito	26.01.2004	D14	B4/5	E. guentheri	ad		no	23,3	14,8	0,8
Dito	26.01.2004	D17	B4/5	E. guentheri	ad		no	24,1	16,2	1,1
Dito	26.01.2004	24-10/04	A3	E. parvus	juv		no	8,3	-	<0,1
Dito	26.01.2004	24-11/04	A3	E. parvus	ad		no	19,0	10,0	0,6
Dito	26.01.2004	24-12/04	A4	E. parvus	ad		no	18,0	19,7	0,6
Dito	26.01.2004		A4	E. guentheri	juv		no	12,1	6,8	0,1
Dito	26.01.2004		A4	E. guentheri	juv		no	11,6	7,0	0,1
Dito	26.01.2004	D15	B9	E. guentheri	ad		no	23,2	16,0	1,2
Dito	26.01.2004	25-1/04	A7	E. parvus	ad	f?	no	24,0	12,4	1,3
Dito	26.01.2004	D16	A8	E. guentheri	ad	f	no	30,0	19,7	2,5
Dito	26.01.2004		A8	E. guentheri	juv		no	6,6	4,0	<0,1
Dito	27.01.2004	26-1/04	A2	E. parvus	ad		no	19,4	12,0	0,9
Dito	27.01.2004	26-2/04	A9	E. parvus	ad		no	19,3	9,9	0,5
Dito	27.01.2004	26-3/04	B2/3	E. parvus	ad		no	20,3	10,4	0,8
Dito	27.01.2004	26-4/04	B3/4	E. parvus	ad?		no	16,7	10,0	0,4
Dito	27.01.2004	22-5/04	B3/4	E. parvus	ad?		yes			
MorroC	02.11.2003	MC1	B2	E. guentheri	ad		no	14,7	10,0	0,4
MorroC	05.11.2003	MC2	B2	E. guentheri	ad	m	no	19,1	13,3	0,7
MorroC	05.11.2003	MC3		E. guentheri	ad	m	no	19,4	13,8	0,7
MorroC	05.11.2003	MC4		E. guentheri	ad	m	no	21,6	13,9	0,9
MorroC	06.11.2003	MC5	A1	E. guentheri	ad	m	no	20,2	12,1	0,6
MorroC	06.11.2003	MC6	C9	E. guentheri	ad		no	19,0	13,9	0,6
MorroC	06.11.2003	MC17	C10	E. guentheri	ad		no	20,6	14,4	0,7
MorroC	06.11.2003	MC8	A8	E. guentheri	ad		no	19,0	13,4	0,7
MorroC	06.11.2003	MC3		E. guentheri	ad	m	yes			
Morro A	29.10.2003		A5/6	E. guentheri	ad	m	no	20,5	15,2	0,7
Morro A	29.10.2003		C1	E. guentheri	ad	m	no	19,6	14,3	1,0
MorroC	13.11.2003	MC9		E. guentheri	ad	m	no	18,4	13,8	0,6
MorroC	13.11.2003	MC10	A7	E. guentheri	juv?	m	no	16,4	11,9	0,5
MorroC	13.11.2003	MC17	C10	E. guentheri	ad	m	yes			
MorroC	13.11.2003	MC11	C10	E. guentheri	ad	m	no	18,7	13,6	0,6
MorroC	13.11.2003	MC12	A8	E. guentheri	ad	m	no	19,9	14,5	0,7

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MorroC	13.11.2003	-	C7	E. guentheri	ad	m	no			
Dito	29.01.2004		C8	E. guentheri	juv		no	13,3	8,1	<0,1
Dito	29.01.2004		A4/5	E. guentheri	juv		no	11,4	6,7	<0,1
Dito	29.01.2004		A6	E. guentheri	juv		no	10,4	5,6	<0,1
MorroC	12.02.2004	MC7	C9/10	E. guentheri	ad		no	20,9	14,5	?
MorroC	12.02.2004	MC14	A1	E. guentheri	ad		no	22,7	14,7	?
Carmo	10.03.2004	CM84	C1/2	E. guentheri	ad	f	no	33,4	24,4	3,0
Carmo	10.03.2004	CM85	C5	E. guentheri	ad		no	20,6	15,4	0,5
Carmo	11.03.2004	CM15	A6	E. guentheri	ad		yes			
Carmo	11.03.2004	CM58	C5	E. guentheri	ad		yes			
Carmo	12.03.2004	CM99	B10/11	E. guentheri	ad		no	21,7	15,6	0,9
Carmo	12.03.2004	CM90	A9/10	E. guentheri	ad		no	21,6	16,0	0,8
Alcides	14.03.2004		C2	E. guentheri	juv		no	14,0	9,9	0,4
Alcides	16.03.2004	A33	B6/7	E. guentheri	ad		no	22,2	15,5	1,0
Alcides	18.03.2004	A34	C1/2	E. guentheri	ad		no	20,9	15,5	0,8
Alcides	18.03.2004	A35	C3	E. guentheri	juv		no	16,9	10,5	0,3
Dito	22.03.2004	D34	A4/5	E. guentheri	juv		no	16,9	11,0	0,5
Dito	22.03.2004	42-2/04	A7/8	E. parvus	juv		no	11,6	6,3	0,2
Dito	22.03.2004	42-3/04	A7/8	E. parvus	juv		no	11,5	6,7	0,2
Dito	26.11.2004	D103	A9	E. guentheri	ad		no	21,2	14,8	0,9
Dito	26.11.2004		A9	E. guentheri	ad		no	-	-	-
Dito	26.11.2004	D105	A10	E. guentheri	ad		no	17,4	11,2	0,5
Dito	26.11.2004	66-27/04	A10	E. parvus	ad		no	22,2	12,6	1,1
Dito	26.11.2004	66-28/04	A11	E. parvus	ad		no	23,0	12,2	1,2
Dito	27.01.2004	26-6/04	C8	E. parvus	ad		no	17,9	10,4	0,6
Dito	27.01.2004		C1	E. guentheri	juv		no	12,0	7,1	<0,1
Dito	27.01.2004	26-9/04	A10/11	E. parvus	juv		no	9,3	4,6	<0,1
Dito	27.01.2004	26-10/04	C2	E. parvus	juv		no	8,7	4,0	<0,1
Dito	27.01.2004		A10	E. guentheri	juv		no	13,6	7,7	0,1
Dito	27.01.2004		C3	E. guentheri	juv		no	12,1	-	-
Dito	27.01.2004	26-13/04	B4/5	E. parvus	ad		no	19,5	10,0	0,8
Dito	27.01.2004	D18	B4/5	E. guentheri	ad	m	no	20,7	14,1	0,8
Dito	27.01.2004	D19	B4/5	E. guentheri	ad		no	20,4	13,9	0,9
Dito	27.01.2004	D4	B0/1	E. guentheri	ad		yes			
Dito	27.01.2004	D20	B1/2	E. guentheri	sub		no	15,8	12,7	0,4
Dito	27.01.2004	D21	B1/2	E. guentheri	ad	f	no	31,9	21,9	2,8
Dito	27.01.2004	D1	A2	E. guentheri	ad	m	yes			
Dito	28.01.2004	D22	B1/2	E. guentheri	ad		no	24,8	16,5	1,1
Dito	28.01.2004	D23	B1	E. guentheri	ad		no	22,2	14,6	1,2
Dito	28.01.2004	D24	B1	E. guentheri	ad		no	18,6	12,9	0,7
Dito	28.01.2004		A4	E. guentheri	juv		no	11,9	6,3	<0,1
Dito	28.01.2004		A9	E. guentheri	juv		no	12,0	7,0	<0,1
Dito	28.01.2004	28-9/04	A9	E. parvus	ad		no	18,5	9,5	0,7
Dito	28.01.2004	D26	C4	E. guentheri	ad	f	no	28,5	20,6	2,5
Dito	28.01.2004	28-12/04	C2	E. parvus	juv		no	10,0	5,0	<0,1
Dito	28.01.2004	28-13/04	C2	E. parvus	juv		no	10,2	4,9	<0,1
Dito	28.01.2004	28-14/04	C2	E. parvus	juv		no	10,9	6,3	<0,1
Dito	28.01.2004	D6	C8	E. guentheri	ad		yes			
Dito	28.01.2004	26-6/04	C9	E. parvus	ad		yes			
Dito	28.01.2004	D28	A10	E. guentheri	ad		no	28,5	20,2	2,1
Dito	28.01.2004	D29	C5	E. guentheri	ad	m?	no	24,9	15,0	1,3
Dito	28.01.2004	29-4/04	C5	E. parvus	ad		no	28,7	11,0	0,8

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Dito	28.01.2004	D30	B10	E. guentheri	ad	m?	no	23,0	16,0	1,0
Dito	28.01.2004	D17	B4/5	E. guentheri	ad		yes			
Dito	28.01.2004	29-7/04	C3	E. parvus	juv		no	8,6	-	<0,1
Dito	28.01.2004	29-8/04	C3	E. parvus	juv		no	8,9	-	<0,1
Dito	28.01.2004	29-9/04	C3	E. parvus	juv		no	10,0	5,3	<0,1
Dito	28.01.2004		C0	E. guentheri	juv		no	11,7	7,1	<0,1
Dito	28.01.2004	29-13/04	C0	E. parvus	juv		no	8,4	-	<0,1
Dito	28.01.2004	D31	B7/8	E. guentheri	ad	f?	no	30,1	21,5	2,3
Dito	29.01.2004	D25	C3	E. guentheri	ad		no	-	-	-
Dito	29.01.2004	D22	B1/2	E. guentheri	ad		yes			
Dito	29.01.2004	D17	B1/2	E. guentheri	ad		yes			
Dito	29.01.2004	D32	B3/4	E. guentheri	ad		no	25,4	17,0	?
Dito	23.03.2004	D35	C0/1	E. guentheri	ad	f	no	31,6	23,9	3,0
Dito	23.03.2004	43-2/04	C3/4	E. parvus	ad?		no	11,7	8,3	0,3
Dito	23.03.2004	43-3/04	C3/4	E. parvus	juv		no	12,3	6,7	0,3
Dito	23.03.2004		C3/4	E. guentheri	juv		no	12,1	7,4	0,25
Dito	23.03.2004	43-5/04	C6/7	E. parvus	juv		no	9,9	5,5	0,2
Dito	23.03.2004	43-6/04	C2	E. parvus	ad		no	19,0	9,7	0,7
Dito	23.03.2004	43-7/04	C2	E. parvus	juv?		no	12,8	7,1	0,3
Dito	23.03.2004		A8	E. guentheri	juv		no	11,4	7,0	0,2
Dito	23.03.2004		A7	E. guentheri	juv		no	11,5	6,4	0,2
Dito	23.03.2004		A7	E. guentheri	juv		no	-	-	-
Dito	23.03.2004	43-11/04	A7	E. parvus	juv		no	12,9	7,9	0,3
Dito	23.03.2004	43-12/04	A6	E. parvus	juv		no	13,9	8,5	0,3
Dito	23.03.2004	43-13/04	A6	E. parvus	ad		no	17,9	9,6	0,4
Dito	23.03.2004	43-14/04	A5	E. parvus	juv?		no	12,9	7,5	0,25
Dito	23.03.2004	43-15/04	A5	E. parvus	ad?		no	14,1	7,6	0,3
Dito	23.03.2004	43-16/04	A5	E. parvus	ad?		no	15,4	7,9	0,35
Dito	23.03.2004	44-1/04	A4	E. parvus	ad		no	17,5	10,2	0,5
Dito	23.03.2004	44-2/04	A4	E. parvus	juv?		no	12,3	6,6	0,15
Dito	23.03.2004	D36	A4	E. guentheri	juv		no	15,4	9,8	0,2
Dito	24.03.2004	D66	C0/1	E. guentheri	ad?		no	18,2	12,5	0,5
Dito	24.03.2004	D38	C1/2	E. guentheri	ad		no	23,7	16,7	1,2
Dito	24.03.2004	45-3/04	C2/3	E. parvus	juv		no	11,5	6,3	0,1
Dito	24.03.2004	D37	B0	E. guentheri	ad?		no	16,5	10,3	0,3
Dito	24.03.2004		B2/3	E. guentheri	juv		no	12,6	8,5	0,15
Dito	24.03.2004		B2/3	E. guentheri	juv		no	9,0	5,9	<0,1
Dito	24.03.2004	45-7/04	C6/7	E. parvus	juv		no	10,0	4,6	<0,1
Dito	24.03.2004	45-8/04	C5/6	E. parvus	juv		no	-	-	<0,1
Dito	24.03.2004		B4	E. guentheri	juv		no	13,6	8,0	0,2
Dito	24.03.2004	45-10/04	B3	E. parvus	juv		no	12,7	7,0	0,15
Dito	24.03.2004		A6	E. guentheri	juv		no	12,1	6,5	0,1
Dito	24.03.2004	43-11/04	A6	E. parvus	juv?		yes			
Dito	24.03.2004	45-13/04	A7	E. parvus	juv?		no	13,2	7,5	0,2
Dito	24.03.2004		A7	E. guentheri	juv		no	13,0	8,0	0,2
Dito	24.03.2004	45-15/04	A8	E. parvus	juv		no	13,5	7,7	0,2
Dito	25.03.2004		A7/8	E. guentheri	juv		no	12,0	7,2	0,1
Dito	25.03.2004		A9	E. guentheri	juv		no	10,9	7,2	0,1
Dito	25.03.2004		B1	E. guentheri	juv		no	10,0	6,1	<0,1
Dito	25.03.2004	46-4/04	B3	E. parvus	juv		no	12,8	6,8	0,2
Dito	25.03.2004		B5	E. guentheri	juv		no	11,0	6,9	<0,1
Dito	25.03.2004		B5	E. guentheri	juv		no	7,0	4,3	<0,1

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Dito	25.03.2004	D35	C0	E. guentheri	ad	f	yes			
Dito	25.03.2004	46-8/04	C0	E. parvus	juv?		no	14,9	7,0	0,2
Dito	25.03.2004	46-9/04	C0	E. parvus	juv?		no	13,3	7,9	0,2
Dito	25.03.2004	D39	C1	E. guentheri	ad		no	26,0	19,4	1,4
Dito	25.03.2004	D40	C2	E. guentheri	ad?		no	15,9	11,4	0,3
Dito	25.03.2004	46-12/04	C2	E. parvus	juv		no	11,1	6,4	0,1
Dito	25.03.2004		C3	E. guentheri	juv		no	12,7	8,0	0,2
Dito	26.03.2004	43-6/04	A2	E. parvus	ad		yes			
Dito	26.03.2004	47-4/04	A3/4	E. parvus	juv		no	10,7	6,3	0,1
Dito	26.03.2004	47-5/04	A4	E. parvus	juv		no	11,1	5,4	0,1
Dito	26.03.2004	D41	A5	E. guentheri	ad?		no	15,3	10,2	0,3
Dito	26.03.2004		A6	E. guentheri	juv		no	10,7	7,2	<0,1
Dito	26.03.2004	47-8/04	C0	E. parvus	juv		no	12,6	6,9	0,2
Dito	26.03.2004		C4	E. guentheri	juv		no	14,0	8,3	0,2
Dito	26.03.2004	D42	C7	E. guentheri	ad		no	23,2	16,4	1,1
Dito	26.03.2004	D43	C9	E. guentheri	ad		no	28,9	21,9	2,1
Dito	26.03.2004		B1	E. guentheri	juv		no	9,9	5,2	<0,1
Dito	26.03.2004	26-3/04	B2/3	E. parvus	ad		yes			
Dito	26.03.2004	46-4/04	B2/3	E. parvus	juv		yes			
Dito	26.03.2004	48-1/04	B2/3	E. parvus	juv		no	13,0	7,5	0,1
Dito	26.03.2004	48-3/04	B3	E. parvus	juv		no	12,7	6,6	0,1
Dito	26.03.2004	48-5/04	B4/5	E. parvus	juv		no	13,9	7,2	0,1
Dito	26.03.2004	48-2/04	B3	E. parvus	juv		no	13,3	7,0	0,1
MorroC	26.10.2004	MC14	A1	E. guentheri	ad	m	yes			
Carmo	08.11.2004	CM100	A1/2	E. guentheri	ad	m	no	21,8	15,8	1,0
Carmo	08.11.2004	CM102	A4	E. guentheri	ad	f	no	29,0	20,9	2,5
Carmo	08.11.2004	CM103	A5	E. parvus?	juv		no	13,4	7,0	0,2
Carmo	08.11.2004	CM104	B5	E. guentheri	ad	m	no	19,4	14,0	0,8
Carmo	09.11.2004	CM105	A3	E. guentheri	ad	m?	no	18,5	11,9	0,6
Carmo	09.11.2004		A7	E. guentheri	juv		no	13,0	8,1	0,3
Carmo	09.11.2004	CM106	A8	E. guentheri	ad	f	no	26,4	18,5	1,7
Alcides	01.12.2004	A54	C7	E. guentheri	ad?		no	16,8	12,0	0,5
Alcides	02.12.2004	A55	C7/8	E. guentheri	ad		no	17,0	12,7	0,6
MorroC	10.01.2005	MC30	A7	E. guentheri	ad	m	no	24,1	15,1	1,2
MorroC	10.01.2005	MC31	A7	E. guentheri	ad	m	no	24,7	17,1	1,3
MorroC	11.01.2005	MC34	A1	E. guentheri	ad	m	no	20,5	14,8	0,9
Carmo	17.01.2005	CM140	A7	E. guentheri	ad?		yes			
Carmo	17.01.2005	CM145	B3	E. guentheri	ad	m	no	22,0	14,0	0,9
Carmo	17.01.2005	CM146	B4	E. guentheri	ad	m	no	22,0	15,4	0,9
Carmo	17.01.2005		C9	Eleutherodactylus sp.	ad		no	15,1	8,2	0,4
Carmo	18.01.2005	CM149	A4	E. guentheri	ad		no	20,3	14,0	0,8
Carmo	18.01.2005	CM150	C5	E. guentheri	ad		no	22,5	16,0	0,7
Carmo	18.01.2005	CM137	C1	E. guentheri	ad		yes			
Carmo	19.01.2005	CM100	A1	E. guentheri	ad	m	yes			
Carmo	19.01.2005		A2	Eleutherodactylus sp.	ad		no	15,8	8,4	0,2
Carmo	19.01.2005	CM152	A3	E. guentheri	ad	f?	no	24,5	17,8	1,2
Carmo	19.01.2005	CM102	A4	E. guentheri	ad	f	yes			
Carmo	19.01.2005	CM153	A4	E. guentheri	ad	m?	no	19,6	13,4	0,5
Carmo	19.01.2005	CM154	A8	E. guentheri	ad	m	no	21,6	15,0	0,9
Carmo	19.01.2005	CM155	A8	E. guentheri	ad	m	no	21,4	15,0	0,9
Carmo	19.01.2005		A11	Eleutherodactylus sp.	ad		no	19,2	10,0	-
Carmo	15.11.2004	CM105	A4	E. guentheri	ad	m?	no	18,6	12,9	0,6

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Carmo	15.11.2004	CM44	A5	E. guentheri	ad	m	yes			
Carmo	15.11.2004	CM106	A6	E. guentheri	ad	m	no	18,4	12,7	0,5
Carmo	15.11.2004	CM107	A10	E. guentheri	ad	m?	no	20,0	13,1	0,7
Carmo	15.11.2004		A10	Eleutherodactylus sp.	ad		no	13,7	7,0	0,2
Carmo	15.11.2004		A10	Eleutherodactylus sp.	ad		no	12,6	7,0	0,3
Carmo	15.11.2004		A10	Eleutherodactylus sp.	ad		no	12,7	6,9	0,3
Carmo	15.11.2004	CM109	B4/5	E. guentheri	ad	m	no	17,8	11,6	0,6
Carmo	15.11.2004	CM110	B4/5	E. guentheri	ad	m	no	23,4	15,4	1,1
Carmo	15.11.2004	CM104	B4/5	E. guentheri	ad	m	yes			
Carmo	15.11.2004	CM111	B4	E. guentheri	ad	m	no	18,3	12,0	0,7
Carmo	15.11.2004	CM112	B5	E. guentheri	ad	m	no	20,0	13,7	0,7
Carmo	15.11.2004		B4/5	Eleutherodactylus sp.	ad	m	no	14,5	8,1	0,2
Carmo	16.11.2004	CM120	A5/6	E. guentheri	ad	m	no	16,5	10,4	0,5
Carmo	16.11.2004	CM121	A6	E. guentheri	ad	m	no	21,9	15,8	1,0
Carmo	16.11.2004	CM122	A7/8	E. guentheri	ad		no	21,9	14,9	1,0
Carmo	16.11.2004	CM112	B5	E. guentheri	ad	m	yes			
Carmo	16.11.2004	CM123	B5	E. guentheri	ad		no	15,3	10,0	0,4
Carmo	16.11.2004	CM124	C5	E. guentheri	ad	m	no	25,7	16,5	1,3
Carmo	16.11.2004		B4/5	Eleutherodactylus sp.	ad	m	no	13,0	7,1	0,2
Carmo	17.11.2004	CM125	A7	E. guentheri	ad	m?	no	18,9	14,1	0,7
Carmo	17.11.2004	CM106	A7	E. guentheri	ad		yes			
Carmo	17.11.2004	CM44	A4/5	E. guentheri	ad	m	yes			
Carmo	17.11.2004	CM126	A6	E. guentheri	ad?		no	18,0	11,3	0,5
Carmo	17.11.2004		A5/6	Eleutherodactylus sp.	ad		no	13,0	6,9	0,3
Carmo	17.11.2004	CM128	B2	E. guentheri	ad	m?	no	23,0	16,8	1,2
Carmo	17.11.2004	CM104	B4/5	E. guentheri	ad	m	yes			
Carmo	17.11.2004	CM82	B4	E. guentheri	ad	f	yes			
Carmo	17.11.2004	CM129	B4/5	E. guentheri	ad?		no	14,7	10,0	0,4
Carmo	17.11.2004	CM130	B8	E. guentheri	ad	m	no	19,5	12,7	0,6
Carmo	17.11.2004	CM131	C9	E. guentheri	ad?		no	13,8	10,5	0,3
Carmo	17.11.2004	CM132	C6	E. guentheri	ad		no	23,8	15,5	1,0
Carmo	17.11.2004	CM133	C7	E. guentheri	ad		no	23,0	16,8	1,3
Carmo	17.11.2004		C7	Eleutherodactylus sp.	ad		no	15,7	8,0	0,3
Carmo	17.11.2004		C5	Eleutherodactylus sp.	ad		no	16,1	8,8	0,5
Carmo	18.11.2004	CM135	A9	E. guentheri	ad	m	no	22,7	16,0	0,9
Carmo	18.11.2004	CM44	A4/5	E. guentheri	ad		yes			
Carmo	18.11.2004	CM136	A6	E. guentheri	ad	f?	no	30,2	21,8	2,7
Carmo	18.11.2004	CM121	A5/6	E. guentheri	ad	m	yes			
Carmo	18.11.2004	CM137	C1	E. guentheri	juv		no	14,5	10,0	0,3
Carmo	18.11.2004	CM124	C5/6	E. guentheri	ad	m	yes			
Carmo	18.11.2004	CM138	C4	E. guentheri	ad	m	no	18,0	13,1	0,6
Carmo	18.11.2004	CM139	C4	E. guentheri	ad	m	no	20,9	14,3	0,9
Carmo	19.11.2004	CM140	A7	E. guentheri	ad?		no	15,8	9,8	0,3
Carmo	19.11.2004	CM141	A6	E. guentheri	ad?		no	12,9	9,0	0,2
Carmo	19.11.2004	CM142	A8	E. guentheri	ad?		no	15,5	10,2	0,3
Carmo	19.11.2004	CM143	B4	E. guentheri	ad	f?	no	31,6	20,6	2,9
Carmo	19.11.2004	CM144	C3	E. guentheri	ad		no	22,6	15,9	1,2
Carmo	19.11.2004	CM124	C5	E. guentheri	ad		yes			
Dito	22.11.2004	D67	C1/2	E. guentheri	ad		no	22,3	15,5	1,1
Dito	22.11.2004	D68	A10/11	E. guentheri	ad		no	20,2	14,3	0,7
Dito	22.11.2004	D69	A4	E. guentheri	ad?		no	15,8	10,1	0,4
Dito	23.11.2004	62-1/04	A4	E. parvus	ad		no	20,0	11,6	0,7

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Dito	23.11.2004	D69	A4	E. guentheri	ad?		yes			
Dito	23.11.2004	D70	A11	E. guentheri	ad		no	18,9	14,0	0,6
Dito	23.11.2004	62-4/04	C0	E. parvus	ad		no	19,1	11,0	0,6
Dito	23.11.2004	D71	C2	E. guentheri	ad		no	17,5	11,0	0,5
Dito	23.11.2004	D72	C5/6	E. guentheri	ad		no	24,2	16,2	1,2
Dito	23.11.2004	D73	C7	E. guentheri	ad		no	23,4	15,5	1,1
Dito	23.11.2004	D74	C7/8	E. guentheri	ad		no	22,2	15,4	1,1
Dito	24.11.2004	D75	A8	E. guentheri	ad?		no	19,9	13,8	0,6
Dito	24.11.2004	D77	C2	E. guentheri	ad	m	no	19,0	13,5	0,7
Dito	24.11.2004	63-3/04	C7	E. parvus	ad		no	19,8	12,2	0,8
Dito	25.11.2004	D76	C0	E. guentheri	ad		no	19,4	13,6	0,7
Dito	25.11.2004	D78	C4/5	E. guentheri	ad?		no	17,0	11,0	0,4
Dito	25.11.2004	D79	C7	E. guentheri	ad		no	21,6	14,4	0,8
Dito	26.11.2004	D80	C0	E. guentheri	ad	m	no	22,9	15,5	1,0
Dito	26.11.2004	D81	C6	E. guentheri	ad		no	21,6	14,6	0,8
Dito	26.11.2004	D73	C6	E. guentheri	ad		yes			
Dito	26.11.2004	D25	C2/3	E. guentheri	ad	f	yes			
Dito	26.11.2004	65-5/04	C3	E. parvus	ad	m?	no	18,5	10,0	0,6
Dito	26.11.2004	65-6/04	C1	E. parvus	ad	m?	no	20,0	10,3	0,6
Dito	26.11.2004	65-7/04	C3	E. parvus	ad		no	18,6	10,4	0,6
Dito	26.11.2004	D82	B6	E. guentheri	ad	f?	no	24,0	16,8	1,2
Dito	26.11.2004	D83	B5	E. guentheri	ad	m	no	19,8	14,1	0,6
Dito	26.11.2004	D84	B5	E. guentheri	ad	m	no	19,1	14,2	0,7
Dito	26.11.2004	D85	B2	E. guentheri	ad	m	no	19,7	14,3	0,6
Dito	26.11.2004	D86	B2	E. guentheri	ad	m	no	21,9	15,6	0,8
Dito	26.11.2004	D87	B3	E. guentheri	ad	m	no	21,5	15,4	0,9
Dito	26.11.2004	D88	B0	E. guentheri	ad		no	25,4	17,9	1,4
Dito	26.11.2004	D89	B0	E. guentheri	ad		no	20,6	14,6	0,9
Dito	26.11.2004	D90	B0	E. guentheri	ad		no	22,8	15,7	1,1
Dito	26.11.2004	D91	B0	E. guentheri	ad		no	24,6	17,4	1,2
Dito	26.11.2004	D92	B4	E. guentheri	ad		no	22,1	15,3	1,0
Dito	26.11.2004	66-4/04	A2	E. parvus	ad		no	17,2	10,2	0,6
Dito	26.11.2004	D93	A2	E. guentheri	ad	m	no	20,2	14,8	0,9
Dito	26.11.2004	D94	A2	E. guentheri	ad	m	no	22,1	15,1	0,9
Dito	26.11.2004	D95	A2	E. guentheri	ad	m	no	21,0	15,0	0,9
Dito	26.11.2004	D96	A2	E. guentheri	ad	m	no	23,3	15,9	1,2
Dito	26.11.2004	D97	A3	E. guentheri	ad	m	no	23,6	16,4	1,1
Dito	26.11.2004	D98	A3	E. guentheri	ad		no	18,2	12,5	0,6
Dito	26.11.2004	66-11/04	A3	E. parvus	ad		no	19,0	11,1	0,6
Dito	26.11.2004	66-12/04	A3	E. parvus	ad		no	17,2	10,7	0,5
Dito	26.11.2004	D99	A3	E. guentheri	ad		no	18,4	12,3	0,6
Dito	26.11.2004	D100	A3	E. guentheri	ad		no	22,0	15,8	0,9
Dito	26.11.2004	D101	A3	E. parvus	ad		no	20,8	11,9	0,8
Dito	26.11.2004	66-16/04	A4	E. parvus	ad		no	16,5	9,6	0,5
Dito	26.11.2004	66-17/04	A4	E. parvus	ad		no	18,0	10,6	0,5
Dito	26.11.2004	66-19/04	A5	E. parvus	ad		no	20,1	12,0	0,7
Dito	26.11.2004	66-20/04	A5	E. parvus	ad?		no	15,3	8,9	0,4
Dito	26.11.2004	66-21/04	A6	E. parvus	ad		no	18,0	10,0	0,6
Dito	26.11.2004	66-22/04	A8	E. parvus	ad		no	21,8	12,3	0,9
Alcides	28.11.2004	A36	A2/3	E. guentheri	ad	m	no	28,8	15,7	1,1
Alcides	28.11.2004	A28	A1	E. guentheri	ad	m	yes			
Alcides	28.11.2004	A37	A8/9	E. guentheri	ad	m	no	19,1	14,9	0,9

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Alcides	28.11.2004	A38	A9	E. guentheri	ad	m	no	19,4	13,5	0,7
Alcides	28.11.2004	A39	A9/10	E. guentheri	ad	m	no	19,5	13,6	0,7
Alcides	28.11.2004	A40	B1	E. guentheri	ad	f	no	24,2	16,8	0,9
Alcides	28.11.2004	A41	B1	E. guentheri	ad	m	no	21,9	15,5	0,8
Alcides	28.11.2004	A42	C8/9	E. guentheri	ad	m	no	24,0	15,5	1,2
Alcides	28.11.2004	A43	C10	E. guentheri	ad	m	no	23,0	16,8	1,1
Alcides	28.11.2004	A44	C6	E. guentheri	ad	m	no	24,0	16,1	1,2
Alcides	28.11.2004	A45	C6	E. guentheri	ad	m	no	24,0	15,5	1,2
Alcides	28.11.2004	A46	C6	E. guentheri	ad	m	no	19,7	13,6	0,8
Alcides	28.11.2004	A47	B2	E. guentheri	ad	m	no	21,1	14,9	0,8
Alcides	28.11.2004	A48	B2	E. guentheri	ad	m	no	22,2	15,3	1,0
Alcides	29.11.2004	A50	B6	E. guentheri	ad	m	no	20,1	13,7	0,8
Alcides	29.11.2004	A51	B4	E. guentheri	ad		no	23,6	16,0	1,1
Alcides	29.11.2004		B5	Eleutherodactylus sp.	juv		no	13,2	8,6	0,3
Alcides	29.11.2004	A52	A8	E. guentheri	ad		no	20,0	14,0	0,9
Alcides	29.11.2004		A4	Eleutherodactylus sp.	ad		no	14,3	8,0	0,4
Alcides	29.11.2004	A53	A3/4	E. guentheri	ad	m	no	20,1	14,5	0,8
Dito	24.01.2005	83-1/05	C0	E. parvus	ad		no	17,6	9,8	0,3
Dito	24.01.2005	D114	C2/3	E. guentheri	ad	m	no	21,4	14,5	0,8
Dito	24.01.2005	D71	C1	E. guentheri	ad		yes			
Dito	24.01.2005	D115	C1	E. guentheri	ad		no	19,1	13,0	0,6
Dito	24.01.2005	D116	A1	E. guentheri	ad		no	28,4	20,7	1,9
Dito	24.01.2005	83-6/05	C0/1	E. parvus	ad		no	20,9	12,7	0,9
Dito	24.01.2005	83-7/05	C8	E. parvus	ad		no	22,5	14,0	1,0
Dito	24.01.2005	D117	C9	E. guentheri	ad	f?	no	28,7	19,2	2,1
Alcides	31.01.2005	A59	A4/5	E. guentheri	ad	m?	no	20,3	15,0	0,9
Alcides	01.02.2005	A60	A2	E. guentheri	ad	m?	no	22,5	14,9	0,9
Alcides	01.02.2005	A59	A4	E. guentheri	ad	m?	yes			
Alcides	01.02.2005	A55	A7/8	E. guentheri	ad		yes			
Alcides	02.02.2005	A61	B3	E. guentheri	ad		no	24,7	17,5	1,2
Alcides	02.02.2005		A4	E. guentheri	juv		no	13,5	7,5	0,2
Alcides	02.02.2005	A53	A4	E. guentheri	ad	m	yes			
Alcides	02.02.2005	A62	A7	E. guentheri	ad	f?	no	27,4	20,2	2,0
Alcides	02.02.2005	A63	A9	E. guentheri	ad	m	no	20,7	15,0	1,0
Alcides	02.02.2005	A64	B10	E. guentheri	ad	m	no	22,5	16,1	1,2
Alcides	02.02.2005	A65	A3/4	E. guentheri	ad	m?	no	21,0	14,8	0,8
Alcides	02.02.2005		A3	Eleutherodactylus sp.			no	19,3	10,4	0,6
Alcides	02.02.2005		A2	E. guentheri	juv		no	-	-	-
Carmo	20.01.2005		A2	Eleutherodactylus sp.	ad		no	17,9	10,3	0,5
Carmo	20.01.2005		A2	Eleutherodactylus sp.	ad		no	20,9	10,7	0,6
Carmo	20.01.2005	CM153	A4	E. guentheri	ad		yes			
Carmo	20.01.2005	CM149	A4	E. guentheri	ad		yes			
Carmo	20.01.2005		A5	Eleutherodactylus sp.	ad		no	17,8	9,9	0,4
Carmo	20.01.2005		B2	Eleutherodactylus sp.	ad		no	18,1	9,6	0,4
Carmo	20.01.2005	CM158	C4	E. guentheri	ad	m	no	21,9	14,0	0,7
Carmo	20.01.2005		C9	Eleutherodactylus sp.	ad		no	16,1	8,1	0,3
Carmo	20.01.2005	CM159	B4	E. guentheri	ad	m	no	23,0	16,4	0,9
Carmo	20.01.2005		B5	Eleutherodactylus sp.	ad		no	17,7	9,6	0,3
Carmo	20.01.2005	CM169	B5	E. guentheri	ad	m	no	21,0	14,7	0,1
Carmo	21.01.2005	CM165	A10	E. guentheri	ad	m	no	25,0	16,3	1,2
Carmo	21.01.2005	CM145	B3	E. guentheri	ad		yes			
Carmo	21.01.2005		C1	Eleutherodactylus sp.	ad		no	14,8	8,5	0,2

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Carmo	21.01.2005		B1	Eleutherodactylus sp.	ad		no	15,0	8,0	0,2
Dito	24.01.2005	D106	B4	E. guentheri	ad	m	no	29,9	22,6	2,7
Dito	24.01.2005	D107	B4	E. guentheri	ad		no	24,5	16,6	1,1
Dito	24.01.2005	82-3/05	B4	E. parvus	ad		no	18,7	10,7	0,5
Dito	24.01.2005	82-4/05	B4	E. parvus	ad		no	17,7	11,0	0,5
Dito	24.01.2005	D108	B5	E. guentheri	ad	m	no	22,3	16,7	0,7
Dito	24.01.2005	D109	B1	E. guentheri	ad		no	23,4	16,4	1,0
Dito	24.01.2005	D110	A3	E. guentheri	ad	f	no	33,7	20,4	3,2
Dito	24.01.2005	D111	A7	E. guentheri	ad	f?	no	29,9	21,4	2,2
Dito	24.01.2005	D112	A2	E. guentheri	ad		no	26,0	18,8	1,7
Dito	24.01.2005	D113	A3	E. guentheri	ad	m	no	24,5	15,8	1,8
Dito	24.01.2005	82-11/05	B11	E. parvus	ad		no	18,5	10,0	0,5
Dito	24.01.2005		B6	E. guentheri	juv		no	9,6	5,8	<0,1
Dito	24.01.2005	D21	B3	E. guentheri	ad	f	yes			
Dito	24.01.2005		B3	E. guentheri	juv		no	11,8	6,6	<0,1
Dito	24.01.2005	D72	C5	E. guentheri	ad	m?	yes			
Dito	24.01.2005		C0	E. guentheri	juv		no	11,8	6,4	<0,1
Alcides	03.02.2005	A66	A9/10	E. guentheri	ad	m	no	20,7	14,2	0,7
Dito	14.02.2005	D101	C4/5	E. parvus	ad	m?	yes			
Dito	14.02.2005	88-2/05	C7/8	E. parvus	ad		no	18,5	10,0	0,7
Dito	14.02.2005	88-3/05	C2	E. parvus	ad		no	18,6	9,9	0,6
Dito	14.02.2005	88-4/05	A4	E. parvus	ad		no	21,3	13,0	0,9
Dito	14.02.2005	88-5/05	C0	E. parvus	ad		no	16,6	9,9	0,6
Dito	14.02.2005		A6	E. guentheri	juv		no	10,0	6,1	0,1
Dito	14.02.2005		B8	E. guentheri	juv		no	9,1	4,8	0,1
Dito	14.02.2005		B8	E. guentheri	juv		no	9,1	4,9	0,1
Dito	14.02.2005	D121	B11	E. guentheri	ad	f	no	32,6	23,4	2,8
Dito	14.02.2005	D122	C1/2	E. guentheri	ad	m?	no	23,8	16,7	1,2
Dito	14.02.2005		C8/9	E. guentheri	juv		no	12,9	8,0	0,3
Dito	14.02.2005	D123	C5	E. guentheri	ad	m?	no	20,9	15,3	0,9
Dito	14.02.2005	D124	C1	E. guentheri	ad	m?	no	22,3	16,5	1,1
Dito	15.02.2005	D125	C2	E. guentheri	ad	m?	no	22,9	16,9	1,1
Dito	15.02.2005	D126	C4/5	E. guentheri	ad	m?	no	22,1	16,0	1,1
Dito	15.02.2005		C0	E. guentheri	juv		no	10,6	6,1	0,1
Dito	15.02.2005	D124	C1	E. guentheri	ad		yes			
Dito	15.02.2005	89-5/05	C1	E. parvus	ad		no	17,7	9,5	0,6
Dito	15.02.2005	89-6/05	C8	E. parvus	ad		no	22,0	12,3	1,1
Dito	15.02.2005	89-7/05	A2	E. parvus	ad		no	21,0	12,4	0,9
Dito	15.02.2005		A2	E. guentheri	juv		no	12,4	7,2	0,2
Dito	15.02.2005	89-9/05	A3	E. parvus	ad		no	18,9	10,6	0,7
Dito	15.02.2005	89-10/05	C4	E. parvus	ad		no	23,4	12,8	1,3
Dito	17.02.2005	D128	B1	E. guentheri	ad	f	no	30,4	22,7	2,6
Dito	17.02.2005	90-2/05	B1	E. parvus	sub		no	19,7	10,4	0,8
Dito	17.02.2005	D129	B4	E. guentheri	ad	f	no	27,5	20,1	2,1
Dito	17.02.2005	90-4/05	B2	E. parvus	ad	m?	no	22,6	13,3	1,1
Dito	17.02.2005	90-5/05	B2	E. parvus	ad		no	22,2	13,0	1,1
Dito	17.02.2005		B2	E. guentheri	juv		no	13,6	8,0	0,2
Dito	17.02.2005		B2	E. guentheri	juv		no	14,6	9,0	0,3
Dito	17.02.2005	89-6/05	C8	E. parvus	ad		yes			
Dito	17.02.2005	90-9/05	C3	E. parvus	ad		no	18,4	10,4	0,6
Dito	17.02.2005	D130	C6/7	E. guentheri	ad	m?	no	21,2	15,0	0,8
Dito	17.02.2005	D131	C4	E. guentheri	ad	f	no	27,3	19,0	1,5

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Dito	17.02.2005	D100	C5	E. guentheri	ad		yes			
Dito	17.02.2005	90-14/05	A6	E. parvus	ad	m?	no	22,5	12,9	1,2
Dito	17.02.2005	91-1/05	A2	E. parvus	ad		no	22,9	13,6	1,2
Dito	17.02.2005		A2/3	E. guentheri	juv		no	8,0	4,3	<0,1
Dito	17.02.2005		A4	E. guentheri	juv		no	10,1	5,7	0,2
Dito	17.02.2005	91-4/05	A4	E. parvus	ad		no	18,2	10,0	0,6
Dito	17.02.2005	D133	A7	E. guentheri	ad	f	no	30,0	21,6	2,6
Dito	17.02.2005	91-6/05	A10	E. parvus	ad		no	18,5	10,3	0,6
Dito	17.02.2005		A4/5	E. guentheri	juv		no	10,8	6,9	0,3
Dito	18.02.2005	92-1/05	A7	E. parvus	ad		no	18,9	10,2	0,7
Dito	18.02.2005	92-2/05	A2	E. parvus	ad		no	24,5	13,2	1,4
Dito	18.02.2005	89-7/05	A2	E. parvus	ad		yes			
Dito	18.02.2005	66-17/04	A3/4	E. parvus	sub		yes			
Dito	18.02.2005	D134	A8	E. guentheri	ad	f	no	30,8	22,6	2,9
Dito	18.02.2005	92-6/05	A7	E. parvus	juv		no	11,0	5,8	0,1
Dito	18.02.2005	92-7/05	A7	E. parvus	ad		no	17,4	10,2	0,6
Dito	18.02.2005	92-8/05	A3	E. parvus	ad		no	16,9	9,2	0,6
Dito	18.02.2005	92-9/05	A6/7	E. parvus	juv		no	10,0	4,7	<0,1
Dito	18.02.2005	92-10/05	A6/7	E. parvus	juv		no	10,5	5,6	<0,1
Dito	18.02.2005	92-11/05	A4	E. parvus	juv		no	10,1	5,1	<0,1
Dito	18.02.2005	92-12/05	A10	E. parvus	ad		no	23,4	13,6	1,4
Dito	18.02.2005	92-13/05	A4/5	E. parvus	juv		no	10,1	5,4	<0,1
Dito	18.02.2005	92-14/05	A4/5	E. parvus	juv		no	10,6	5,2	<0,1
Dito	18.02.2005	D130	C6	E. guentheri	ad		yes			
Dito	18.02.2005	D135	C8	E. guentheri	ad		no	27,6	20,2	1,7
Dito	18.02.2005	D101	C3/4	E. parvus	ad		yes			
Dito	18.02.2005	D136	C0/1	E. guentheri	ad		no	21,1	16,9	1,0
Dito	18.02.2005	93-9/05	B1/2	E. parvus	ad?		no	18,0	9,9	0,7
Carmo	28.02.2005	CM82	B2	E. guentheri	ad	f	yes			
Carmo	28.02.2005	CM169	B2	E. guentheri	ad	m?	no	23,0	16,9	0,9
Carmo	28.02.2005	CM170	A8	E. guentheri	ad	m?	no	21,6	15,1	0,9
Carmo	28.02.2005		A4	E. guentheri	juv		no	11,0	6,2	0,1
Carmo	28.02.2005		C3	Eleutherodactylus sp.	juv		no	9,3	4,7	<0,1
Carmo	28.02.2005		A11	Eleutherodactylus sp.	ad		no	14,3	8,2	0,3
Carmo	01.03.2005	CM172	C10	E. guentheri	ad		no	23,0	15,6	0,9
Carmo	01.03.2005		A7/8	E. guentheri	juv		no	11,8	7,5	0,1
Carmo	02.03.2005	CM173	B3	E. guentheri	ad		no	21,8	15,8	1,0
Carmo	02.03.2005	CM174	C8	E. guentheri	ad		no	23,7	16,2	1,2
Carmo	02.03.2005		C7	E. guentheri	juv		no	10,0	5,0	<0,1
Carmo	02.03.2005		B2	E. guentheri	juv		no	6,8	3,9	<0,1
Carmo	02.03.2005	CM175	C9	E. guentheri	ad	f	no	26,7	20,1	1,8
Carmo	05.04.2005	CM185	B9	E. guentheri	ad		no	25,9	18,1	1,6
Carmo	05.04.2005	CM82	B2/3	E. guentheri	ad	f?	yes			
Carmo	05.04.2005		A7	E. guentheri	juv		no	15,0	9,7	0,2
Carmo	05.04.2005	CM102	A5	E. guentheri	ad	f?	yes			
Carmo	05.04.2005	CM106	A5	E. guentheri	ad		yes			
Carmo	05.04.2005		C3	Eleutherodactylus sp.	ad		no	21,3	10,5	0,7
Carmo	06.04.2005		A11	E. guentheri	juv		no	14,8	9,5	0,3
Carmo	06.04.2005		B11	E. guentheri	juv		no	12,1	6,7	0,1
Carmo	06.04.2005	CM186	A1	E. guentheri	ad		no	23,6	16,0	1,2
Carmo	06.04.2005	CM187	A4	E. guentheri	ad	f?	no	27,9	19,9	2,2
Carmo	06.04.2005	CM188	A6	E. guentheri	ad	m?	no	22,0	16,0	1,2

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Carmo	06.04.2005		B6	E. guentheri	juv		no	10,2	5,7	0,1
Carmo	06.04.2005		A5	E. guentheri	juv		no	13,1	8,1	0,2
Carmo	06.04.2005	CM106	A5	E. guentheri	ad		yes			
Carmo	06.04.2005		A5	E. guentheri	juv		no	14,9	8,8	0,2
Carmo	06.04.2005		B3	Eleutherodactylus sp.	juv		no	12,7	6,8	0,1
Carmo	07.04.2005	CM143	B2	E. guentheri	ad	f?	yes			
Carmo	07.04.2005	CM189	A2	E. guentheri	ad		no	28,9	21,2	1,9
Carmo	07.04.2005	CM188	A6	E. guentheri	ad	m?	yes			
Carmo	07.04.2005		B1	E. guentheri	juv		no	11,7	7,9	0,1
Carmo	03.03.2005	CM179	B5	E. guentheri	ad		no	19,9	14,6	0,7
Carmo	03.03.2005	CM150	A3	E. guentheri	ad		yes			
Carmo	03.03.2005	CM142	A8	E. guentheri	ad		yes			
Carmo	03.03.2005		A8	E. guentheri	juv		no	12,4	7,2	0,2
Carmo	03.03.2005		B7	E. guentheri	juv		no	9,5	5,2	<0,1
Carmo	04.03.2005	CM125	B7/8	E. guentheri	ad	f	yes			
Carmo	04.03.2005	CM180	B9/10	E. guentheri	ad		no	26,1	18,7	1,3
Carmo	04.03.2005	CM106	A6	E. guentheri	ad		yes			
Dito	07.03.2005	D140	C1	E. guentheri	ad	f	no	28,9	21,4	2,3
Dito	07.03.2005		C0	E. guentheri	juv		no	11,2	6,6	0,1
Dito	07.03.2005		C0	E. guentheri	juv		no	10,7	5,9	0,1
Dito	07.03.2005	101-5/05	C0	E. parvus	ad		no	23,3	12,7	1,2
Dito	07.03.2005	89-5/05	C0	E. parvus	ad		yes			
Dito	07.03.2005	62-4/04	C0	E. parvus	ad		yes			
Dito	07.03.2005	101-8/05	C3	E. parvus	juv		no	11,5	5,8	0,2
Dito	07.03.2005	90-5/05	B1/2	E. parvus	ad		yes			
Dito	07.03.2005	101-10/05	A5	E. parvus	ad		no	23,4	13,0	1,3
Dito	08.03.2005	D142	B0/1	E. guentheri	ad	m?	no	23,5	16,2	1,1
Dito	08.03.2005		C8/9	E. guentheri	sub		no	14,4	9,8	0,3
Dito	08.03.2005	D143	A8	E. guentheri	ad	f	no	34,0	23,0	3,3
Dito	08.03.2005	101-10/05	A5	E. parvus	ad		yes			
Dito	08.03.2005	66-22/04	A7	E. parvus	ad		yes			
Dito	08.03.2005	89-9/05	A2/3	E. parvus	ad		yes			
Dito	08.03.2005	62-4/04	C0	E. parvus	ad		yes			
Dito	08.03.2005	101-5/05	C0	E. parvus	ad		yes			
Dito	08.03.2005	89-5/05	C0	E. parvus	ad		yes			
Dito	08.03.2005	D144	C0	E. guentheri	ad	f	no	19,3	20,8	2,1
Dito	08.03.2005		C0	E. guentheri	juv		no	10,8	6,6	0,1
Dito	09.03.2005	D71	C1/2	E. guentheri	ad	f	yes	28,0	19,8	1,9
Dito	09.03.2005	D146	C9	E. guentheri	ad	f	no	31,6	22,3	3,0
Dito	09.03.2005	D147	C9	E. guentheri	ad	f	no	28,7	20,0	2,1
Dito	09.03.2005	D148	A6	E. guentheri	sub?		no	19,5	12,6	0,6
Dito	09.03.2005	D140	C1	E. guentheri	ad	f	yes			
Dito	09.03.2005	D123	C4/5	E. guentheri	ad	m?	yes			
Dito	09.03.2005	103-7/05	A5	E. parvus	juv		no	11,7	6,1	0,1
Dito	09.03.2005	24-12/04	A4/5	E. parvus	ad		yes			
Dito	09.03.2005	101-10/05	A5	E. parvus	ad	f?	yes			
Dito	09.03.2005	62-4/04	C0	E. parvus	ad	m?	yes			
Dito	09.03.2005		C0	E. guentheri	juv		no	15,0	9,8	0,3
Dito	10.03.2005		C0	E. guentheri	juv		no	11,6	6,5	0,1
Dito	10.03.2005		A2	E. guentheri	juv		no	13,3	9,0	0,2
Dito	10.03.2005	D115	C1-2	E. guentheri	ad	m?	yes			
Dito	10.03.2005	89-9/05	A3	E. parvus	ad		yes			

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Dito	10.03.2005	104-5/05	A4	E. parvus	ad	f?	no	23,1	12,5	1,2
Dito	10.03.2005	104-6/05	B4-5	E. parvus	juv		no	12,1	6,5	0,2
Dito	10.03.2005	104-7/05	B2-3	E. parvus	ad		no	22,2	12,9	0,9
Dito	10.03.2005	24-12/04	A4/5	E. parvus	ad	m?	yes			
Dito	10.03.2005	104-9/05	A5	E. parvus	juv		no	12,1	6,0	0,1
Dito	10.03.2005	46-8/04	C0	E. parvus	ad	f?	yes	23,0	12,2	0,9
Dito	10.03.2005		C0	E. guentheri	juv		no	11,7	7,0	0,1
Dito	10.03.2005	82-3/05	B3	E. parvus	ad	m?	yes	17,5	10,1	0,6
Dito	11.03.2005	D151	C9	E. guentheri	ad	f	no	29,9	22,0	2,1
Dito	11.03.2005	D152	C9	E. guentheri	ad	f	no	30,2	21,6	2,7
Dito	11.03.2005	D148	A6	E. guentheri	ad	m?	yes			
Dito	11.03.2005	D123	C4/5	E. guentheri	ad	m?	yes			
Dito	11.03.2005		B1	E. guentheri	juv		no	9,4	5,4	0,1
Dito	11.03.2005		C0	E. guentheri	juv		no	13,7	8,6	0,2
Dito	11.03.2005		B1	E. guentheri	juv		no	8,7	5,4	0,2
Dito	11.03.2005	105-8/05	A2	E. parvus	ad		no	22,6	13,4	0,1
Dito	11.03.2005	105-9/05	B5	E. parvus	ad	m?	no	18,8	9,7	0,6
Dito	11.03.2005	D101	A2/3	E. parvus	ad	f?	yes			
Dito	11.03.2005	105-11/05	B3	E. parvus	juv		no	13,2	7,5	0,2
Alcides	15.03.2005	A67	A4/5	E. guentheri	ad	f?	no	29,7	22,5	2,3
Alcides	15.03.2005		A7	E. guentheri	juv		no	8,4	4,3	0,1
Alcides	17.03.2005	A68	C2	E. guentheri	ad	f?	no	22,4	14,8	0,9
Alcides	17.03.2005		C3/4	E. guentheri	sub		no	-	-	-
Carmo	04.04.2005		A4	E. guentheri	juv		no	13,2	8,4	0,2
Carmo	04.04.2005	CM181	A7	E. guentheri	ad		no	28,8	19,1	1,9
Carmo	04.04.2005		B5	E. guentheri	juv		no	12,0	7,3	0,1
Carmo	04.04.2005	CM105	A4	E. guentheri	ad		yes			
Carmo	04.04.2005	CM104	B6	E. guentheri	ad		yes			
Carmo	04.04.2005	CM106	A5	E. guentheri	ad		yes			
Carmo	04.04.2005		A5	E. guentheri	juv		no	13,5	9,5	0,3
Carmo	04.04.2005		C3	E. parvus	juv		no	14,2	6,8	0,2
Carmo	04.04.2005		A8	E. parvus	juv		no	12,0	6,3	0,2
Carmo	04.04.2005		A2	E. parvus	ad		no	20,5	11,2	0,7
Carmo	05.04.2005	CM183	B5/6	E. guentheri	ad	f?	no	31,3	20,9	2,5
Carmo	05.04.2005		C11	E. guentheri	juv		no	12,5	7,2	0,1
Carmo	05.04.2005	CM184	B10/11	E. guentheri	ad	f?	no	29,3	20,4	2,2
Carmo	10.03.2004	CM83	B3	C. ornatus	ad?		no	28,1	13,4	2,0
Carmo	10.03.2004	CM28	B3	C. ornatus	ad?		yes			
Carmo	10.03.2004	CM73	C4	C. ornatus	ad?		yes			
Carmo	10.03.2004	CM86	C5	C. ornatus	juv		no	28,6	13,0	1,0
Carmo	10.03.2004	CM87	C7/8	C. ornatus	juv		no	28,3	12,1	1,5
Carmo	10.03.2004	CM88	C9/10	C. ornatus	ad?		no	36,0	16,0	2,5
Carmo	11.03.2004	CM89	C1/2	C. ornatus	ad?		no	33,2	15,5	2,4
Carmo	11.03.2004	CM71	A5	C. ornatus	ad?		yes			
Carmo	11.03.2004	CM91	C9	C. ornatus	ad?		no	29,1	14,5	2,9
Carmo	11.03.2004	CM92	C9	C. ornatus	ad?		no	28,8	13,1	1,5
MorroC	25.10.2004	MC17	A1	C. ornatus	ad		no	51,4	26,0	8,3
MorroC	25.10.2004	MC15	A1	C. ornatus	ad?		no	38,9	17,7	4,2
Carmo	09.11.2004	CM107	B4/5	C. ornatus	ad?		no	35,5	15,4	2,9
Carmo	15.01.2004	CM45	B2/3	C. ornatus	sub?		no	32,0	15,0	2,6
Carmo	15.01.2004	CM46	B8/9	C. ornatus	ad?	m?	no	53,4	24,8	11,0
Carmo	15.01.2004	CM48	C8	C. ornatus	juv		no	28,5	13,2	1,5

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Carmo	15.01.2004	CM51	B5	C. ornatus	juv		no	35,0	15,1	2,9
Carmo	15.01.2004	CM54	A2	C. ornatus	juv		no	24,7	12,4	1,4
Carmo	16.01.2004	CM60	A5/6	C. ornatus	ad		no	50,0	23,7	11,5
Carmo	16.01.2004	CM61	A5/6	C. ornatus	juv		no	25,4	11,5	1,2
Alcides	19.01.2004	A1	C2	C. ornatus	juv		no	27,1	11,0	1,2
Alcides	19.01.2004	A6	A4	C. ornatus	juv		no	24,7	11,0	1,0
Alcides	20.01.2004	A9	B7	C. ornatus	ad		no	53,6	25,3	11,1
Alcides	21.01.2004	A15	C2	C. ornatus	ad	m?	no	48,0	21,8	7,7
Alcides	21.01.2004	A20	A8	C. ornatus	ad		no	64,6	30,4	17,9
Alcides	21.01.2004	A26	C5	C. ornatus	ad	m	no	59,0	26,4	15,5
Alcides	23.01.2004	A30	B1	C. ornatus	juv		no	25,1	11,2	1,2
Alcides	23.01.2004	A6	A5	C. ornatus	juv		yes			
Alcides	23.01.2004	A26	C5	C. ornatus	ad	m	yes			
Alcides	23.01.2004	A31	A5/6	C. ornatus	ad	m	no	53,7	26,8	13,8
Dito	25.01.2004	D3	A2	C. ornatus	ad	m	no	56,6	27,6	14,4
Carmo	15.11.2004	CM108	C4	C. ornatus	ad?	m?	no	34,1	16,3	3,4
Carmo	15.11.2004	CM20	C8	C. ornatus	ad	m?	yes			
Carmo	16.11.2004	CM119	A5/6	C. ornatus	ad		no	38,5	17,7	4,8
Carmo	17.11.2004	CM119	A5/6	C. ornatus	ad		yes			
Carmo	17.11.2004	CM127	A1/2	C. ornatus	ad		no	37,0	16,8	4,0
Carmo	17.11.2004	CM134	B7	C. ornatus	ad		no	34,9	16,7	3,2
Dito	26.11.2004	D102	A8	C. ornatus	juv		no	25,1	11,8	1,1
Alcides	28.11.2004	A49	B2	C. ornatus	juv		no	18,9	8,0	0,6
Alcides	02.12.2004	A56	A4	C. ornatus	juv		no	21,7	9,8	0,7
Alcides	02.12.2004	A57	A5	C. ornatus	juv		no	18,1	7,1	0,6
MorroC	14.12.2004	MC26	PFB2	C. ornatus	ad		no	54,9	27,3	13,0
MorroC	17.12.2004	MC27	PFB4	C. ornatus	ad	f	no	89,9	37,0	50,6
MorroC	12.01.2005	MC35	B6	C. ornatus	ad	f?	no	84,3	36,0	48,8
MorroC	12.01.2005	MC26	PFE1	C. ornatus	ad	m?	yes			
MorroC	12.01.2005	MC36	B9	C. ornatus	ad	m?	no	69,1	30,9	22,8
Carmo	17.01.2005	CM147	B8	C. ornatus	juv		no	23,3	10,5	0,9
Carmo	17.01.2005	CM148	C9	C. ornatus	sub		no	35,6	17,4	3,1
Carmo	18.01.2005	CM151	B2	C. ornatus	juv		no	25,0	10,3	0,8
Carmo	19.01.2005	CM156	B5	C. ornatus	juv		no	26,8	12,6	1,5
Carmo	19.01.2005	CM157	C7	C. ornatus	ad		no	47,7	21,0	7,4
Morro C	05.11.2003	MC1	C3	C. ornatus	ad	f	no	70,7	35,0	27,1
Carmo	13.01.2004	CM5	C5	C. ornatus			no	33,7	16,2	2,8
Carmo	12.01.2004	CM6	B6	C. ornatus		m?	no	56,6	26,0	12,9
Carmo	12.01.2004	CM8	C3	C. ornatus			no	28,9	12,4	1,5
Carmo	12.01.2004	CM9	C3	C. ornatus			no	29,3	13,7	2,1
Carmo	13.01.2004	CM13	B8/9	C. ornatus			no	34,0	15,9	3,0
Carmo	13.01.2004	CM21	C6	C. ornatus			no	44,3	21,4	6,8
Carmo	14.01.2004	CM25	A10	C. ornatus	juv		no	27,0	11,6	1,1
Carmo	14.01.2004	CM26	A6	C. ornatus	juv		no	24,8	11,2	1,0
Carmo	14.01.2004	CM27	A6	C. ornatus	juv		no	25,0	10,7	1,0
Carmo	14.01.2004	CM28	B6	C. ornatus			no	34,1	16,8	3,2
Carmo	14.01.2004	CM29	B8	C. ornatus	ad?		no	42,3	19,5	4,5
Carmo	14.01.2004	CM30	B8	C. ornatus	sub?		no	33,6	17,4	2,3
Carmo	14.01.2004	CM33	C8	C. ornatus			no	34,2	14,9	2,5
Carmo	14.01.2004	CM34	B5	C. ornatus	juv?		no	27,5	12,5	1,5
Carmo	14.01.2004	CM35	B8	C. ornatus	juv?		no	27,8	13,0	1,5
Carmo	14.01.2004	CM36	C7	C. ornatus			no	33,7	15,5	2,8

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Carmo	15.01.2004	CM37	B5	C. ornatus	juv		no	26,8	12,0	1,4
Carmo	15.01.2004	CM42	B9	C. ornatus	ad	m	no	58,6	28,2	16,4
Carmo	15.01.2004	CM43	B9	C. ornatus	juv		no	36,6	16,8	3,3
Dito	25.01.2004	D8	A3/4	C. ornatus	ad		no	54,5	26,2	14,5
Dito	25.01.2004	D7	C3	C. ornatus	ad	m	no	55,1	26,6	16,2
Dito	25.01.2004	D11	A2	C. ornatus	ad		no	71,2	31,6	28,6
Dito	27.01.2004	D7	B0/1	C. ornatus	ad		yes			
Dito	27.01.2004	D3	A2	C. ornatus	ad		yes			
Dito	28.01.2004	D25	A5	C. ornatus	juv		no	30,0	14,5	1,3
Dito	28.01.2004	D27	C9	C. ornatus	juv		no	26,7	11,7	1,5
Dito	29.01.2004	D8	A3/4	C. ornatus	ad		yes			
Dito	29.01.2004	D33	D9	C. ornatus	juv		no	30,0	14,4	?
Carmo	08.03.2004	CM76	A2	C. ornatus	ad?		no	39,6	18,9	4,5
Carmo	08.03.2004	CM69	A6/7	C. ornatus	juv		no	31,9	13,0	2,5
Carmo	08.03.2004	CM70	C2	C. ornatus	ad?		no	38,1	17,4	4,0
Carmo	08.03.2004	CM71	A5	C. ornatus	juv		no	30,2	13,8	2,0
Carmo	09.03.2004	CM72	B6	C. ornatus	ad?		no	36,9	17,3	4,0
Carmo	09.03.2004	CM70	C4	C. ornatus	ad?		yes			
Carmo	09.03.2004	CM73	A7/8	C. ornatus	ad?		no	36,9	17,5	3,5
Carmo	09.03.2004	CM74	A10	C. ornatus	ad?		no	34,9	15,5	3,0
Carmo	10.03.2004	CM75	A8	C. ornatus	juv		no	28,7	12,5	1,5
Carmo	10.03.2004	CM77	A5	C. ornatus	ad?		no	36,5	16,7	4,0
Carmo	10.03.2004	CM78	A10	C. ornatus	ad?		no	41,3	18,7	3,5
Carmo	10.03.2004	CM79	A2/3	C. ornatus	ad?		no	31,0	14,8	2,5
Carmo	10.03.2004	CM80	A6	C. ornatus	ad?		no	34,3	15,2	3,5
Carmo	10.03.2004	CM69	A6	C. ornatus	ad?		yes			
Carmo	20.01.2005	CM160	C9	C. ornatus	sub		no	40,5	18,7	4,6
Carmo	20.01.2005	CM161	C9	C. ornatus	juv		no	31,0	14,1	2,1
Carmo	20.01.2005	CM162	C4	C. ornatus	juv		no	26,6	12,5	1,5
Carmo	20.01.2005	CM163	C6	C. ornatus	juv		no	32,2	15,8	2,7
Carmo	20.01.2005	CM164	C2	C. ornatus	juv		no	27,4	12,7	1,7
Carmo	20.01.2005	CM165	C10	C. ornatus	juv		no	35,3	16,9	3,2
Carmo	20.01.2005	CM166	C1/2	C. ornatus	juv		no	27,0	12,6	1,4
Carmo	20.01.2005	CM167	B10	C. ornatus	sub		no	38,0	18,0	4,3
Carmo	20.01.2005	CM168	B10/11	C. ornatus	juv		no	33,5	14,5	2,3
Carmo	21.01.2005	CM166	B1	C. ornatus	juv		no	27,9	12,0	1,3
Carmo	21.01.2005	CM167	C6	C. ornatus	ad	f?	no	55,1	25,8	13,5
Carmo	21.01.2005	CM168	B8	C. ornatus	juv		no	30,0	14,0	2,0
Dito	24.01.2005	D118	B2	C. ornatus	sub		no	41,4	20,0	5,9
Dito	24.01.2005	D102	A7/8	C. ornatus	ad		yes			
Dito	24.01.2005	D119	C9	C. ornatus	juv		no	27,9	11,9	1,6
Dito	24.01.2005	D120	B4	C. ornatus	juv		no	30,8	12,6	1,7
Alcides	31.01.2005	A58	B7	C. ornatus	juv		no	22,7	10,5	0,8
Dito	15.02.2005	D127	C1/2	C. ornatus	sub?		no	29,8	13,5	2,0
Dito	17.02.2005	D132	C0	C. ornatus	juv		no	30,1	13,9	2,0
Dito	18.02.2005	D137	C0/1	C. ornatus	juv		no	24,8	11,0	1,2
Dito	18.02.2005	D138	A2/3	C. ornatus	sub		no	31,2	14,3	2,3
Dito	18.02.2005	D139	C7	C. ornatus	sub		no	45,0	16,2	2,9
MorroC	23.02.2005	MC38	PFE1	C. ornatus	juv		no	27,6	13,0	1,4
MorroC	24.02.2005	MC39	PFA5	C. ornatus	juv		no	33,1	15,5	2,7
Carmo	28.02.2005	CM171	C10	C. ornatus	sub		no	30,2	13,9	2,1
Carmo	01.03.2005	CM162	C4	C. ornatus	sub		yes			

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Carmo	02.03.2005	CM88	C8	C. ornatus	ad		yes			
Carmo	02.03.2005	CM176	C4/5	C. ornatus	juv		no	6,1	11,1	1,2
Carmo	02.03.2005	CM177	B6	C. ornatus	sub		no	31,7	13,2	1,8
Carmo	02.03.2005	CM178	C7	C. ornatus	ad	m	no	53,1	24,3	12,3
Dito	07.03.2005	D141	C0	C. ornatus	ad		no	43,5	20,9	5,7
Dito	08.03.2005	D145	C0	C. ornatus	sub		no	29,5	13,0	1,8
Dito	09.03.2005	D132	C0	C. ornatus	sub		yes			
Dito	09.03.2005	D100	A1/2	C. ornatus	sub		no	35,9	15,7	3,1
Dito	10.03.2005	D149	B3	C. ornatus	sub?		no	40,5	19,0	3,9
Dito	10.03.2005	D150	B6	C. ornatus	sub?		no	42,9	20,0	5,1
Alcides	15.03.2005	A67	A5	C. ornatus	sub		no	28,5	12,4	1,6
Carmo	04.04.2005	CM182	A2	C. ornatus	sub		no	35,6	16,2	3,1
Carmo	04.04.2005	CM80	A5	C. ornatus	ad		yes			
Carmo	07.04.2005	CM190	C2/3	C. ornatus	sub		no	29,1	13,0	1,6

Appendix II

Lebenslauf

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Familienstand
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Berufliche Tätigkeit

seit 01/2003	wissenschaftlicher Mitarbeiter am Helmholtzzentrum für Umweltforschung, Department Naturschutzforschung
01/2001 – 12/2002	Universität Halle, Institut für Zoologie – Stipendiat (Untersuchungen zur Höhenadaptation der Waldeidechse im Nationalpark Hochharz)
07/2000 – 10/2000	wissenschaftlicher Mitarbeiter am Helmholtzzentrum für Umweltforschung, Department Naturschutzforschung

Studium

10/1993 – 03/2000	Studium der Biologie, Martin-Luther-Universität Halle-Wittenberg

Schwerpunkte: Zoologie (Tierökologie, Herpetologie), Genetik, Geographie, Limnologie

Abschluss Diplom
Thema der Diplomarbeit: Ökologische Untersuchungen an einer isolierten Population der Mauereidechse, *Podarcis muralis* (Laurenti, 1768) bei Leipzig

Schule

09/1990 – 08/1993	Abitur am Sportgymnasium Halle
09/1981 – 08/1990	Grund- und Oberschule Kurt Arndt Halle

Leipzig, 17.12.2007

Henning Steinicke

Eidesstattliche Versicherung

Hiermit erkläre ich, Henning Steinicke, an Eides statt, dass die vorliegende Dissertation selbstständig und ohne fremde Hilfe verfasst wurde. Alle verwendeten Hilfsmittel und Quellen wurden als solche gekennzeichnet.

Leipzig, 17.12.2007

Henning Steinicke