Field and Laboratory Methods in Primatology

SECOND EDITION

Building on the success of the first edition and bringing together contributions from a range of experts in the field, the second edition of this guide to research on wild primates covers the latest advances in the field, including new information on field experiments and measuring behaviour. It provides essential information and advice on the technical and practical aspects of both field and laboratory methods, covering topics such as ethnoprimatology; remote sensing; GPS and radio-tracking; trapping and handling; dietary ecology; non-invasive genetics and endocrinology. This integrated approach opens up new opportunities to study the behavioural ecology of some of the most endangered primates and to collect information on previously studied populations.

Chapters include methodological techniques; instructions on collecting, processing and preserving samples/data for later analysis; ethical considerations; comparative costs and further reading, making this an invaluable tool for postgraduate students and researchers in primatology, behavioural ecology and zoology.

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A Practical Guide

SECOND EDITION

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To Ymke Warren, dedicated primatologist and conservation biologist, 1970–2010

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Foreword

It is a pleasure and a privilege to contribute to this second edition of *Field and Laboratory Methods in Primatology*. The first edition was published only eight years ago, in 2003, so it is a clear sign of success that a second edition should follow so rapidly in its wake. I know from personal experience that many primate field workers, particularly those embarking on their maiden study, found the first edition very useful. So this new, updated version will surely be very welcome. Those who appreciated the well-coordinated team effort in the first edition will be pleased to see that the line-up of chapters and authors has remained very much the same. The editors, Joanna Setchell and Deborah Curtis, have once again marshalled the contributions with a sure hand. The original twenty-one chapters have been retained, with minor shifts in authorship here and there. The only substantial change is the addition of a new chapter (Chapter 11) by Zuberbühler & Wittig on field experiments, in recognition of the growing importance of this approach. The editors note that a primary aim of this volume is 'to encourage fields of research that are currently under-exploited . . . and to address the (often neglected) broader cultural and legal implications of fieldwork'. It is important here that the editors therefore hope not only to provide a basic practical guide to methods but also to influence the future course of research. Whereas the first edition was undeniably very successful as a guidebook for researchers, it is less clear whether it has had a significant impact on overall strategy. In my view, after only eight years it is too early to know; but I believe that in the future we will look back and see this book as a crucial milestone in the development of primate field research.

Findings from field studies of primate behaviour and ecology have not only made many significant contributions to primatology as such but have also fed into discussions of human evolution. In an

entirely different direction, they have also become increasingly important for conservation biology. Primates typically inhabit tropical or subtropical forests, and their relatively high profile makes them prominent indicator species for the frighteningly rapid process of deforestation that is a mounting problem for conservation generally. Reliable data on primate behaviour and ecology raise awareness and constitute one of the tools used in modern biology as increasing resources are devoted to the battle against extinction. Encouragingly, over the eight years that have elapsed since the first edition was published, primate field workers have devoted increasing time and energy to conservation issues.

Field studies have progressively expanded to cover the entire order Primates at varying depths, yielding an impressive array of data. Yet, despite this veritable explosion in primate field studies, relatively little attention has been devoted to synthetic treatments of methods. An early guide produced by the Subcommittee on Conservation of Natural Populations in Washington (1981), which focussed on ecological aspects, became unavailable long ago. Apart from that, prior to publication of the first edition of *Field and Laboratory Methods in Primatology*, there was no single published source for even a basic set of methods required for primate field studies. That practical guide to field methods and certain allied laboratory procedures, including contributions from many key players, was therefore sorely needed and warmly welcomed. Primate field workers have since had a single source providing invaluable practical guidance. It is of, course, becoming increasingly easy to track down basic documentation through the internet. This was already obvious in 2003 from the numerous websites cited in individual chapters of the first edition, and dramatic improvements have taken place over the past eight years. But carefully distilled advice for primate fieldworkers remains an extremely valuable commodity found only in *Field and Laboratory Methods in Primatology*.

Primate field studies have made remarkable progress over the past 75 years since anecdotal accounts first gave way to systematic data collection. The initial transition to objective reporting was marked by Carpenter's classic field study of the behaviour and social relations of howler monkeys (1934). This was followed by a series of detailed field studies of the natural behaviour of individual primate species, focussing on Old World monkeys living in relatively open habitats (e.g., baboons, patas monkeys, vervets) and our closest relatives, the apes (notably chimpanzees). For many years, a binoculars-and-notebook

approach prevailed, but the emphasis was very much on careful compilation of detailed behavioural observations over extended periods.

Some 30 years passed before another major transition, spurred by innovative field studies of birds, was marked by the seminal publication of Crook and Gartlan (1966). These authors were the first to generate a basic but comprehensive classification of primate social systems and to examine possible evolutionary developments in relation to ecological factors. This quickly led on to the key concept of primate socioecology and instigated a new wave of primate field studies in which quantitative data were systematically collected for both behaviour and selected ecological variables (notably those connected with diet). Eisenberg *et al.* (1972) further consolidated the basic aim of generating an overall comparative framework for primate field studies.

At this stage, it was recognized that reliable methods for collecting unbiased quantitative data are crucially important. Careful attention to objective, well-defined methods to guarantee collection of reliable quantitative data was undoubtedly a key development in the history of primate field studies. Altmann's fundamental (1974) publication on behavioural sampling surely played a pivotal rôle in transforming the approach taken to data collection in the field. Martin and Bateson (1986) later provided an influential guide to methods of behavioural observation for use both in the field and in captivity. Although now taken almost for granted, the shift towards focal animal sampling as the method of choice – because it is explicitly designed to exclude observational bias – was one of the most prominent features of primate field studies after 1974. In parallel, it was also realized that careful quantification of ecological variables is essential. This, in turn, led to the clear realization that a field study of any chosen primate species should cover at least one annual cycle in order to encompass seasonal variation. Indeed, because year-to-year differences can be marked, primate field studies should ideally cover a period of several years for proper assessment of the rôle of ecological factors. Long-term field studies of individual primate species are in any case especially valuable, as evolutionary arguments depend on reproductive success, which is optimally measured over an individual's entire lifetime. Because primates are relatively long-lived mammals, the ideal requirements for long-term study are very difficult to meet. But an increasing number of primate field studies are beginning to meet that very exacting standard, and it is encouraging to see that further progress has been made in this respect over the past eight years.

It did not take long before quantitative data from several detailed, long-term studies of primate behaviour and ecology were brought together in an influential book edited by Clutton-Brock (1977). This book, in addition to presenting overviews from individual field studies, provided results from overall comparative analyses of data on group size and composition, ranging behaviour and diet. These comparisons revealed several general quantitative principles of primate ecology and social organization (see also Clutton-Brock & Harvey, 1977; Martin, 1981). A decade later, the process of synthesizing quantitative data from a wide range of primate field studies was further advanced by another edited volume (Smuts *et al.*, 1987). More recently, a synthetic work produced by Sussman (1999; 2000) systematically presented information from a very wide spectrum of field studies. This was followed in 2007 by a 44-chapter book described as the first edited volume to offer a comprehensive overview of primatology since 1987 (Campbell *et al.*, 2007). The value of that volume as a reference work is underlined by the fact that a second, revised and expanded, edition has just been published (Campbell *et al.*, 2011).

In an accompanying development, primate field studies were progressively transformed from basic fact-finding exercises to problem-oriented investigations. This was directly reflected in the title of another edited volume (Sussman, 1979) that was published soon after Clutton-Brock's 1977 compendium. Sussman's volume marked a significant shift towards primate field studies specifically designed to investigate particular issues that were seen to be of theoretical importance, such as intraspecific variation in behaviour between study sites or distinctions between sympatric species. A number of single-author synthetic treatises have also been produced over the years, notably by Jolly (1985; the second edition of a book originally published in 1972), Fedigan (1982), Richard (1985) and Dunbar (1988).

For various reasons, coverage of primate species both in field studies and in synthetic works has generally been conspicuously uneven. For many years, there was a heavy emphasis on higher primates, predominantly on Old World monkeys and apes. At first, studies concentrated on species that either inhabit open habitats (particularly savannah-living Old World cercopithecine monkeys) or are relatively closely related to humans (i.e. apes). Thereafter, increasing attempts were made to include a number of New World monkeys, which are all exclusively forest-living. Carpenter's classic study of howler monkeys in Panama (1934) was, in fact, notable not only for its pioneering rôle but also because it exceptionally involved a forest-living New World

monkey species. Despite the fact that they account for a quarter of extant primate species and markedly extend the adaptive and temporal range of primates, prosimians (lemurs, lorises and tarsiers) were largely neglected for some time. The few prosimian species selected for initial detailed studies were monkey-like in being relatively large-bodied and diurnal in habits. One practical reason for this is that most prosimians are small-bodied, nocturnal and forest-living and therefore relatively difficult to study. However, there was also a measure of deliberate neglect because of the myopic view that prosimians are of marginal importance. In fact, studies of prosimians yield a far richer foundation for comparative studies.

In the 1970s, an important insight emerged from the first detailed studies of nocturnal prosimian species: these 'solitary' primates actually have well-developed social networks involving occasional encounters between individuals at night and nest sharing by day (Charles-Dominique, 1977; Bearder & Martin, 1980; Bearder, 1987). Prosimians show certain special features that are completely lacking among higher primates, particularly with respect to activity pattern. As noted by Erkert in his chapter on chronobiology (Chapter 18), most primates are either clearly diurnal (active from dawn to dusk) or clearly nocturnal (active from dusk to dawn). Most prosimians are nocturnal. Simian primates (monkeys and apes) are typically diurnal; owl monkeys (*Aotus*) provide the only exception. Thus, study of adaptations for nocturnal life among primates is necessarily largely confined to prosimians. Moreover, some prosimians (*Eulemur* and *Hapalemur*) show a highly unusual pattern of activity, including both diurnal and nocturnal phases. In a relatively late development, this distinct activity pattern was clearly recognized and defined as cathemerality (Tattersall, 1988). Field studies have only recently begun to reveal the significance of cathemeral behaviour (Curtis & Rasmussen, 2006). Studies of nocturnal prosimians also led to certain methodological innovations, most notably radio-tracking, which is still far more commonly used for nocturnal than for diurnal primates. One welcome development has been partial eradication of the previous general neglect of prosimians in primate field studies. It is noteworthy for instance, that the first volume of Sussman's synthetic survey (1999) was devoted almost entirely to prosimian primates. This reflects both increased awareness and marked growth in studies devoted to prosimians in recent years. It is particularly pleasing to see a dramatic improvement in our understanding of nocturnal tarsiers, most notably through the studies conducted by Gursky (2007).

A further extension to problem-oriented primate field studies arose through explicit attention to sociobiological hypotheses. Various core concepts of sociobiology, most notably kin selection, inclusive fitness, reciprocal altruism and sexual selection, are clearly of direct relevance to primate behaviour. It is therefore understandable that field studies have increasingly been designed to test sociobiological hypotheses. However, it should be noted that it is exceedingly difficult to collect adequate data for convincing tests of sociobiological interpretations from long-lived, slow-breeding animals such as primates. Only a few primate studies have been continued long enough to yield data on lifetime reproductive success, which are ideally required to test many arguments about selective advantage of individual behaviour patterns.

Lest it be thought that the development of primate field studies has followed a simple linear trajectory of unmitigated progress, it should also be emphasized that some important aspects have to some extent fallen by the wayside. One prominent example is provided by studies designed to explore proximate causation, which typically require some form of field experimentation. Although this is a very promising approach, it has been relatively little used (Kummer, 2002). A number of excellent studies have illustrated the particular value of field playback experiments employing natural vocalizations and manipulating them in various ways (see, for example, Cheney & Seyfarth, 2007; Semple, 1998; Semple *et al.*, 2002). But the experimental approach remains relative rare in primate field studies. So the addition of a new chapter specifically dealing with field experiments in this second edition of *Field and Laboratory Methods of Primatology* is a well-chosen improvement. Effective experiments require very careful design, so the guidelines provided are extremely useful. As various studies have shown, experiments with primates under natural conditions provide unique opportunities for probing the primate mind.

The most recent methodological milestone in primate field studies, still ongoing, has arisen through the availability of various relatively new techniques. Some of these new techniques are technological in nature (e.g. coupling of radio-tracking with automatic activity recording, Chapters 10, 18; GPS, GIS and remote sensing, Chapter 4); others are attributable to a combination of new methods with non-invasive collection of samples (e.g. hormone assays, Chapter 20; genetic typing, Chapter 21). In particular, a tripartite combination of field observations with hormone assays and genetic testing (essential for reliable inference of paternity) has opened up new possibilities for

testing long-established notions regarding the relationship between social behaviour and reproduction. Excellent examples of combined approaches are provided by studies of female cycles, mating behaviour and paternity in free-living Hanuman langurs and Barbary macaques (Heistermann *et al.*, 2001; Brauch *et al.*, 2008).

Despite the wide array of available methods reviewed in the first edition of *Field and Laboratory Methods in Primatology*, helpfully updated in this revised version, there is still considerable scope for greater integration into new studies. It is, for instance, regrettable that detailed investigation of food items has not moved ahead faster and on a broader front. As Lucas and colleagues note in Chapter 13, threats to wild primate populations mean that many opportunities to collect valuable data may be missed for ever. Numerous possibilities for studying the physical and chemical properties of food items are effectively reviewed in Chapters 13 and 14 and deserve to be applied more widely. In my view, the best way to develop a feel for these topics is to read the excellent book that Lucas published in 2004, after the first edition of the present volume appeared. (For some reason, Lucas was too modest to cite his own book in either of the two chapters on which he is lead author.) There are also many opportunities for new research in the realm of primate vocalizations, notably in the ultrasonic range. As Geissmann and Parsons note in Chapter 16, there have been rapid advances with respect to suitable equipment. Indeed, things have moved so fast that some state-of-the-art equipment recommended in 2003 is no longer manufactured. Last but not least, it would surely be rewarding for field primatologists to make greater use of techniques such as GPS, GIS and remote sensing. My own dream is that one day it might be possible to sit in my office in Chicago and enjoy real-time monitoring of primate behaviour and ecology, with data streaming back through satellite links.

Primate field studies have become increasingly complex because of the high standards now set for objective, bias-free data collection and the steadily growing spectrum of available ancillary techniques. The need for thorough advance preparation has hence become particularly acute. It is increasingly difficult for a single investigator to cope with the demands of a modern field study, so there is an increasing trend towards field studies involving teamwork. Extensive advance preparation has now become obligatory across the board, and the chapters in this book provide many useful indications to help in this. It cannot be emphasized enough that timely application for research approval and permits is a key part of any preparation. The basic design

of any study naturally requires very careful thought. As it is now also customary for a primate field study to address particular issues or hypotheses that have been identified in advance, there are fairly strict constraints on study design from the outset. Ways of achieving statistical independence in any data collected must be carefully considered. As several authors in this volume stress, advance preparation should also include training in relevant skills, expert advice and prior familiarization with particular techniques and equipment where appropriate. If animals are to be trapped, appropriate training before departure for the field is essential.

Increasing needs for careful advance planning of primate field studies are challenging because it is also important to maintain some degree of flexibility when dealing with unpredictable field conditions. The best-laid plans can be upset by unexpected circumstances and developments in the field. It is all very well to invest time and energy in advance preparation and training, but field studies also demand adaptability and the ability to respond with inspired improvization. For this and several other reasons, as Curtis *et al.* note in the introductory chapter, it is best to conduct a pilot study at the proposed field study site. A dry run prior to the main study is particularly necessary when there is no prior history of comparable fieldwork at that site.

This volume highlights an issue of central importance for any modern field study in clearly emphasizing ethical responsibilities and appropriate early decision-making by fieldworkers. Awareness of ethical aspects has progressively increased over the years, partly because of rapidly growing concern about conservation issues but also because of mounting sensitivity to animal welfare in a very general sense. In the first place, proper compliance with regulations for permissions and permits is mandatory for ethical, not just practical, reasons. Fieldworkers are 'ambassadors'. They have a duty to promote understanding for conservation and animal welfare by their actions both at home and abroad. Applications for CITES permits, in particular, may be time-consuming and occasionally vexatious (notably when the thorny topic of export/import of urine and faecal samples is involved), but it is imperative to show respect for international legislation that was introduced to control international trade in endangered species. Suitable prior training in certain techniques (e.g. handling of animals and taking blood samples) is also important in this context, as it can significantly enhance animal welfare.

Another key area that involves several ethical aspects is the decision whether or not to capture animals (see, for example,

Chapters 7, 8, 10 and 19). In this respect, too, fieldworkers serve as ambassadors. So it is essential that any capture programme should be properly authorized and conducted with evident concern for animal welfare. If the decision is made to capture animals as part of a field study, every effort should be made to maximize information that can be collected without prejudice to the subjects. While a captured animal is appropriately immobilized, it is possible to take standard measurements, check on health and reproductive condition and take various samples (e.g. dental casts, ectoparasites, plucked hairs, blood samples, X-rays; Chapters 7, 8 and 9). Indeed, the fieldworker is arguably bound by obligation to the scientific community to maximize collection of biological information from captured animals, provided that physical intervention and risk are minimized. One productive possibility that usually requires retention of animals in captivity is measurement of basal metabolic rate (BMR). As explained by Jutta Schmid (Chapter 19), BMR can be measured under field conditions using portable equipment. Here, a modified approach offers advantages regarding the level of disturbance imposed on study subjects (Genoud *et al.*, 1997). A nestbox with a built-in thermal jacket can be used as a metabolic chamber, and air can be sampled and assayed by drawing rather than pumping it through the box. This avoids the need for hermetic sealing of the metabolic chamber, with all the attendant complications. Ideally, any measurements should be conducted over a single rest period. Retention of an animal in captivity should always be kept to a strict minimum because it may disrupt social interactions.

One of the greatest benefits of capturing animals is undoubtedly the opportunity to apply various kinds of marking to facilitate recognition of individuals, provided that such marking is conducted with a proper concern for animal welfare (Chapter 10). In particular, radiotracking can be used, dramatically increasing the reliability of individual identification and the ease with which study animals can be located. This may facilitate the process of habituation if stress is minimized during capture. However, prominent questions of animal welfare arise in this context too: careful consideration must be given to the size and method of attachment of the transmitter package. Moreover, timely recapture must be reliably feasible in order to remove the package in due course. Removal of transmitter packages from all animals by the end of a field study is absolutely essential, but regrettably this is a topic that is still inadequately reported or discussed (Chapter 10).

Another crucial area is that of taxonomy (Chapter 9). All primate fieldworkers should give due attention to taxonomy in designing and

conducting their studies. Findings may contribute to the general database that feeds into continued refinement of primate taxonomy. In addition, correct identification of the taxon under study may directly affect the outcome. An example is provided by Richard's study of two sifaka populations in Madagascar (1974). At the time, those two populations were identified as subspecies of *Propithecus verreauxi* (*P. v. verreauxi* and *P. v. coquereli*). The field study was specifically designed to examine variability in behaviour and ecology within a single primate species. However, twenty-five years later analyses of mitochondrial DNA sequences revealed that these two populations in fact belong to two distinct clades of sifakas. The degree of genetic divergence between *verreauxi* and *coquereli* suggests a species-level divergence (Pastorini *et al*., 2001). Two separate species are now recognized in a widely used primate classification (Groves, 2005). Hence, a study explicitly designed to examine intraspecific variability has turned out to be an investigation of interspecific differences instead.

Ethical issues also arise with taxonomy. As Groves and Harding (Chapter 9) discuss, taxonomic aspects are fundamental to any fieldwork on primates. This is particularly true if any contribution is made to conservation measures, so investigators may be said to have an obligation to collect data and specimens that will help refine taxonomy. But this is precisely where a major ethical issue arises. Current museum-based taxonomic practice is explicitly based on a strategy of collecting reference specimens, and type specimens play a fundamental rôle in formal recognition of species and subspecies. The question that must now be posed is whether it is ethically justifiable to continue to collect primate specimens (other than incidental finds) from the field specifically to contribute to reference collections. This question is, of course, particularly acute where severely threatened populations are involved.

In fact, many investigators would simply rule out further collection of primate specimens for museum reference purposes, even for species that are still relatively common. This matter still needs proper debate among primatologists, indeed among zoologists generally, to establish generally acceptable guidelines. The fact of the matter is that formal recognition (including publication) of a new primate species or subspecies currently requires at least one reference specimen. In the absence of such a specimen, newly discovered primate taxa may remain in limbo. In principle, it should now be possible to design an acceptable reference base (e.g. combining photographs, measurements taken on the live animal, dental casts, field X-rays, plucked hairs and

genetic typing) that no longer requires collection and preparation of a cadaver. However, there is a pressing need for formal international agreement on some alternative system if we are to accept that collection of museum specimens is no longer mandatory for taxonomic recognition. As Groves and Harding state, the fourth edition of the *International Code of Zoological Nomenclature*, which took effect on 1 January 2000, specifies that a type specimen must be 'an animal, or any part of an animal'. Some progress has been made since the publication of the first edition of this book. DNA samples have been used as type specimens for a few primate species and even photographs have been accepted for this purpose. If it should prove possible to design an acceptable system to replace collection of classical reference specimens, the need for effective broad-based sampling from live animals in primate field studies would become even greater.

In closing, I want once again to emphasize the need to consider what happens when the investigator returns home after completing a long-term primate field study in a distant foreign country. Quite apart from its scientific benefits, a long period spent abroad for this purpose has a particular value as a stimulating (if often challenging) life experience that broadens the investigator's horizons and permits an external perspective on that investigator's own culture. However, it is not often realized that the investigator may suffer a fairly acute form of culture shock on returning home. This 're-entry syndrome' (a term coined by one of the respondents) was specifically reported by Hinde (1979) in a hard-to-obtain publication based on replies to a questionnaire that he distributed to gauge the overseas experiences of recent graduates and others. Completed questionnaires concerning the first field experience lasting 5–24 months were received from 65 people in four groups (30 primatologists, 7 social anthropologists, 5 modern linguists and 21 participants in Voluntary Service Overseas), most of whom replied to the questionnaire within two years after returning from the field.

Hinde's survey incidentally revealed some important basic points about primate field studies. Significantly, respondents generally emphasized the value of prior training in methods of data collection and of previous field experience, thus emphatically underlining the value of appropriate preparation and pilot work. In Hinde's words: 'Proper preparation is crucial. Problems must be formulated, data collection methods outlined and practised, and the fieldworker trained in the skills necessary for his project.' Prior language training was also identified as a valuable asset. Most of the primatologists were

very positive about their field experiences, although they reported that the first three months or so in the field tended to be quite problematic. It is noteworthy that half of the primatologists thought that they worked too hard because of self-imposed work schedules (which may account for 'Fieldworker's Procrastination Syndrome', recognized by Bearder and Nekaris in Chapter 22). Many of the primatologists and anthropologists thought that a break after three to six months would be a sensible measure. Academic isolation was a serious problem for many respondents, and a key factor was presence or absence of effective local support at the field study site. Hinde noted: 'It is desirable, but not usually possible, for research supervisors to visit research students in the field – if possible in the early phases of their study. If that is not possible, it is an asset to have a supervisor who knows the study area, and who keeps in as close touch as possible by correspondence.'

The most striking point to emerge from Hinde's survey (1979), however, was the high frequency with which respondents reported feeling some kind of disorientation or alienation after returning home. This was specifically mentioned by 23 primatologists (77%), by all of the anthropologists, by 3 modern linguists (60%) and by 13 VSO workers (62%). The 're-entry syndrome' thus identified involved culture shock in relation to 'civilized society' and the perception of its fast pace, difficulties with social interaction and difficulties in settling down to work (reported by half the primatologists). Clearly, re-adapting to the home culture after completion of a field study is also a serious issue that deserves attention as part of the experience of fieldwork. At the very least, recognition of the fact that this is a widespread phenomenon and hence a shared experience may make it easier for returning primatologists to cope with this additional challenge.

As a final note, I would like once again to make a personal tribute to all of the dedicated primate fieldworkers who have braved tough and demanding conditions – including 're-entry syndrome' – to build the truly impressive hoard of information that is now available. They have performed a major service to the academic community and are increasingly contributing in a major way to conservation biology. I pass on my very best wishes to the next generation of fieldworkers, who will surely be involved in studies of ever-increasing complexity, but who at least will have the revised version of this comprehensive methodological survey to guide them.

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