Present Directions and Future Prospects in Southern African Ornithology

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Birds are probably the best know class of animals. As a group, they are conspicuous, widespread and ecologically diverse, thereby rendering them amenable to investigation. The result is a wealth of basic information on their geographical distributions, habitat preferences, foods, breeding habits and life histories, much of which has been collected by skilled and enthusiastic amateur naturalists. These data in turn have provided the foundations for the very substantial contributions made by ornithologists to the development, testing and refinement of many fundamental concepts in the fields of population and community ecology, biogeography, behaviour, speciation and evolution.

Much basically descriptive information is available on the biology of Southern African birds. We now need syntheses and studies which will further the development of basic principles, particularly those relevant to the problem of conserving biotic diversity.

Ornithologists have also been at the forefront of the nature conservation movement. Birds, being aesthetically pleasing and conspicuous features of the environment, have attracted wide public interest and involvement in their welfare, and have been used to promote public awareness of environmental problems and the need for conservation. They have also proved to be relatively sensitive indicators of environmental change and deterioration: the insidious effects of chlorinated hydrocarbons, for example, being more immediately apparent in bird populations than in most other animal groups.[1] Additionally, ornithologists have been among the first to meet the challenge of formulating detailed conservation principles from apparently esoteric biological concepts: for example, the application of island biogeography theory to the design of nature reserves.[2]

These achievements mark ornithology as being a very vital and fertile field of human enquiry. Yet if ornithology is to remain as one of the leading biological sciences there must be an ongoing review of those problems and issues in biology to which the study of birds can make a significant contribution. In a Southern African context, the 21st anniversary of the Percy FitzPatrick Institute of African Ornithology provides an appropriate occasion on which to conduct such a review. Accordingly, I will briefly survey what I see as the current state of Southern African ornithology, focusing on some of the gaps and future research needs. The survey is not intended to be a complete review of all the available local ornithological literature but rather is aimed at identifying the main directions of current research and those areas where knowledge and understanding are lacking. Finally, since the Percy FitzPatrick Institute is one of the few ornithological institutes in the world, and the only one in the southern hemisphere. I will consider specifically the rôle that it can play in meeting these challenges.

Current state of ornithological knowledge

Southern Africa can count as being one of the ornithologically better known regions of the world, due largely to a history of scientific investigation dating back to the late 1600s. Most, if not all, of the species in the region have been described and classified, and the taxonomy is relatively stable. However, very few thorough systematic studies have been carried out (for examples, see refs 3 – 5), so that the systematic relationships among species and higher taxa are not necessarily well understood. Allied to this has been an almost complete lack of research into comparative anatomy:[6,7] studies of functional anatomy have been only marginally better served.[8-10] A knowledge of systematic relationships is of fundamental importance in zoogeographic studies and in providing some insight into the palaeoecological events which may have influenced speciation. In this regard, more attention needs to be given to the relatively large amounts of sub-fossil avian material that is available. Analyses of these remains would give some information on the former distribution of species, as well as some indication of the nature of past environmental change.[11,12]

Current research into systematics is focused mainly on the study of geographic variation in plumage coloration and morphology within species.[13,14] Most of this effort has been confined to the description and naming of subspecies, frequently on the basis of apparently arbitrarily-chosen characters. The general lack of statistical analyses, or any other basis for deciding which differences are in fact significant, makes it difficult to evaluate these studies objectively. Reference is often made to apparent correlations between the variation and particular environmental variables but these have seldom been quantified,[15] or the mechanisms determined. To the best of my knowledge, none of the studies have demonstrated that the variation in question is genetically determined rather than environmentally controlled during development. None the less, the designation of subspecies does provide a set of working hypotheses about the population structure of a species and future research needs to be directed towards testing these hypotheses.

Much more is known about the broad distribution patterns and general biology of individual species. Many breeding biology studies have been carried out, often supplemented with data on behaviour and diet (for examples, see refs 16 – 23). Of the 689 bird species breeding south of the Zambezi and Cunene rivers, only about 14% can be classed as unknown, in the sense that basic biological information is lacking on a number of aspects of their distribution, habitat requirements, food, behaviour and breeding. Most of these species are peripheral in their distribution. In contrast, five percent of the species can be considered to be very well known, having been the subjects of intensive investigation over a number of years, while a further 26% can be classed as being well known, in that we have considerably more than just the basic biological data on them. Seabirds, waterbirds (including ducks and geese) and birds-of-prey figure prominently among these species. For the remaining 55% of the species only basic biological data are available.

A relatively large number of regional and local bird books and checklists have been published, from which it is possible to obtain a broad picture of a species' distribution.[14,24-31] Bird distributions have been mapped on a quarter-degree square basis in Natal[32] and the Transvaal (MS housed at the Transvaal Museum, Pretoria). The distribu-

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tion of selected birds-of-prey has been similarly mapped in the Cape Province.[33] An atlas of coastal bird distribution is currently in preparation and a mapping scheme for the avifauna of the Orange Free State has been mooted. These atlasing schemes are supplemented by avifaunal lists for particular localities published in the now-defunct *South African Avifaunal Series* and its successor, *Southern Birds*. These studies provide an invaluable base from which future changes in the distribution of individual species can be monitored.

The ecological distribution of birds is known only in the very broadest terms.[34,35] Most of the studies have concentrated on describing the avifauna associated with particular vegetation types, often within a zoogeographical framework. While these studies have been useful in revealing the relationships of the Southern African avifauna with those of other regions in Africa, they do not explain why the avifaunal communities are structured as they are, or what determines why certain species are confined to particular vegetation types or zoogeographic regions. Correlations have been noted between bird distribution patterns and temperature,[36-39] but the causal mechanisms have not been demonstrated.

The avifaunal communities of particular habitats have been described in a number of studies (for examples, see refs 40–45). Generally, these have tended to be descriptive, simply listing the species that occur, together with their relative abundances. In some cases the component species have been classified on the basis of their food preferences but these preferences have seldom been quantified. A number of attempts have been made to correlate the number of co-occurring species with aspects of vegetation structure and floristic diversity.[46-48] For example, in the fynbos vegetation of the south-western Cape Province, the number of species at a site is closely correlated with simple indices of vegetation structure based on the principal components of vegetation height and half-height,[47] though floristic diversity also appears to be important (W. R. Siegfried, personal communication). Obviously, such correlations will be higher for some trophic groups than others, depending on the way particular resource categories vary with vegetation structure. Thus, for insectivorous birds, vegetation structure appears to be of primary importance in determining the numbers of co-existing species and individuals: taller vegetation contains a greater number of discrete sites at which insects can occur and on which foraging birds can specialize. Some studies have attempted to quantify the use of both vertical and horizontal components of vegetation structure by individual species.[49,50]

The above studies describe the effects of ecological interactions between species and with their resources. However, in order to understand community structure and organization, studies are needed of the population processes involved. The questions as to what determines the number of species that can coexist at a site, the mechanisms by which coexistence or exclusion is achieved, and the turnover of species between sites, have barely begun to be considered locally, though they have been central questions in much of the ecological research done elsewhere. Cody's study[47] of community structure in the fynbos is an exception, though even it goes only part of the way towards explaining the evolutionary and ecological determinants of diversity patterns. Rather than continue to focus on the community as a whole, it might be more profitable to concentrate on the question of how species' guilds* are structured and organized. This would encourage greater attention to be paid to the nature of the resources, the factors determining the degree of consumer specialization on them, and the mechanisms and outcomes of competitive interactions among guild members. A considerable amount of information is available on the diets of Southern African birds but most of it comes from casual and often limited observations.[51] Many of the feeding ecology studies that have been carried out have sought simply to describe the diets of particular species in detail, the results frequently being based on analyses of crop or stomach contents,[53-57] regurgitations of undigested material,[58-62] insect remains in faeces,[63] prey remains at nests or feeding sites,[64-66] or direct observations of feeding birds.[67] Seldom has the degree of bias in the particular method used been evaluated. Most of the studies have been done on seabirds, waterbirds and birds-of-prey, groups from which material can be readily obtained. In spite of these studies, we know very little about what determines diet breadth in any species, how it varies seasonally and geographically, and how it is affected by the presence or absence of competitors. Nor do we know how the feeding niche is partitioned within a species or whether different phenotypes exploit parts of it differentially.

In some studies, specific differences in diet, mean item size, foraging methods or preferred feeding areas have been interpreted as the means by which ecologically related species coexist. Implicit in this is the assumption that these patterns have evolved, and are maintained, by interspecific competition. However, competition is only one of the factors that may influence diet breadth. The array of potential food items, the energetic costs and benefits of exploiting individual items, and the behavioural processes involved in maximizing net energy gain through the appropriate choice of food, may also be important.

There have been a number of studies of feeding behaviour which focus on hunting methods, foraging-time budgets, foraging energetics and efficiency,[60,68-71] as well as on the influence of morphology and experience on diet composition.[55,72] More such studies are needed, particularly where they are linked to studies of the spatial distribution, quality, quantity, renewal rates and temporal patterns of availability of the resources being exploited. Allied to this is the need for studies on the interactions between consumers. Merely demonstrating differences in diet between ecologically similar species does not necessarily serve to indicate the existence of competition or the processes involved. At best, they reflect only the outcomes of such interactions.

Few studies have attempted to relate diet to the abundance and availability of prey[55,59,60] with the aim of understanding how this might constrain prey selection. A further aim in some instances has been to assess the impact of predation on the prey population. Such studies have been particularly prominent in fisheries research[52,59,60] but their short duration, general lack of information on the dynamics of the prey populations, difficulties inherent in measuring prey availability, as opposed to prey abundance, and the assumptions involved in estimating predator energy requirements, have tended to limit the success of these studies.

The positions of birds in the trophic webs of ecological systems, and the magnitude and patterns of energy and nutrient flow through the various populations, are fundamental to understanding the functional rôles of birds in these systems. A number of recent studies have begun to investigate these relationships in terrestrial, coastal and marine-island ecosystems.[73-76] Generally, birds appear to play a relatively minor rôle in the energy transfer of terrestrial ecosystems, this amounting to much less than 1% of estimated net primary production in a number of studies.[73] The consumption of energy by birds in coastal and marine ecosystems, as a proportion of net primary production, may be greater but precise figures are not yet available. In marine-island ecosystems birds seem to be particularly important in transfering minerals from the marine to the island ecosystems. On Marion Island, for example, birds are responsible for much of the nitrogen and phosphorus imported into the system.[77]

Although the energy and nutrient contributions of birds to most terrestrial ecosystems may be relatively small, birds can influence ecosystem structure and functioning in other ways. Some species are important predators of particular prey populations (for example, Black Eagles *Aquila verreauxi* prey almost exclusively on the

*guild: a group of ecologically related species which exploit a set of resources in similar ways.

hyraxes *Procavia capensis* and *Heterohyrax brucei*[22]), exerting both direct (through population reduction) and indirect (through influencing the behaviour of the prey population and localizing its activities in time and space) pressures. Some species are brood parasites of other birds,[18] though we currently understand very little of the consequences of this for the host populations. Smith's work in Panama[78] suggests that these might be exceedingly complex. A number of species play important rôles as scavengers, thereby influencing the rates of carcass reduction and possibly the patterns of disease transmission. Scavengers are especially prominent in Africa, with its abundant and diverse large-mammal fauna, and the interrelationships between these species is only now beginning to attract the attention that they deserve.[79] Many bird species associate with large mammals, in some cases forming symbiotic relationships with them.[80] Birds may also serve as pollinators and seed dispersers of both indigenous and alien plants,[71,81-83] thereby influencing plant success, population structure and distribution. However, we currently understand very little about the detailed ecological consequences of such interactions. Much of the current work is descriptive and is focused on the patterns at community level rather than on the processes at population level. The consequences of these interactions at community and ecosystem levels are potentially far-reaching and research designed to elucidate the mechanisms and quantify the effects of these interactions holds exciting prospects and many implications for the task of conserving such systems.

Fundamental to any study of population processes is the need to understand the dynamics of the study population and the factors influencing reproductive success and mortality. Data on clutch sizes, nesting and breeding success, number of breeding attempts per year, age-specific mortality rates, age at first breeding, average life expectancy and net reproductive rates are available for only a very few local species, including the Cattle Egret *Ardeola ibis*,[84,85] Laughing Dove *Streptopelia senegalensis*[86-88] and Cape Sparrow *Passer melanurus*.[89-91] Less complete data are available for a considerable number of other species but these data have not been synthesized in order to identify where the gaps in our knowledge are. This needs to be done so that the outstanding information can be collected and a general picture of the population dynamics of these species obtained. One caveat though is necessary. Much of the information has been collected from often widely scattered localities, at different times and for limited durations. The results therefore reflect only average values. It is very unlikely that in a region as climatically variable as Southern Africa the concept of average reproduction and mortality rates has much biological significance. It is much more likely that these population characteristics will vary through time, with periods of high reproduction and others of high mortality. We need to know therefore the extent to which these factors vary geographically and temporally, particularly in relation to yearly variations in climate and changing ecological conditions. In this respect, it will be necessary to encourage long-term studies designed to answer these and other questions.

Most of the information on longevity and mortality patterns comes from the recovery of marked individuals of known age. A bird ringing scheme has operated in Southern Africa since 1948 and a considerable amount of potentially useful information has been collected since then. Over 940 000 individuals of nearly 740 species have been ringed, of which about 14 000 have been recovered. Yet there have been relatively few analyses of these data. Some attempts have been made to construct life-tables and calculate average annual mortality rates for individual species.[84,87,89,91-95] Other studies have concentrated on describing the migration systems of transcontinental migrants[96-99] and the regional movements of local species.[100-103] Analyses of the data for other species are needed, if only to evaluate the potential worth of the data collected to date by the South African ringing operations.

An adjunct to bird ringing activities has been the study of feather moult and body mass fluctuations. Many moult studies have been published[98,104-111] and a synthesis of these would be useful. Most of the studies have simply described the timing and progression of moult but the factors influencing these patterns have usually been a matter for speculation. Moult in some African birds takes a considerable length of time[20,107,111] and may even overlap with the breeding schedule.[112] The significance of this is not clear but it may reflect the energetic and nutrient costs of feather replacement in relation to the availability of adequate food to meet these costs. No studies have been done locally on the measurement of these costs and the capacity of the birds to meet them, other than a brief study of body composition and energy metabolism of moulting eudyptid penguins on Marion Island.[113]

Fluctuations in body mass occur on a daily and seasonal basis, reflecting changes in energy intake, storage and expenditure in relation to environmental conditions, food availability and activities such as breeding, moulting and migration. Comprehensive analyses of mass changes in relation to these factors have not been done locally. Premigratory fattening in waders has been studied and the results used to predict flight ranges, and therefore migration routes, of these birds.[98,114] Pre-breeding increases in body mass have been reported for some species, including the Cape Cormorant *Phalacrocorax capensis*,[115] Black Duck *Anas sparsa*[116] and various *Euplectes* species,[117] indirectly indicating the energy cost of reproduction. Although the energy costs of incubation have been measured in a number of studies,[118-121] the energy costs associated with breeding as a whole have been estimated for only one species.[122] This study indicated an excess of energy expenditure over consumption, accompanied by a decline in body mass. Post-breeding troughs in body and pectoral muscle mass have been noted in some small songbirds.[123] None the less, considering the frequency with which body mass data are collected, it is surprising that there have not been more studies designed to investigate body mass changes in relation to fluctuations in resources and events in a species' annual cycle.

Ecophysiological research on birds in Southern Africa has focused largely on the maintenance of ionic balance[124-127] and the regulation of body temperature by birds inhabiting thermally extreme environments.[127-132] Other studies have focused on the interactions between parental behaviour, the eggs, nest and a fluctuating external environment, and how egg and nest temperatures are maintained within narrow limits.[118-121,131-134] These studies have all served to indicate the importance of behaviour in temperature regulation. However, we are only beginning to relate these costs and savings to a bird's total energy budget and to explore the implications of these for the use of resources in fluctuating and unpredictable environments.

Energy-demanding events such as breeding and moulting usually take place during the most favourable times of the year, being scheduled so that they do not overlap and impose excessive demands on a bird. This presumes a degree of environmental predictability. However, ecological conditions in Southern Africa appear to be a lot less predictable and, despite the wealth of information on the breeding seasons of birds in the region,[135-139] we do not fully understand the interplay of environmental factors that determine the timing of these events.[140] Ultimately, birds should breed at that time of the year when the probability of raising young to independence is greatest but this may be modified by the physiological state of the female and her ability to obtain food to produce eggs.[123,141] Thus there should be proximate cues that predict conditions suitable for breeding. Rainfall and the state of the vegetation are those most frequently noted[135,137,139] though there has been very little endocrinological research done locally to support this. One study, on Cape Cormorants,[115] has implicated changes in photoperiod. This, however, may have only an anticipatory function, with precise adjustments coming from more immediate indicators of future environmental conditions.

There have been many studies on the breeding biologies of individual species.[16-23,142-144] Most of these have been largely descriptive, focusing on the duration of various phases in the breeding cycle, the rôles and behaviour of the sexes, nesting and breeding success, and some of the factors that might influence these. Seabirds, waterbirds and birds-of-prey have received most attention. A number of papers have contributed to the debate on the causes and significance of sibling competition and related reductions in brood size,[143-148] but most of the studies have not been designed to answer specific questions. However, if we are to understand the interplay of environmental and genetic factors that influence a species' reproductive rate, we will need to know how particular demographic parameters (such as egg size, clutch size, and number of broods per year) vary in relation to environmental conditions, particularly in regions of unpredictable climate. A rich body of theory has been developed to account for the known patterns, derived mostly from studies done in northern temperate and wet tropical regions, and their relevance needs to be tested more widely.

We also need to know the patterns of nesting and breeding success, the timing and sources of mortality and how these vary in relation to habitat, nest site, brood size and time of year. Some information already exists in the literature, other potentially relevant data are available in the Southern African Ornithological Society's nest record card scheme. The quality of these data has not been checked, though a pilot study is underway. Nevertheless, sufficient data ought to be available with which to attempt some syntheses and thereby identify the gaps in our knowledge. It is worth re-emphasizing, however, that such analyses provide information on only average values for reproductive success. We need more studies that reflect the variations that exist between individuals, geographically and with time.

Reproductive rate is influenced also by the social organization and behaviour of a species through modifying an individual's access to resources such as food, mates and nest sites, and by involving the individual in additional energy expenditure on social interactions. A wide variety of mating and spacing systems has been recorded, some of which have been studied locally. These include studies of monogamous species which may be territorial (some waterfowl,[149] birds-of-prey,[22,150] and insectivorous passerines[151]), non-territorial (many ducks[152] and sandgrouse[153]) or colonial nesters (many seabirds[144] and herons[154]), as well as species that are polygynous (Ostrich *Struthio camelus*,[155] Comb Duck *Sarkidiornis melanotos*,[156] Maccoa Duck *Oxyura maccoa*,[157] and various *Euplectes* species[158]) and polyandrous (African Jacana *Actophilornis africana*[159]). In addition, there are a number of cooperatively breeding species in which individuals, who are related to varying degrees, cooperate in the rearing of the offspring of the breeding pair and, in some cases, in the defence of a group territory. Cooperative breeding has been recorded in at least 52 African bird species (30 of which occur in Southern Africa) and is suspected in a further 74.[160] The phenomenon appears to be most prevalent in savannas, which may be related to the varying productivity and strong seasonality of this environment. A few studies, mostly of limited duration, have been done locally,[155,161,162] though a number of species are being studied intensively elsewhere in Africa. We need to encourage similar detailed investigations here.

The ecological determinants of animal mating systems are relatively well understood. The key factors appear to be the spatial dispersion of critical resources, the temporal availability of potential mates, and the costs and benefits of gaining access to these. The various costs and benefits have seldom been determined completely, largely because of the difficulties of relating energy costs to fitness benefits. Since natural selection operates through an individual's lifetime genetic contribution to succeeding generations, studies of limited duration are not going to measure these costs and benefits successfully. We need to look at the functioning of social systems, and the performance of individuals in them, over numbers of years. Only then will the subtlety and complexity of the interactions between individuals competing for reproductive success be fully revealed.

Long-term studies are also needed if the nature of the advantages to cooperatively breeding individuals, and the ecological and social factors determining them, are to be understood. For most species, we are not yet able to answer convincingly questions on whether 'helpers' actually help and, if they do, then what the respective advantages and disadvantages are to the parents, helpers and offspring. In addition to the basic data on the reproductive output of groups in relation to group size, composition, age and experience of the group members, habitat quality and other factors, detailed information is also needed on the behaviour, dispersal, survival and reproduction of the individuals within these groups. Southern African ornithologists, having a large number of cooperatively breeding species from which to choose, could contribute significantly to advances in this rapidly developing field.

A knowledge of how social interactions are mediated is important to understanding the workings of a particular species' social system. Most of the local research on avian communication systems has been devoted to descriptions of display repertoires in various species, the structure of individual displays, the context in which they occur, and their apparent functions.[154,163-168] In some instances the presence and form of homologous displays in closely related species have been used to help clarify systematic relationships,[149,157,166] and to see how the species are behaviourally separated.[168] Only a few studies have considered the communication system in an ecological context: examining individuals' communication needs, how these are met, and how both social and environmental factors influence the form of the displays.[149,156,157] Other studies have sought to explain particular vocal displays and plumage patterns in terms of their rôles in interspecific communication,[169-171] the displays being interpreted as a means of manipulating the behaviour of other species. We know very little about the same phenomenon in the context of intraspecific communication.

Implicit in a number of studies of the communication systems of closely related species is the assumption that specifically distinct displays and plumage patterns have evolved in response to selection for the maintenance of reproductive isolation of the species.[158,169] This concept has been criticized by Paterson,[172,173] who argues instead that such features have evolved to ensure fertilization through precise mate recognition. This concept has a number of important implications. First, as Paterson has stressed, the specific-mate recognition system (SMRS) will be highly resistant to both directional and disruptive selection in large populations. Thus any characters associated directly or indirectly with the SMRS will generally be protected from selection. Just how much variation is sheltered in this way is not known because we do not have a clear idea of what comprises the SMRS of a species, or if the characters associated with it are invariable through time. Does the SMRS consist merely of a small number or sequence of displays, or does it consist of a broad spectrum of characters? Does it include features such as the so-called secondary sexual characters, which according to conventional wisdom are products of epigamic and intersexual selection? There is clearly a need for more detailed descriptions and analyses of communication systems, involving studies of both the SMRS and the other communication needs of an individual involved in complex and subtle interactions with conspecifics.

Secondly, the question is raised as to whether alternative alleles can be fixed by selection in large populations. The assumption that widespread, morphologically and behaviourally undifferentiated populations are panmictic remains untested and the alternative, that many species comprise small, local populations, has yet to be disproved. Much more work is needed on

Black Eagle with six-week-old eaglet [Peter Steyn].

Lanner Falcon [W. R. Tarboton].

Cape Gannets on Malgas Island [Peter Steyn].

Black Heron [W. R. Tarboton].

Blackshouldered Kite [W. R. Tarboton].

Cape Rockjumper [Peter Steyn].

Table 1. Employment of ornithologists[a] in southern Africa in 1981.

	Permanent staff		Temporary and contract appointments				
Organization(s)	Research[b]	Admin.[c]	Research associates[d]	Research assistants[e]	Post-graduates[f]	Others[g]	Total
Museums (8)	10	2	2			2	16
Universities (10)	4	3	2		8	5	22
PFIAO	2	2	11	9	11		35
Nature Conservation (7)	7	2		1		6	16
Government departments (2)	2					2	5
SAOS[h]						10	10
Total	26	9	15	10	19	25	104

[a]Defined here as those persons whose current research involves work on birds, or who have a professional interest in birds. [b]Includes teaching staff. [c]Includes those scientists whose job commitments limit their research and teaching to less than 50% of their work time. [d]Includes postdoctoral and visiting researchers, persons holding honorary appointments and those persons carrying out relatively independent research for purposes other than for obtaining a higher degree. [e]Includes technicians and those persons employed to assist others in their research. [f]Includes persons currently registered for a higher degree. [g]Includes persons who are engaged in ornithological research part-time but who are employed in a different capacity. [h]Includes those members of the South African Ornithological Society who are carrying out independent research in an avocational capacity.

the population structure of species if these issues are to be resolved.

Finally, by recognizing species as collections of individuals sharing common mate-recognition systems, how does this influence our current taxonomic views of Southern African birds? We have come full circle: perhaps the confident remarks expressed in the opening paragraphs will, in time, need revision.

Manpower and organization

There are at least 104 ornithologists active in Southern Africa today (Table 1). (For the purposes of this discussion an ornithologist is taken to be a person who is currently working on birds, or who has a professional interest in birds.) The majority (54%) are employed at the universities, with most of them working in the Percy FitzPatrick Institute at the University of Cape Town. Equal numbers of ornithologists are employed by the museums and nature conservation authorities, though a number of those working in nature conservation do so in some other capacity. Furthermore, the number of ornithologists in each of the conservancies is unequal, some having a number of researchers in this field, others having one or none. The estimated current annual expenditure on ornithological research, including support services, exceeds R1 million.

The number of self-motivated amateur ornithologists is also noteworthy and many of them have made significant contributions to our knowledge. The Southern African Ornithological Society currently has about 3000 members, many of whom help in various projects such as the Nest Record Card scheme, bird ringing and atlasing. Thus there does not appear to be any shortage of manpower, though a better geographical spread of expertise would be beneficial: nearly 40% of the professional ornithologists work in the south-western Cape and in marine programmes.

Despite the relatively large number of professional ornithologists, only about one-third of them are in permanent employment, 35% of them in administrative posts. Twenty-four percent of ornithologists are employed in some other capacity than as ornithologists, so that their research is essentially part-time. The remainder (42%) are employed on contract or are conducting postgraduate research and thus lack job security. A number of these researchers are funded through the national scientific programmes coordinated by the CSIR and thus are involved in cooperative, multidisciplinary research.

The main cooperative projects currently being undertaken involve extensive participation by the Percy FitzPatrick Institute in the multidisciplinary research programmes developed by the South African Scientific Committee for Antarctic Research (SASCAR) and the South African National Committee for Oceanographic Research (SANCOR). These include studies of the rôles of seabirds in the transport of minerals and energy to and within the Marion Island terrestrial ecosystem; studies on the Prince Edward and Gough islands of the population dynamics of selected seabird species in relation to the dynamics of their prey populations; participation in the Southern Ocean programme, which focuses on the spatial and temporal distribution of Antarctic seabirds with particular reference to their potential rôle as indicators of krill and other living marine resources; and studies on the feeding ecology of seabirds in the Benguela Current system. Some cooperative research, on the distribution and seasonal changes in waterfowl populations and wetland habitats, is being undertaken by the various provincial nature conservation departments in South Africa. However, the potential for more extensive cooperation between these bodies, and with other interested parties, has yet to be fully exploited.

There are a number of cooperative projects involving amateur ornithologists. These include the recently completed survey of the distribution of birds in Natal; the Vulture Study Group, devoted to research and conservation of Southern African vultures; and the Western Cape Wader Study Group, involved in the study of migration routes, local movements, moult and body mass fluctuations of palaearctic waders. Cooperation between amateur and professional ornithologists occurs in many other studies on a less formal basis. Mention should also be made of the South African Bird Ringing Unit (SAFRING), which administers and coordinates bird ringing in Southern Africa, an activity in which amateur ornithologists play a major rôle.

The future

The main conclusion to be drawn from this review is that we know a considerable amount about the Southern African avifauna, probably much more than is generally realized. However, much of the information is largely descriptive and relatively little advance has been made locally towards the development and testing of concepts designed to explain these observations. Ornithology as a whole is rich in concepts, most of which have been developed from research done in northern temperate regions, but how applicable these are to local conditions has seldom been critically tested. Consequently, our knowledge of the causes and mechanisms of the phenomena that we observe remains superficial. The primary task therefore facing ornithologists in Southern Africa must be to build on this foundation of empirical knowledge and develop a body of principles concerning the ways in which birds function in African environments and the consequences of this functioning at population, community and ecosystem levels.

In the first instance we need syntheses of existing information, along the lines of the recent reviews by Grimes,[160] on cooperative breeding in African birds, and by Dean and Macdonald,[80] on African bird/mammal associations. Such reviews help clarify the broad patterns, emphasize areas where information is still lacking, and raise questions that should stimulate the framing and testing of hypotheses, thereby providing a focus for future research. Some of the subjects on which there would appear to be sufficient data to warrant at least preliminary syntheses include the timing and duration of avian breeding seasons, with focus particularly on differences between species, and within species in different habitats; geographic trends in clutch size, breeding success and number of breeding attempts per season in particular species; patterns of survival and longevity; the patterns, timing and duration of moult in African birds, and the phenomenon of moult/breeding overlap.

Secondly, there is a need for greater emphasis on question-orientated research and on the formulation and testing of hypotheses. The process of asking the right questions, or deciding which observations need to be explained and what types of explanation are required, is important, since the nature of the question can influence markedly success in obtaining an answer. More attention also needs to be given to identifying what information is needed in order to test a particular hypothesis and its alternatives, to the planning of experiments and field studies designed to provide that information, and to the analysis and interpretation of the results.

Thirdly, there is a need to encourage longer-term studies similar to those being carried out on the Black Eagle[22,146] and Jackass Penguin *Spheniscus demersus*.[129,165,174] Too much of the work undertaken to date has been short-term and superficial, with many of the questions raised by such studies never having been followed up. For example, questions concerning the significance of particular breeding systems, the factors involved in regulating populations, and the processes determining the structure and organization of communities, will never be satisfactorily answered until we have completed long-term studies of known individuals, populations and communities.

The prospects for long-term research would be substantially improved if there was greater guarantee of long-term funding and concomitant job security for researchers. Much current ornithological research is sustained by funds granted for short, 1 – 3 year, contract or postgraduate studies, which is not conducive to the planning, establishment and maintenance of long-term research.

What are likely to be some of the more rewarding research fields in African ornithology? I have already indicated some of the areas where our knowledge or understanding is poor or non-existent and any of these would be worth investigating. However, I believe that we should look more closely at those questions and subjects which will complement work being done elsewhere. This means concentrating on those fields of research where we can provide a different perspective to a more general problem. In this respect, some of the ways in which tropical and subtropical avifaunas differ from those in more temperate regions include generally smaller clutch sizes; greater longevity; greater deferred maturity; extensive cooperative breeding; more complex mating systems; different mechanisms triggering breeding and moult; slower moult and a higher incidence of moult/breeding overlap; more specialized frugivores; nectivory; a wide range of interspecific feeding associations; and a wider array of ecological opportunities resulting in a greater variety of guilds, more species per guild and a large size-range of species in these guilds. In addition, there are many large, long-lived birds having low intrinsic rates of population increase whose population dynamics need to be studied, particularly as these species are most vulnerable to disturbance, loss of habitat and exploitation. Research into any of these problems by local ornithologists could contribute substantially to the development of theory in these fields.

At the same time, there is an urgent need for conservation-orientated research which will contribute to the maintenance of biotic diversity and the preservation of ecosystem functioning. In ornithology, there is first a need to determine the distribution and status of all bird species in Southern Africa, giving priority to endemic species and to species which are considered to be threatened. This will provide information on which species and areas most require conservation action. These studies can either be done by documenting the distribution of all species in a region[32] or detailing the distribution and status of individual species or groups.[33,175-178] Secondly, there is a need for studies of the ecological processes and interactions from which ecosystem functioning stems. These include studies of population interactions;[179] community composition and dynamics; the patterns of movement, and the use of different resources in space and time; the functional rôles of birds in ecosystems (as competitors, predators, pollinators, seed dispersers etc.); and the temporal changes in the size, structure and distribution of populations. Such studies help to define the boundaries to ecosystems and thus the location, configuration and minimum size of areas to be conserved. Thirdly, there is a need for management-orientated studies which will provide information on the dynamics of both threatened[179-183] and exploited populations so that the management of these can be improved.[184,185]

In summary, therefore, I see the main objectives of future ornithological endeavour in Southern Africa to be to develop and test concepts what will lead to a better understanding of the biology of the avifauna, and to promote its conservation. In what ways can ornithologists in the museums, nature conservancies, universities and other organizations cooperate in achieving these aims? Essentially, their rôles are complementary, though there is a lack of coordination that tends to offset this advantage. There is a need for ornithologists to get together more frequently to discuss their research and find a basis for cooperation. The holding of structured workshops at one or two-year intervals would provide the most constructive forum for discussion.

The achievement of these aims is also hampered by the fragmentation of expertise and facilities. Outside the south-western Cape professional ornithologists tend to work in relative isolation. There is a need to seek ways of alleviating this situation, perhaps by developing regional centres where library facilities and study material can be brought together, thereby providing a focus for ornithological activity. This would also have the advantage of making the curation and archiving of material easier. At present, there is a disturbing attrition of this material since most museums appear to lack the funds and personnel to ensure that all their collections are adequately maintained.

What rôle can the amateur ornithologist play in these developments? To a large extent, the current strength of Southern African ornithology owes much to the talented and sustained input from amateur ornithologists. Many of them have contributed significantly to our knowledge, either through independent research or through their participation in cooperative activities such as the Nest Record Card and Bird Ringing schemes. We need to ensure that as the corps of professional ornithologists increases, and as research techniques become more specialized, cooperation between amateur and professional is maintained to their mutual advantage. Many amateurs are motivated to do some research but they need advice and encouragement, at least initially. There is a need for a list of suitable projects from which amateurs can draw, if necessary, and professional ornithologists can help considerably in this regard. Finally, the knowledge and commitment of amateurs can be greatly enhanced by their participation, with professionals, in workshops and seminars. The Southern African Ornithological Society is well placed to act as an interface in this regard.

The rôle of the Percy FitzPatrick Institute

The Percy FitzPatrick Institute of African Ornithology is one of only a few ornithological institutes in the world and the only one of its kind in the southern hemisphere. As such it is uniquely placed to promote the continued development of ornithology in the region. There is little doubt that, since its establishment 21 years ago, it has had a major impact on the growth of ornithological research both through its own research output (Fig. 1) and by stimulating and encouraging other researchers. I have already indicated that there is a need for greater coordination between researchers (itself a product of the growth of ornithology) and I believe that the Institute is best placed to assume the rôle of coordinator and so promote the most efficient use of our ornithological resources.

Much of the research being carried out at the Percy FitzPatrick focuses on the functional rôles played by birds in ecosystems. Approximately three-quarters of this work is currently being carried out on coastal and seabirds, particularly on Marion Island and in the Southern Ocean. This reflects the more conspicuous rôle that these birds play in such environments, as well as the Institute's geographic position and the tradition of marine biological research at the University of Cape Town. This research has been highly productive and has established South Africa as one of the foremost nations

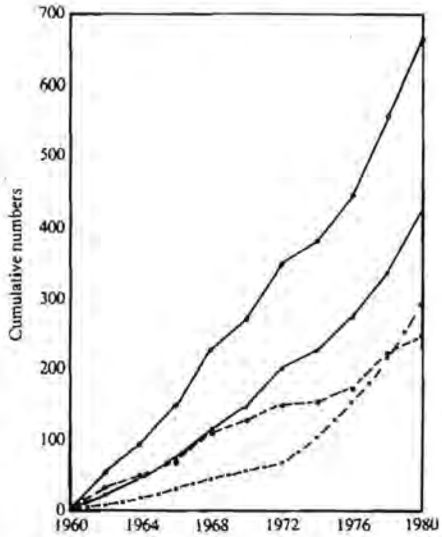

Fig. 1. Cumulative increase in the numbers of publications (o——o), full-length scientific papers (■——■), short communications and popular articles (o—o) and personnel (■ — ■) at the Percy FitzPatrick Institute, 1960 – 1980.

in Antarctic research. However, there are many problems in terrestrial ecology to which the Institute should also give some attention. There is a need to develop long-term, multifaceted programmes similar to those being carried out in the Antarctic. Not only would this give the Institute a more visible presence as an institute of African ornithology but it would provide the leadership and source of inspiration that are needed if we are to fulfil our aims.

This review constitutes part of the commemoration of the 21st anniversary of the establishment of the Percy FitzPatrick Institute of African Ornithology and is based largely on the proceedings of a workshop on the Future of Southern African Ornithology held at the University of Cape Town in February 1981. The workshop was organized jointly by the Percy FitzPatrick Institute and the Committee for Nature Conservation Research of the National Programme for Environmental Sciences of the CSIR. Nevertheless, the views expressed in this article do not necessarily reflect those held by these organizations. I thank all the participants in the workshop, especially A. F. Boshoff, J. Cooper, A. C. Kemp, J. A. Ledger, I. A. W. Macdonald, W. R. Siegfried, W. R. Tarboton and C. J. Vernon for their contributions. Parts of this draft were read by S. K. Frost, A. C. Kemp and W. R. Siegfried, to whom I am grateful.

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