The role of behavioural ecology in southern Africa

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In their stimulating article, Lawes and du Plessis [I] ask if there is a role for the discipline of behavioural ecology (that is, seeking evolutionary explanations for behavioural decisions made by organisms in their natural environment) in southern Africa. Their focus was South Africa, which they rightly stated was the only country in Africa with a 'reasonable tradition of behavioural ecology' where most of the work was pursued by resident sci~ntists. We would like to dispel any possible misinterpretation that it is the only country in Africa where such work is undertaken, and we offer further arguments why behavioural ecology has an important role to play in future research in Africa.

In Namibia, we may be unique in having the only non-governmental organisation in Africa with the purpose of promoting the study of behavioural ecology. The Namibian Evolutionary Ecology Group (NEEG), founded in 1990, was set up for the sole purpose of encouraging and stimulating research with evolutionary questions and approaches in mind. We have been assisted greatly by input from Uppsala University's behavioural ecology group in Sweden, whose biennial forays into southern Africa inject large doses of enthusiasm and expertise into NEEG's annual meetings, now in their fifth year. These meetings have attracted foreign and local biologists alike, with professors Nick Davies, Tim Birkhead, Staffan Ulfstrand, Anders Mj1jller and Ian Jamieson among our keynote speakers.

Our intention is to point out that other regions in southern Africa do see behavioural and evolutionary ecology as important enough to invite and encourage interaction with researchers such as these, despite the damper put on any form of evolutionary teaching at the primary or secondary school levels. We heartily agree with Lawes and du Plessis that African universities must turn around this evolutionary vacuum by promoting behavioural' ecology courses within their curricula, to expose students to the best experimental designs, methods and results emanating from behavioural ecology research. British behavioural ecologist, Robin Dunbar, has gone as far as suggesting that biology should be used as the key introduction for students to the sciences (and scientific method) ahead of maths, chemistry and other 'hard sciences' because students can identify with, and understand, it more easily.[2]

The question is, does such research actually assist science in Africa, or is it indeed a luxury[3] or too sexy! for southern African countries? We offer several ways in which behavioural ecology can enhance, and has enhanced, ecological research and training in Africa and elsewhere. Of these, possibly the most important to scientific progress is the exposure of African scientists to research methodology, particularly experimental design, which is generally lacking in southern Africa. There is a perception among some southern African biologists, for example, that 'why' (rather than how or when) questions are impossible to answer. For some, formulating questions at aU has proved difficult and this may explain why descriptive 'science' is so frequent here. With classic experimental field manipulations such as those devised by Andersson[5] to elucidate the evolution of animal ornaments, those of Mj1jller[6] to understand how and why parasites influence reproduction and sexual selection in birds, and simple assays to determine reproductive decisions among humans in traditional African societies,? we can not only ask such questions, but now have the methods and models to answer them.

The second and most practical reason for promoting behavioural ecology within southern Africa is the information it can provide in respect of urgent conservation-related problems. Just as one cannot fix a malfunctioning car without understanding the way cars in general function, so one cannot manage an ecosystem without understanding the natural processes that formed it and function within it. A better understanding of these processes is a part of the goal of a behavioural ecology approach. There are several examples: the first is the development of simple methods to assess accurately genotypic/phenotypic quality in game populations (through measures of fluctuating asymmetry[8]), for the purposes of choosing appropriate animals to translocate, cull, breed or even auction. A second example is the development of conservation policies for lions, which includes the modelling of trophy hunting quotas, based on behavioural studies of grouping patterns, co-operation and predation.[9,10] A third conservation example is exposing the hidden dangers of sustainably harvesting second-hatched siblicidal eagle chicks (or eggs), as once illegally practised in Zimbabwe, [II] because of possible effects on future fitness.[12] Another spinoff is using research tools such as nest boxes, initially designed to enhance the behavioural study of poorly known endemic birds in Namibia, but which rapidly increase breeding populations. Increases may result in the future sustainable harvesting of species such as illegally traded parrots[13] to solve conservation problems. Both our knowledge base and possible conservation options are thus immediately enhanced through a behavioural ecology approach. Finally, studies of mating systems and the often highly skewed copulation success of polygynous male mammals and birds[14,15] provide very important insights into realistic estimates of viable population sizes and conservation genetics.[16] Such species may be endemics with critically low populations or economically important (tourist-attracting) species exhibiting persistently low populations within national parks.[17] Even when data are collected for mainly descriptive purposes, they may then be used in retrospect to provide critical support for more esoteric, but interesting questions on evolutionary design,[18] that probably could not be answered in any other country.

Perhaps the greatest contribution which this discipline can make to the development of the southern African subregion is the insights it provides into human behaviour and ecology. This may be best exemplified by the many successful applications of 'optimal foraging theory' to hunters in traditional societies. Such studies provide a robust explanation of both why particular species are hunted and the extent to which that hunting is sustainable.[19,2o] This theory correctly predicts how hunting patterns change with the adoption of new technologies (such as shotguns),[21] which can be especially useful in explaining counter7intuitive changes (for instance, where there is a decline rather than an increase in harvesting rates for some species). The potential of foraging theory is not limited only to the hunting of game; a recent study used this theory to explain patterns of illegal fuelwood collection in a protected area in

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Malawi.22 Other approaches in behavioural ecology can also provide useful insights into subsistence practices, as recently illustrated by the demonstration that Gabbra pastoralists (in Kenya) manage their herds of livestock in precisely the right way to maximise the long-term survival of their households.23The results of studies such as these have an invaluable contribution to make to the development and implementation of more efficient practices in natural resource management.

Moreover, other aspects of human welfare stand to benefit from the promotion of behavioural ecology. For example, this approach has already been used to investigate fertility and mortality differentials among Ngamiland Herero pastoralists in Botswana,24 with potentially important implications for local population planning and health services. Similarly, current behavioural ecology research among the Nama pastoralists of southern Namibia aims to illuminate family support networks.25 By explaining the pattern of resource flow through these informal social security systems, it may be possible to enhance many aspects of rural development. An understanding of such systems is likely to be particularly important in a year when E1 Nifio threatens widespread drought throughout southern Africa, when the effective distribution of drought aid to prevent both human malnutrition and the loss of livestock becomes an urgent priority.

These three broad categories covering research methods, conservation biology and human development are a sample, not an exhaustive list, of areas where behavioural ecology can assume economic as well as conservation-related relevance for developing nations with increasing pressure being placed on their limited resources. Others that fall under the umbrella of evolutionary ecology include understanding the behavioural effects of habitatJragmentation on declining populations, understanding the effects of sociaVpopulation structure on mate-finding and signalling within small populations (for instance schools of whales), and understanding speciation processes and the behaviour and genetics of founder populations and their resilience to possible extinction.

With considerable work in Namibia - such as the effects of de-homing on social behaviour in black rhino, *Diceros bicomis,26* infrasonic communication among elephants, *Loxodonta africana,27* the effects of asymmetry in horn size of oryx, *Oryx gazella,8* the adaptations and counter-ploys used by egg-dumping birds in ephemeral wetlands, predation risk decisions made by foraging baboons, *Papio ursinus,28*effects of plant asymmetry on insect oviposition choice29and the remarkable ability of human (Jul'Hoan San) trackers30to re-construct accurately the hunting strategies and kills of leopards, *Panthera pardus,* to understand asociality in leopards31. we believe that Namibia has something to offer the rest of Africa on both the evolutionary ecology and conservation biology fronts. While descriptive studies do have a role to play, we hope the days of only descriptive studies are numbered, and those providing insightful answers to precise questions through modelling and correlational and experimental approaches will become more numerous (and valued) in the next millennium.

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