



# Trends in behavioural ecology: Putting South African research in a global perspective

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South Africa remains at the leading edge of scientific publishing on the African continent, yet few analyses of publication patterns exist outside the biomedical field. Considering the large number of protected areas and mammalian guilds within the country, I examined trends in South African ecological research as it pertains to the behaviour of mammals. I assessed the topics and taxonomic focus of mammalogists at South African institutes over the span of 15 years (2001–2015), and contrasted local research with the shifting focus of international behavioural research. This review of more than 1000 publications indicates that South African based researchers exhibit a strong tendency towards field-based research, as opposed to laboratory-centred experiments. In terms of topical focus, local ecologists place significant weight on the behavioural categories of mating, social and foraging behaviour – reflecting a global priority for these topics. This finding contrasts with an increased emphasis on animal cognition and communication research in the international research arena, including field-based studies on these themes. I make suggestions on how behavioural ecologists in South Africa can align themselves with global trends while also continuing to distinguish those facets that make South African behavioural ecology unique.

### Significance:

- This review is the first of behavioural ecology in South Africa.
- Suggestions are made for where South African researchers can profitably shift research focus.
- International trends in behavioural ecology are highlighted.

## Introduction

South Africa remains at the forefront of scientific publishing on the African continent, with Life Sciences contributing strongly to these research outputs.<sup>1</sup> Within this broader discipline, we also have the relatively unique advantage of direct access to intact mammalian guilds<sup>2</sup> inside well-managed protected areas<sup>3</sup> – a factor that has stimulated significant mammalogical research in the country. However, no broad meta-analysis of local publishing patterns currently exists, and by some accounts few South African researchers are investigating mammalian behaviour: within the Zoological Society of Southern Africa, the Ethology research group was short-lived<sup>4</sup>, and in the past 15 years only one paper on mammalian behaviour has been published in South Africa's top multidisciplinary journal, the *South African Journal of Science*<sup>5</sup>. This is surprising, as evolutionary biology is thriving in South Africa<sup>6</sup> and behavioural ecology is by definition the integration of evolutionary biology with the observation of animal behaviour. Since 1963<sup>7</sup>, when Tinbergen created his seminal framework for studying behaviour (traditional 'ethology') in an evolutionary context, the study of behavioural ecology has thrived internationally<sup>8</sup>. How well, then, is South African research represented within this field?

I reviewed the study of mammalian behaviour in South Africa, describing trends in behavioural ecology over the course of 15 years (2001–2015) and highlighting the evolution of this discipline. As a framework, I use the 10 themes of behavioural ecology recently developed by Berger-Tal and colleagues<sup>9</sup> as an accurate reflection on the specialities within this research field. I discuss specific strengths and weaknesses of behavioural ecology research in South Africa and indicate opportunities for continued growth.

## Methodology

I conducted an extensive survey of international literature on mammalian behavioural ecology using the SCOPUS database. Search terms were deliberately broad to encompass all literature (articles/review papers) from 2001 to 2015 that included the term "behav\*" and "mammal\*" in the title, abstract or keywords. In addition, I constructed a list of all mammalian families, thereby creating a search phrase to check if any of the mammalian families were included in the title, abstract or keywords of the publication. An initial search specifying these broad terms yielded 11 330 articles and review papers. This figure is an indication of the number of publications that describe behaviour, but is likely an exaggeration of the research that deals specifically and exclusively with mammalian behaviour.

I refined my search to compare South African research with the international literature, and created two publication databases. In the first, I specified that the author affiliation had to include "South Africa". These authors may have had multiple affiliations, and affiliation with a South African institute did not necessarily imply this was their primary place of work. I compiled a second database of international research that explicitly excluded authors with South African affiliations. In the second database, I limited the search to journals that focus specifically on animal behaviour: *Behavioral Ecology* (impact factor (IF)=3.177, from <http://www.citefactor.org/> accessed on 24 November 2016), *Animal Behaviour* (IF=3.137), *Applied Animal Behaviour Science* (IF=1.691), *Advances in the Study of Behaviour* (IF=2.692), and *Behavioral Ecology and Sociobiology* (IF=2.35). Furthermore, I included publications on mammalian behaviour that featured in the top three multidisciplinary journals, to ensure that I did not ignore research with the putative highest impact. These journals were: *Science* (2013 IF=31.477), *Nature* (2013 IF=42.351), and *Proceedings of the National Academy of Sciences of the United States of America*

(2013 IF=9.423). Once the articles were extracted from the SCOPUS database, I analysed all abstracts to exclude papers that did not focus on, or explicitly include mammalian behavioural ecology. This process produced a total of 371 South African papers and 901 international publications. This refined selection of South African papers suggests that at least 3.3% of all articles on mammalian behaviour include South African affiliations (371 out of 11 330). Importantly, as I was selective in the outlets for international publications in particular, the latter database did not constitute all international publications on mammalian behaviour – it is a reflection of the articles appearing in the more respected and subject-specific journals, and therefore indicative of broader trends in the field.

Within these databases, I examined the taxonomic breadth of study species as well as the focus on different techniques or approaches in the local and international literature. To aid the thematic analyses, I performed text mining to identify the most common keywords, using the 'tm' package<sup>10</sup> in RStudio for Mac (version 0.99.903). Finally, I pooled the papers for each database into three 5-year blocks: (1) 2001–2005; (2) 2006–2010; and (3) 2011–2015, and used the 10 behavioural themes identified in a recent review<sup>9</sup> to guide my assessment of changing trends.

## Findings and discussion

### Overview: South African contributions

South African researchers contributed to >3% of the global literature on mammalian behavioural ecology, which is higher than the 1% contribution that sub-Saharan African countries make to global scientific research in general.<sup>11</sup> As the original database of articles on mammalian behaviour was likely an exaggerated number (I did not go through all 11 330 abstracts to ascertain each study's focus), the true proportion of South African affiliations will be even higher. The majority of South African papers were primary research articles, with local authors publishing review papers at a somewhat higher rate (2.5% of the South African database) than international authors (1.5% of the international database). While it is positive to see this contribution to the synthesis of the field, South African ecologists appear to have had a smaller impact than international scientists: only 13.2% of our research has been cited more than five times per year, in contrast to nearly one third (31.7%) of international articles being cited at the same rate. The South African ecologists who publish in top multidisciplinary journals (e.g. Slotow et al.<sup>12</sup>) often base their research on long-term field data, that is, studies that continue beyond a three-year project.

While many local and international publications claimed to investigate behaviour in an evolutionary context, South African researchers were more likely to address the ultimate causes and consequences of behaviour (in contrast to proximate or mechanistic causes of behaviour). South African authors tend to study species within the broader ecological context, incorporating aspects of the habitat<sup>13</sup>, ecosystem<sup>14</sup>, and the survival/fitness value<sup>15</sup> of different behaviours. Population dynamics and population-level analyses were common in South African research, often including genetic analyses of population structure.<sup>16</sup> In one third (36.4%) of South African papers<sup>17,18</sup>, authors linked behaviour to conservation, compared with a much more limited focus on conservation in the international literature (1.8% of the literature, e.g. Palphramand et al.<sup>19</sup>). South African researchers therefore appear to align themselves well with calls for the integration of behaviour and conservation.<sup>9</sup> Furthermore, many South African researchers conducted experiments in their behavioural research, with nearly half (46.1%) of experiment-driven articles based on field studies.<sup>20,21</sup>

By contrast, in the international literature, 83.7% of experiments took place in captive or laboratory-based settings<sup>22</sup>, and a further 5.4% of these experiments utilised domestic or farmed animals<sup>23</sup>. International scientists often followed a mechanistic approach to the analysis of mammalian behaviour, with a large proportion of publications investigating causes and consequences of behaviour on a cellular level.<sup>24</sup> These authors also frequently studied the mechanisms of circadian rhythms<sup>25</sup> and echolocation<sup>26</sup>, which are largely absent from the South African database. International researchers exhibited a high interest in animal welfare research<sup>27</sup>, likely reflecting the prevalence of captive species in their taxonomic repertoire.

The most popular taxonomic clade in both databases was Rodentia; however, international studies concentrated on laboratory rodents<sup>28</sup>, contrasting with a much broader focus in South African research (including mole rats<sup>14</sup> and *Rhabdomys*<sup>29</sup> species). Carnivores were also prominent study subjects, with meerkats (*Suricata suricatta*) dominating both databases.<sup>30,31</sup> Internationally, canids<sup>32</sup> and spotted hyenas (*Crocuta crocuta*<sup>33</sup>) featured strongly in behavioural research, whereas South African researchers more often investigated Felidae<sup>34</sup>. Antelope<sup>35</sup> and small carnivores outside the Herpestidae family<sup>36</sup> were amongst the least studied taxa.

### Dominant themes: Foraging, reproduction and social behaviour

Research in most thematic areas increased over the review period (Table 1), signifying a growing trend for researchers to address multiple themes within one study. South African and international authors largely agreed in terms of the top three thematic areas: foraging, reproductive and social behaviour (Table 1, Figure 1). In contrast to international trends, in which indirect analysis of foraging behaviour was rarely represented<sup>37</sup>, many South African researchers use indirect methods such as scat<sup>38</sup> and isotope analyses<sup>39</sup> to describe foraging behaviour. Foraging ecology in the South African literature is therefore often restricted to dietary studies, with nuanced assessments of foraging behaviour – such as habitat selection<sup>13</sup> or strategic responses to environmental variation<sup>40</sup> – remaining uncommon.

Locally and internationally, research on mating and reproductive behaviour often assesses the hormonal correlates of reproductive success and/or helping behaviour. While common in the international literature<sup>41</sup>, the endocrinology of reproduction is particularly widespread in the South African database (for example see Marneweck et al.<sup>15</sup>). In both databases, much of the research focuses on reproductive control or suppression<sup>42</sup>, including rarely documented abortion<sup>43</sup>.

Within the theme of social behaviour, relatively few researchers examined social behaviour and social structure as a goal in itself. Sociality was nearly always linked to other aspects of an animal's behavioural ecology, such as anti-predator and foraging behaviour<sup>44</sup>, or competition<sup>45</sup>. The social behaviour of solitary species or solitary foragers was also examined fairly often by both local<sup>46</sup> and international authors<sup>47</sup>. The progression of this theme, beyond the basic description of social systems in gregarious species, is likely a reflection of the maturity of sociobiology as a research discipline.

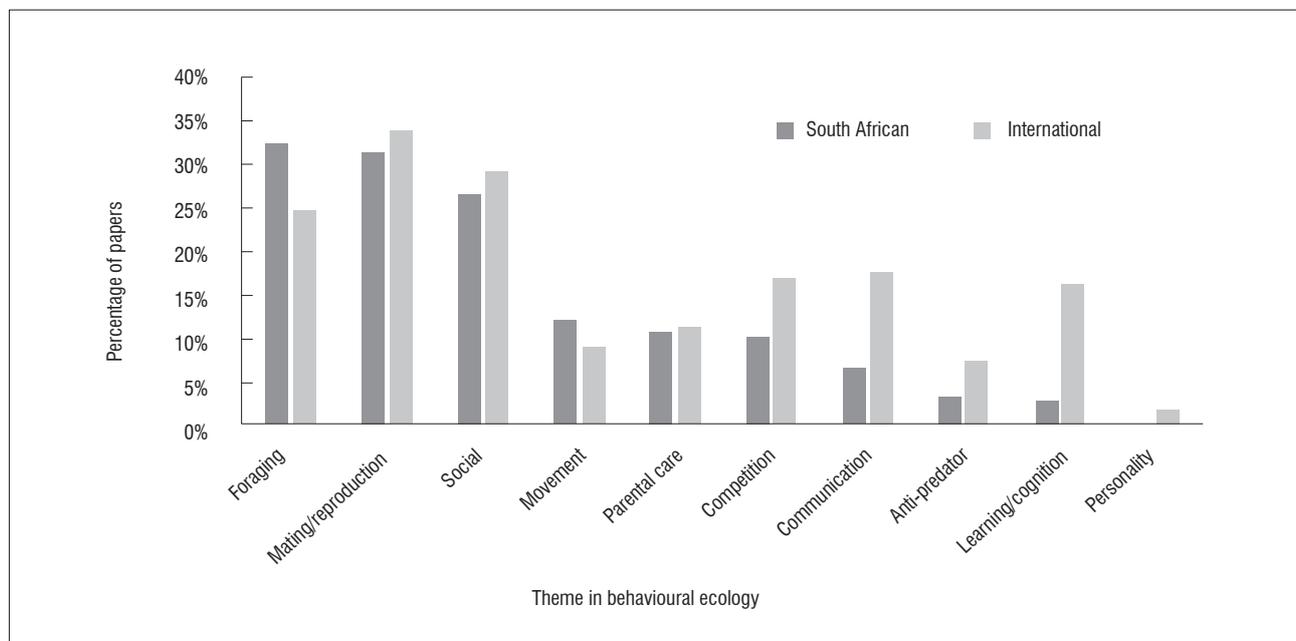
### Discrepancies: Communication, cognition and behavioural syndromes

A sharp contrast emerged between South African and international literature in terms of the next two high-priority themes. Internationally, communication and cognition were topics that featured in 17.7% and 16.1% of all articles, respectively. Comparatively speaking, South African authors largely have ignored these themes in the past 15 years, with only 2.7% of papers focused on learning and cognition, and 6.5% of publications investigating mammalian communication. The few South African publications examining mammalian cognition follow international trends in terms of topic, highlighting innovative behaviour in wild mammals<sup>48</sup>, and exploring the link between stress and cognition<sup>49</sup>. One unusual study concluded that large brain size in dolphins was driven less by cognitive demands, than by low water temperatures.<sup>50</sup> This South African study stands in sharp contrast to seminal international articles linking brain size to sociality<sup>51</sup> and – more rarely – the demands of complex foraging<sup>52</sup>. Within the theme of mammalian communication, South Africans agree with international research in preferentially studying acoustic signals<sup>53</sup>, above other communication modalities<sup>54</sup>.

Over the review period, the theme of animal personality, or behavioural syndromes, was not investigated even once by South African mammalogists. The bulk of international publications ( $n=14$ ) on the topic of personality appeared after 2010, although no papers on the theme appeared in the multidisciplinary journals *Science* or *Nature*. Mammalian personality or temperament is most often examined in the context of stress response<sup>55</sup>, survival<sup>56</sup> and fitness<sup>57</sup>.

**Table 1:** The percentage of papers published within each behavioural theme, across three 5-year blocks. South African papers include at least one South African author, whereas international papers were those works published without South African (co-)authors.

Theme	%South African papers			%International papers		
	2001–2005	2006–2010	2011–2015	2001–2005	2006–2010	2011–2015
Foraging	26.2	35.5	32.1	23.04	23.69	26.62
Mating/reproduction	24.6	33.3	32.1	29.57	35.54	37.74
Social	20.0	30.5	25.5	25.65	27.55	33.44
Movement	6.2	12.8	13.3	9.57	6.06	11.69
Competition	9.2	7.1	12.7	11.74	17.91	19.48
Parental care	10.8	11.3	9.7	4.78	14.88	11.69
Communication	1.5	6.4	8.5	16.52	18.18	17.86
Learning/cognition	0	2.1	4.2	16.52	14.33	17.86
Anti-predator	0	4.3	3.6	8.26	6.89	7.14
Personality	0	0	0	0.43	0.55	3.90



**Figure 1:** The percentage of articles and review papers examining 10 different themes within the discipline of behavioural ecology. South African authors' outputs between 2001 and 2015 are contrasted with the papers produced by non-South African (international) researchers over the same period.

The discrepancies between South African and international trends are less severe in the remaining five themes, and both databases present a similar distribution of topics. There are a few subtle distinctions in focus area. In terms of competitive behaviour, South African authors examine interspecific interactions<sup>58</sup> more often than international scientists do<sup>59</sup>. Within the theme of anti-predator behaviour, it is interesting to note that only international researchers appeared to consider the consequences of humans and human infrastructure for anti-predator behaviour<sup>60</sup>, while vigilance<sup>61</sup> remains a common focus across both databases. I could find no remarkable distinctions between South African and international researchers in the study of mammalian migration and dispersal. Finally, in terms of parental care, the primary focus of both data sets was on

maternal care, with South Africans<sup>48</sup> assessing paternal care more often than international authors<sup>62</sup>.

### The way forward

In a very practical sense, South African mammalogists are making optimal use of the accessible 'walk-in' laboratory available in the country's conserved areas and relatively intact ecosystems. A prominent focus on conservation-related research suggests that these researchers are cognisant of the risk of losing these fauna, and are actively directing projects to meet the challenges of a human-dominated global landscape. It is important to note, however, that using 'conservation' as a key term in research does not imply that practical solutions to conservation-

related problems are presented. Indeed, other reviewers<sup>9</sup> have pointed out that researchers who wish to have a positive impact on conservation challenges need to consciously conduct research that proposes, examines and practically explains answers to conservation-related questions. This is unfortunately not currently the norm in South African (or international) conservation biology.

Whereas behavioural ecology in South Africa is currently on firm footing, local researchers' impact can be more profound if we consciously adopt a more integrated approach. In a recent review, Bateson and Laland<sup>8</sup> highlighted that behavioural ecologists tend to ask specific behavioural questions in isolation, rarely combining a proximate and ultimate angle within a single study. This challenge remains despite the fact that Tinbergen<sup>7</sup> advocated for integration over 50 years ago, and South African researchers appear to be as guilty of this narrow theoretical scope as international researchers are. We could start addressing this challenge by building on our strengths. In the South African literature, the most cited research often addresses movement and foraging ecology (predation, in particular), and we have a strong national focus on studying carnivores. We could – and should – move beyond the study of movement and foraging behaviour (see also Young and Shivik<sup>63</sup>), building on the unique strengths of this mammalian order. For example, carnivores exhibit paternal care – a rarity amongst mammals<sup>64</sup> – more frequently than other mammals, yet we know almost nothing about the physiological drivers and consequences of this behaviour<sup>65</sup>. New studies should examine movement and foraging behaviour from both a proximate and ultimate angle, assessing the physiological covariates of dispersal and breeding behaviour, as well as the longer-term consequences of these individual decisions for fitness and population dynamics. Furthermore, while South African researchers already display a positive tendency to study heterospecific interactions, these studies are often performed on either a population level (e.g. Codron et al.<sup>39</sup>), or much smaller scale<sup>68</sup>. It is likely that collaborative research across study sites would enable us to assess inter-specific competition and collaboration on both a fine and large scale.

South African researchers appear slow to respond to some changing international trends that could open up new research and funding avenues. Specifically, local mammalogists pay scant attention to the themes of mammalian communication and cognition, contrasting with international trends. Importantly, international interest in the topic of animal cognition is far higher than this review would suggest, considering that I excluded subject-specific journals such as *Animal Cognition* (IF=1.122) from the review. Further, studies on mammalian communication and cognition are prominent amongst the most-cited papers in the international literature. Animal communication and cognition are, in many ways, closely linked. Not only is communicative complexity deemed indicative of cognitive complexity<sup>66</sup>, but researchers often use animal signals in experiments designed to examine particular aspects of animal cognition<sup>67</sup>. South African authors could benefit from looking beyond the topics that have sustained local behavioural ecology for a long time, and steer some research focus into the minds and communicative abilities of our rich mammalian fauna. Of particular interest would be linking these themes with conservation biology.<sup>68</sup> For example, basic associative learning experiments can be used to train naïve animals to avoid predators<sup>69</sup> or avoid novel, toxic prey species<sup>70</sup>. Knowledge of how prey animals detect predators using olfactory, visual or acoustic cues could potentially improve the management of direct human–wildlife conflict: acoustic deterrents have been used to reduce crop raiding by elephants<sup>71</sup>, and prey avoidance of predator faeces<sup>72</sup> suggests that such chemical cues can be used to deter some pests.

Another significant difference between South African and international research is that international scientists place a big emphasis on mechanistic studies of behaviour, often in captive study populations. This is particularly true for the behavioural research showcased in the top multidisciplinary journals, *Nature* and *Science*. Although this focus is likely a pragmatic response to the local paucity of wildlife, such controlled conditions open up novel research opportunities. The study of animal personality, for example, is largely rooted in laboratory or captive studies, and has only recently become more mainstream as a

topic that has serious implications for animal survival and evolution.<sup>73</sup> There are endless possibilities for investigating the unique physiology and behaviour of our local fauna, particularly smaller species that may more readily adapt to captive environments. Already, some novel South African led research has emerged from research into captive mammals, such as an examination of how rising environmental temperatures impact sleep behaviour in bats (*Epomophorus wahlbergi*<sup>74</sup>). Certainly, local researchers could also tap into the international fascination with the mammalian brain, potentially through active collaboration with medical researchers who have access to high-end scanning equipment.

South African researchers' successful scientific exploitation of our abundant natural resources may have inadvertently created a research blindspot in that we literally do not look closer to home to investigate the myriad ways in which mammals respond to humans and human infrastructure. With humans often living inside or adjacent to protected areas in South Africa, and tourism being a primary source of national income, studying the direct and indirect interaction between humans or human infrastructure and wildlife is becoming imperative. At the moment, South African researchers have not looked much further than crop raiding or the negative impacts of primates 'invading' human-modified areas.<sup>75,76</sup> Thus, we typically concentrate on the negative impacts of human–wildlife on humans and largely ignore the impact of humans on the behaviour of local wildlife. Directions of research could include describing the behaviour of various species in urban areas<sup>77</sup>, or assessing responses to humans as tourists<sup>78</sup>, road users<sup>80</sup> and scientific observers<sup>79</sup>.

South African behavioural ecologists would undeniably benefit from more collaboration between institutions, locations and fields of expertise. We still tend to work in silos (the majority of South African articles stemmed from the Mammal Research Institute of the University of Pretoria), and even concentrate on specific geographical locations, ignoring nature reserves that do not form part of the 'Big Five' national parks.<sup>80</sup> Funding bodies should also consider encouraging long-term field projects, which generate insights into the evolution of behaviour that no short-term approach could yield. Simultaneously, South African researchers should not ignore the possibilities inherent in well-designed laboratory and captive research that enable the detailed assessment of proximate corollaries of animal behaviour. We will not, however, make any great leaps forward without conversation. The time may be right for the revival of the Ethology research group as part of the Zoological Society of Southern Africa.

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