Forum

Descriptive versus explanatory hypotheses in evolutionary research;

a potentially concerning bias exemplified by research into the evolution of social organisations in Carnivores

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In this note I want to point out a potentially concerning bias in evolutionary hypothesis testing. In evolutionary research, deductive hypothesis testing is the most common way of achieving information on causal relationships (QUINN & DUNHAM 1983; LOEHLE 1987). Two general classes of hypotheses can be identified in research on trait evolution, although these may not always be explicitly stated. Hypotheses of the first class are descriptive in that they specifically relate to how traits have evolved. These hypotheses typically focus on evolutionary trajectories, but may also include rates of evolutionary change or the nature of the evolutionary process itself (PAGEL 1997). Hypotheses of this class are often tested using phylogenetic methods (e.g., SWOFFORD & MADDISON 1987; MADDISON 1994; SCHLUTER 1995; SCHLUTER et al. 1997; PAGEL 1999), and generally make no assumptions regarding the causes for evolutionary events. Hypotheses belonging to the second class, on the other hand, are explanatory in that they focus on explaining why a particular evolutionary process has occurred. These hypotheses therefore rest on an assumption that a specific course of evolution has taken place. They are generally analysed using a fitness maximization framework, and in contrast to descriptive hypotheses are not frequently tested using phylogenetic approaches (WADE & KALISZ 1990). While these two lines of inquiries in theory could be at least partly coupled, so that studies designed to test one class of hypothesis may render information about the other class, such coupling is by nature asymmetric in that studies designed to test descriptive hypothesis may render information regarding the causes for the evolutionary events (i.e. explanatory hypotheses) while it is very difficult to derive information regarding the course of evolution from studies designed to test the causes for evolutionary events (e.g., GOULD & LEWONTIN 1979, but see WADE & KALISZ 1990 for examples where this may not be the case). Therefore, it appears logical that a suite of descriptive hypotheses first should be identified and then thoroughly tested before explanatory hypotheses should be defined to explain the causes for a specific evolutionary process (Fig. 1). For instance, in a cladistic reconstruction of the origin of primate sociality, MÜLLER & THALMAN (2000) contradicted the generally accepted view of a dispersed harem system, i.e. a solitary social organisation in which the range of one male contains several female ranges, as the basis from which the diverse array of primate social groups have evolved (MARTIN 1981). Subsequently it has been recognized that the previously assumed ancestral solitary social organisations in primates show a considerable intra- and interspecific variation (KAPPELER & VAN CHAIK 2002). This realization caused a shift in focus from research explicitly looking for explanations into the formation of spatially cohesive social groups (reviewed in VAN CHAIK 1983; TERBORGH & JANSON 1986) towards framing and testing explanatory hypotheses related to the evolution and maintenance of a much wider range of social organisations (KAPPELER & VAN CHAIK 2002). Although this shift did not necessarily dismiss previous work relating primarily environmental factors to the evolution of primate social groups, it highlighted a serious gap in the general understanding of how social organisations in primates are regulated and maintained that previously had gone unnoticed. This exemplifies why it is often critical to first test and understand the trajectory of evolutionary processes before the causal mechanisms behind trait evolution are approached using deductive hypothesis testing.

The mammalian order Carnivora is a well studied group partly because of the charismatic characteristics of many carnivore species, but also due to a wide variety of morphological, ecological and behavioural adaptations (EWER 1973; BEKOFF et al. 1984). In particular, much research effort has been directed towards understanding the evolution of carnivore social organisation, with a disproportionate amount of empirical work being directed towards the large group living species, such as the African lion (*Panthera leo*), the grey wolf (*Canis lupus*) and the African Wild dog (*Lycaon*

pictus) (e.g., MECH 1970, PACKER et al. 1988, CREEL & CREEL 2002). As a consequence, much research has focused on explaining why these large animals live in stable social groups, and limited attention has been given to how they evolved into becoming social (DALERUM 2007). In this note I present a brief review of research on the evolution of carnivore social organisation as an example where explanatory hypotheses seems to have been widely discussed, suggested and tested before the descriptive hypotheses that they rely on have been firmly tested and confirmed. I highlight two potentially serious effects of such biased research efforts on our ability to understand evolutionary processes.

Review of research on carnivore social evolution

I used ISI Web of Knowledge (http://www.isiknowledge.com) to search for studies that have investigated the evolution of carnivore social organisations. The data base used for the search covered the years 1956 to 2009. The literature search revealed 45 articles that contained the search terms 'Carnivora' or 'carnivore' and 'social evolution' or 'sociality' and 'evolution'. I complemented these results with 8 books and book chapters that are classical references in the subject. I carefully scored each study into at least one of 5 classes as follows;

(0) No identification or test of hypotheses regarding the evolution of carnivore social organisations. The study was not included for this note.

(1) Identifying descriptive hypotheses regarding the evolution of carnivore social organisations. The study clearly identified hypothesis regarding the trajectory of the evolution of social organisations.

(2) Testing descriptive hypotheses regarding the evolution of carnivore social organisations. The study clearly stated one or several descriptive hypotheses of the evolution of social organisations, and explicitly tested it/these using empirical data.

(3) Identifying explanatory hypotheses regarding the evolution of carnivore social organisations. The study clearly identified one or several hypotheses relating to the causes for evolutionary transitions in social organisations.

(4) Testing explanatory hypotheses regarding the evolution of carnivore social organisations. The study clearly stated one or several hypotheses relating to the causes for evolutionary transitions in social organisations, and tested it/these with empirical data.

For the studies that tested hypotheses, I also scored whether the hypotheses were supported or not by the research. Of the 53 identified studies, 17 were found to have developed or explicitly tested either descriptive or explanatory hypotheses regarding carnivore social evolution. These studies are listed in appendix 1.

Of the 17 studies identified to have either described or tested hypotheses regarding the evolution of carnivore sociality, only 2 (12% of the 17 studies) identified descriptive hypotheses, whereas 4 (24%) tested descriptive hypotheses. Only 1 tested evolutionary trajectories across the whole Carnivora (DALERUM 2007), and with the exception for one single species study (RATNAYEKE et al. 2002), no study found conclusive support for the tested evolutionary trajectories (MUNOZ-DURAN 2002;

VERON et al. 2004; DALERUM 2007). Similarly, only 4 (24%) of the studies presented explanatory hypotheses for the evolution of carnivore social organisations. However, the vast majority of publications, 12 out of the 17 (71%) tested these explanatory hypotheses, and the majority of these studies (9 out of 12) presented support for the evolutionary explanations that they tested (Fig. 2). Similarly to research in primate social evolution, the majority of these explanatory studies tested explanations for the formation of complex and cohesive social groups from a solitary ancestry.

Implications for interpreting evolutionary research

Although this review was not exhaustive, it revealed a prevailing bias in research on the evolution of carnivore social organisations, with the majority of studies focusing on finding empirical support for hypothesis explaining the causes for evolutionary trajectories. Although such a bias may not necessarily be of concern, it could be problematic if the underlying descriptive hypotheses have not been adequately supported. This appears to be the case for research on the evolution of carnivore social organisations, where a very low proportion of studies focused on testing descriptive hypotheses empirically, and only a single species study was found to lend support for any of these hypotheses. I therefore suggest that research into the evolution of carnivore social organisation may be regarded as an interesting example where explanatory causes for evolution appears to have been widely examined before the evolutionary trajectories they are attempting to explain have been robustly supported.

If these biases are common across evolutionary research, we face a great challenge in changing our research focus from explaining why specific evolutionary events occurred into finding support for how they occurred. Such a shift would not be controversial, since many hypotheses regarding evolutionary trajectories are deeply founded but not necessarily empirically supported by the scientific community (e.g., WHITE 2003), and imaginative explanations regarding the adaptive causes for trait evolution are often more interesting to address than pathways of evolutionary change (GOULD & LEWONTIN 1979). Moreover, even if single studies provide support for a specific evolutionary process, as in the presented example, such limited support does not provide strong evidence even if they are backed up by statistical inference (IOANNANIDIS 2005). Therefore, a series of studies preferably has to render independent support for a single descriptive hypothesis prior to any explanatory hypotheses being developed to explain it. If this does not occur, I suggest that the resulting misdirection in research focus could significantly hamper our ability to understand evolutionary processes in two significant ways.

First, any explanatory hypothesis, which is supported empirically or not, must be regarded with great caution if the descriptive hypothesis it rests on has not been appropriately supported. Consequently, much research effort may be directed towards studies that will not necessarily advance our understanding of evolutionary processes. By directing focus either on the evolutionary processes itself, or on causes for evolutionary processes that have been supported by rigid scientific investigation, we will not loose limited scientific resources on investigations that could be intellectual dead ends. Second, by prematurely developing explanatory hypotheses, there will be a tendency to accept underlying descriptive hypotheses prior to an appropriate number of competing hypotheses regarding evolutionary processes have been explored (for carnivore social evolution, see for instance DALERUM et al. 2006; DALERUM 2007). Therefore, a lack of focus on developing competing hypotheses of evolutionary pathways may cause the loss of important progress in developing novel theory for pathways of evolutionary change.

To conclude, I propose that research into the evolution of social organisations within the order

Carnivora represents a cautionary example where a logical order of evolutionary hypothesis testing appear to not have been followed. I suggest that such premature focus on causes for trait evolution could severely hamper our understanding of evolutionary processes, and subsequently that evolutionary biologists should pay greater attention to the cumulative support for hypotheses describing how traits have evolved before they develop and test hypotheses to explain why the traits under concern have evolved along a specific trajectory.

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MARTIN R.D. 1981. Field studies of primate behaviour. *Symposia of the Zoological Society of London* 46: 287–336.

MECH L.D. 1970. The wolf. The ecology and behaviour of an endangered species. *Minneapolis: University of Minnesota Press.*

MÜLLER A.E. & THALMANN U. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biological Reviews of the Cambridge Philosophical Society* 75: 405-435.

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PACKER C., HERBST L., PUSEY A., BYGOTT J.D., HAMBY J.P., CAIRNS S.J. & BORGEHOFF MULDER M. 1988. Reproductive success of lions, pp. 1988. In: Clutton-Brock T.H. Edt. Reproductive success, studies of individual variation in contrasting breeding systems. *Chicago: Chicago University Press.*

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RATNAYEKE S., TUSKAN S.A. & PELTON M.R. 2002. Genetic relatedness and female spatial organization in a solitary carnivore, *Procyon lotor*. *Molecular Ecology* 11: 1115-1124.

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VERON G., COLYN M., DUNHAM A.E., TAYLOR P. & GAUBERT P. 2004. Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Molecular Phylogeny and Evolution* 30:582-598.

WADE M.J. & KALISZ S.C. 1990. The causes of natural selection. *Evolution* 44: 1947-1955.

WHITE T. 2004. Early homonids – Diversity or distortion? *Science* 299:1994-1997.

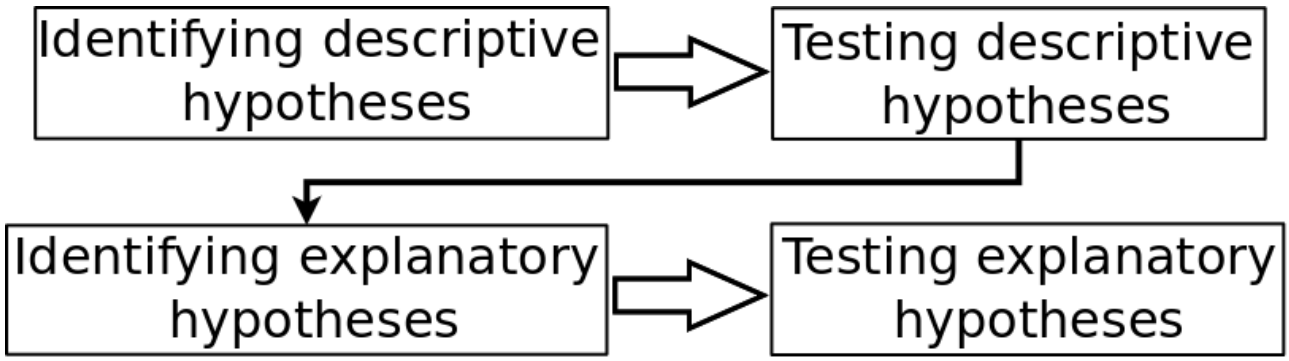

Fig. 1.- Conceptual flow chart for hypotheses testing in evolutionary research. Identifying and testing explanatory hypotheses are often not meaningful unless the descriptive hypotheses they rest upon have been appropriately supported and tested against a sufficient number of alternatives.

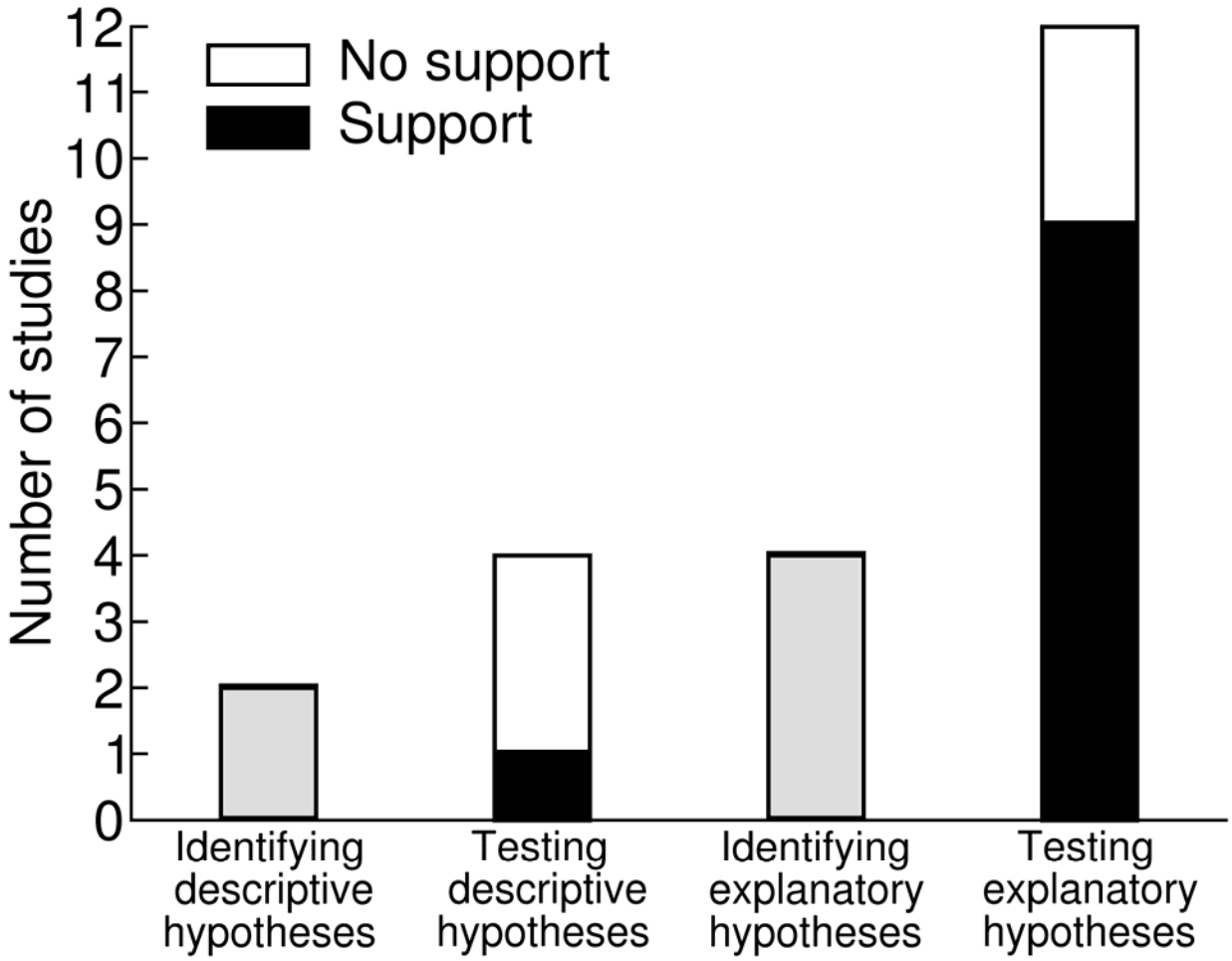

Fig. 2.- Studies of carnivore social evolution distributed among four different classes of evolutionary research; studies developing descriptive hypotheses, studies testing descriptive hypotheses, studies developing explanatory hypotheses, and studies testing explanatory hypotheses. Studies testing hypotheses are scored as to weather the research supported the hypothesis in question or not. Studies were identified from searches in ISI Web of Knowledge (http://www.isiknowledge.com) that contained the search terms “Carnivora” or “carnivore” and “social evolution” or “sociality” and “evolution”, as well as 8 landmark studies not identified by this search.

Appendix 1. Studies extracted from ISI Web of Knowledge (http://www.isiknowledge.com) that contained the search terms “Carnivora” or “carnivore” and “social evolution” or “sociality” and “evolution”, as well as landmark studies not identified by the search. Each publication was scored the research into 5 classes; no identification or test of the evolution of carnivore social organisations (publication was not included in analyses), (1) identification of descriptive hypotheses regarding the evolution of carnivore social organisations, (2) testing of descriptive hypotheses regarding the evolution of carnivore social organisations, (3) identification of explanatory hypotheses regarding the evolution of carnivore social organisations, (4) testing of explanatory hypotheses regarding the evolution of carnivore social organisations.

Reference	Type of hypotheses testing*	Conclusive
Bekoff M. et al. 1984. Ann Rev Ecol Syst 15:191-232.	4	Yes
Creel S, Macdonald DW. 1995. Adv Stud Behav 24:203-257.	3,4	No
Dalerum F. 2007. J Zool 273:90-97.	1,2	No
da Silva J. et al. 1993. Oecologia 95:558-564.	4	Yes
da Silva J. et al. 1994. Behav Ecol 5:151-158.	4	Yes
Gittleman JL. 1989. Pp 183-207 In Carnivore Behavior, Ecology and Evolution (Gittleman ed.). Cornell. Univ. Press.	4	No
Gorman ML. 1979. J. Zool 187:65-73.	4	Yes
Gusset M. 2007. Mammalia 71:80-82.	4	Yes
Kleiman DG, Eisenberg JF. 1973. Anim Behav 21:637-659.	1,3	N/A
Macdonald DW. 1983. Nature 301:379-384.	3,4	Yes
Moehlman PD. 1989. Pp 143-163 In Carnivore Behavior, Ecology and Evolution (Gittleman ed.). Cornell. Univ. Press.	4	Yes
Munoz-Duran J. 2002. Evol Ecol Res 4:963-991.	2	No
Packer C. 1986. Pp 492-451 in Ecological aspects of social evolution (Rubenstein and Wrangham eds.) Princeton Univ. Press.	3,4	Yes
Ratnayeke S. et al. 2002. Mol Ecol 11:1115-1124.	2	Yes
Sandell M. 1989. Pp 164-182 In Carnivore Behavior, Ecology and Evolution (Gittleman ed.). Cornell. Univ. Press.	4	No
Veron G. et al. 2004. Molec Phylog Evol 30:582-598.	2	No
Wagner A. et al. 2008. Anim Behav 75:1131-1142.	4	Yes

*) 1 – Developing descriptive hypotheses, 2 – Testing descriptive hypotheses, 3 – Developing explanatory hypotheses, 4 – Testing explanatory hypotheses