International Journal of Science Education

ISSN: 0950-0693 (Print) 1464-5289 (Online) Journal homepage: http://www.tandfonline.com/loi/tsed20

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To cite this article: Rianne Pinxten, Mathieu Desclée & Marcel Eens (2016): Upper secondary and first-year university students' explanations of animal behaviour: to what extent are Tinbergen's four questions about causation, ontogeny, function and evolution, represented?, International Journal of Science Education, DOI: 10.1080/09500693.2016.1239139

To link to this article: http://dx.doi.org/10.1080/09500693.2016.1239139

Published online: 05 Oct 2016.

INTERNATIONAL JOURNAL OF SCIENCE EDUCATION, 2016
http://dx.doi.org/10.1080/09500693.2016.1239139

Upper secondary and first-year university students' explanations of animal behaviour: to what extent are Tinbergen's four questions about causation, ontogeny, function and evolution, represented?

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ABSTRACT
In 1963, the Nobel Prize-winning ethologist Niko Tinbergen proposed a framework for the scientific study of animal behaviour by outlining four questions that should be answered to have a complete understanding: causation, ontogeny, function and evolution. At present, Tinbergen's framework is still considered the best way to guide animal behavioural research. Given the importance in science instruction of demonstrating how scientists work and ask questions, we investigated to what extent Tinbergen's questions are addressed in biology textbooks in secondary education in Flanders, Belgium, and represented in upper-secondary and first-year university students' explanations of behaviour in general and of specific animal behaviours. Our results revealed that teaching of animal behaviour mainly addresses ontogeny and causation, and that Tinbergen's framework is not explicitly referred to. Students typically addressed only one or two questions, with the majority addressing causation or both causation and ontogeny when explaining behaviour in general, but function or causation and function when explaining specific animal behaviours. This high prevalence of function may be due to teleological thinking. Evolution was completely neglected, even in university students who had recently completed an evolution course. Our results revealed that transfer of the concepts of ontogeny and evolution was (almost) absent. We argue why Tinbergen's framework should be an integral part of any biology curriculum.

ARTICLE HISTORY
Received 26 April 2015
Accepted 17 September 2016

KEYWORDS
Animal behaviour education; Tinbergen's four questions; secondary education; knowledge transfer

Introduction

Science involves not only knowledge but also a process. Learning of science by students is thus better supported if textbooks and instruction address not only scientific knowledge, but also scientific practices in the field (Bednekoff, 2005; Wilke & Straits, 2005; DiGiuseppe, 2014). The purpose of emphasising scientific practices during instruction is to help students develop a deeper understanding of science by demonstrating to them how

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scientists in the domain work, how they ask questions and examine the hypotheses raised (Bell, Smetana, & Binns, 2005). Hence, an important goal in biology and science education is to demonstrate, and teach, students how to ask the right scientifically oriented questions, depending on the specific domain. Research on inquiry-based learning, which also involves students learning to ask questions and formulate hypotheses, has revealed that most students appear to have difficulties with this specific skill (Schwartz, Lederman, & Crawford, 2004). In the biology curriculum, demonstrating, and experiencing, scientific practices is in particular useful for an adequate understanding of physiology, animal behaviour or ecology (Kremer, Specht, Urhahne, & Mayer, 2014).

Animal behaviour provides a great opportunity to learn science because students can directly observe animals and draw on their everyday experiences when formulating hypotheses (Bednekoff, 2005). So, teachers can readily use observation of animals to emphasise how scientists ask questions and frame and test hypotheses about animal behaviour. With respect to the scientific study of animal behaviour, it is generally agreed upon that four different questions should be answered to have a complete understanding: causation, ontogeny, function and evolution (Bateson & Laland, 2013a; Tinbergen, 1963; see below for more details). Hence, students learning about animal behaviour should be informed about this four-questions' framework as a tool to study animal behaviour. Emphasising these questions and the practices leading to answering them during instruction will also support a deeper understanding of the topic of animal behaviour itself.

In addition, another important cognitive skill central to deep conceptual understanding in animal behaviour, and sciences in general, is knowledge transfer. The cognitive skill of knowledge transfer (i.e. the ability to apply knowledge learned in one context to other novel contexts or to use it generatively) is thus also a fundamental goal in science education (Mayer, 2002). However, science education research has shown that most students have numerous difficulties regarding knowledge transfer (Anderson & Schönborn, 2008). For example, Pugh, Koskey, and Linnenbrink-Garcia (2014) recently described the patterns of transfer displayed by high school biology students learning about natural selection over time and concluded that transfer and duration of transfer were fairly limited. Natural selection is an important major concept in biology. As part of the larger concept of evolution, it is considered a threshold concept that integrates the learning of many sub-concepts and is necessary to make sense of the field of biology (Dobzhansky, 1973).

In this study, we specifically focus, within the subdomain of animal behaviour, on two cognitive skills that are important in the context of science education: the ability to ask the right scientific questions, in particular the extent to which Tinbergen's four questions are represented in biology textbooks and in students' explanations of behaviour, and the ability to transfer knowledge. Animal behaviour is agreed upon as an important major domain or concept in Biology. It is at the heart of the National Research Council's (NRC's) grand challenges for biology (NRC, 2010), since all of these challenges have strong behavioural elements. The latter was emphasised in a recent National Science Foundation (NSF) white paper (NSF Workshop, 2012).

Animal behaviour and Tinbergen's four questions

Behaviour is one of the most important properties of living organisms. Elucidating the mechanisms underlying behaviour and understanding its evolution represent major intellectual challenges in modern biology. As behaviour is that part of an organism by which it interacts with its environment, it can be considered as the bridge between the molecular and physiological aspects and the ecological aspects of biology (Levitis, Lidicker, & Freund, 2009), and thus as the most synthetic of all life sciences. Current research on animal behaviour has an inherent integrative and multidisciplinary nature involving scientific disciplines such as psychology, neuroscience, physiology, immunology, anthropology, evolutionary biology and ecology (Dugatkin, 2014; Ryan & Wilczynski, 2011) and hence promotes the development of new conceptual approaches in biology overall.

In his classic paper 'On aims and methods of Ethology' (Tinbergen, 1963), the Nobel Prize-winning ethologist Niko Tinbergen was the first to propose a research framework for the scientific study of behaviour by outlining the four different types of questions or problems that are raised by the study of behaviour (see also Martin & Bateson, 2007):

(1) What is the mechanism that causes the behaviour (*causation*)? How do internal and external causal factors elicit and control behaviour in the short term?
(2) How does the behaviour develop during the lifetime of the individual (*ontogeny*)? What factors influence the way in which behaviour develops during the lifetime of the individual and how do the developmental processes work?
(3) What is the function (Tinbergen originally called this survival value) of behaviour (*function*)? What is the current use or survival value of behaviour? How does behaving in a particular way help the individual to survive? How does behaviour help the individual to reproduce in its physical and social environment? The latter focus on reproduction was originally not included in Tinbergen's paper.
(4) How did it develop over the history of the species (*evolution*)? What factors might have been involved in moulding the behaviour over the course of evolutionary history? How can comparisons between different species help to explain that history?

The classification of these four questions is one of Tinbergen's most enduring legacies, in that he highlighted the value of a comprehensive, multifaceted understanding of a characteristic, with answers to each question providing complementary insights (Bateson & Laland, 2013a). Although Tinbergen was concerned with behaviour, the four questions broadly apply to any characteristic in living systems. The biological function and causation concern current problems, whereas individual development and evolution are historical (Tinbergen, 1963). The causation and development questions are also often referred to as proximate (or how-questions), because they focus on understanding the immediate causes of behaviour. The functional and evolutionary questions are often grouped as ultimate (or why-questions), because they require evolutionary reasoning and analyses (Martin & Bateson, 2007). Niko Tinbergen always has put emphasis on asking the right question and on having a clear idea of what would count as an answer. In his view, no question was worth asking unless at the same time it was clear how an answer could be obtained (Stamp Dawkins, 2014).

Despite the major advances that have occurred in the study of animal behaviour since the publication of Tinbergen's paper in 1963, his four questions still remain fundamental ethological tools (Strassmann, 2014). Indeed, on the occasion of the 50th anniversary of the publication of Tinbergen's paper, leading behavioural biologists have reflected on the four questions and evaluated scientific work they encouraged (Bateson & Laland, 2013a, 2013b; Nesse, 2013; Stamp Dawkins, 2014; Taborsky, 2014). Their general conclusion was that, at present, the specific framework that Tinbergen outlined is still a very good way for guiding and organising behavioural research. This is also nicely phrased in the foreword of the 'Tinbergen Virtual issue' in *Ethology* (Fulmer & Hauber, 2013):

> The how-s of causation and development and the why-s of phylogeny and function remain fundamental ethological tools. Today, physiological and cognitive causation is explored by using whole-brain scanners in awake and behaving animals, and ontogenetic studies explore extended phenotypes and epigenetic influences, whereas phylogeny is investigated with complete genomic data, and fitness is measured as life-time reproductive success of animals tracked by satellites.

Indeed, at present, almost every modern textbook on animal behaviour quotes Tinbergen's framework with approval (Alcock, 2013; Bolhuis & Giraldeau, 2005; Ryan & Wilczynski, 2011).

Educational practice for animal behaviour

Textbooks play a significant role in secondary education (Weiss, Pasley, Smith, Banilower, & Heck, 2003). In many cases, the course textbook constitutes the 'delivered' curriculum, determining what teachers teach and students learn (Chiappetta & Koballa, 2002). As emphasised by DiGiuseppe (2014), in terms of science education, science textbooks continue to make an important contribution (Stern & Roseman, 2004), purportedly accounting for 75–90% of instruction and 90% of all teacher-assigned homework (Chiappetta, Ganesh, Lee, & Phillips, 2006).

Given that introductory classes in biology should prepare students for advanced classes and help them appreciate current research in the field, Bednekoff (2005) examined how well introductory biology textbooks used in higher education in the USA reflect knowledge and practice in the field of animal behaviour. He concluded that the treatment of animal behaviour clearly illustrated that the practices of teaching do not, unfortunately, match the practices of conducting animal behaviour research in the laboratory or the field. He also reported that approximately half of the textbooks did not even mention proximate and ultimate causes.

At present, scientific research on animal behaviour education in secondary (i.e. high school) education, and more specifically on the extent to which Tinbergen's four questions are explicitly addressed or referred to, is scarcely available. We are aware of only one study that has explicitly examined educational practice for behavioural biology in secondary education in Europe. Van Moolenbroek, Boersma, and Waarlo (2005) investigated the chapter about behaviour in the most frequently used Dutch biology textbooks and concluded that behavioural biology in secondary education was largely outdated, and hence should be innovated. The textbooks did not emphasise the dynamic and complex character of behaviour nor were any links to other scientific fields mentioned. Although the causation, ontogeny and function of behaviour were referred to, while the evolution of behaviour was generally neglected, there was no explicit reference to Tinbergen's four questions as a tool for studying animal behaviour. In addition, Van Moolenbroek (2012) stated that the lack of structure by Tinbergen's four questions and the absence of relationships between behavioural biology and other disciplines in biology textbooks used in secondary education would not be adequate for students' understanding of animal behaviour. Unfortunately, the effect of the Dutch educational practices on secondary students' understanding of animal behaviour was not investigated.

The present study

The major goal of the present study was therefore to explore the extent to which Tinbergen's four questions are addressed in the current educational practice for behavioural biology in secondary education in Flanders, the northern region of Belgium, and in students' explanations of behaviour after they have been taught about animal behaviour.

In Belgium, the mainly Dutch-speaking Flanders region and the French-speaking Walloon region are both largely autonomous regions, also with respect to the educational curriculum. Secondary education in Flanders has a uniform structure. Students enter the first of six grades in secondary education around the age of 12. The six grades are grouped into three cycles of two grades. The topic of animal behaviour is programmed in the fourth grade (2nd year of the second cycle) of secondary non-vocational education. What should be taught is indicated in the single attainment target about animal behaviour, 'B-5. Illustrate with examples the difference between innate and learned behaviour', set by the Flemish Ministry of Education (Attainment targets for Biology, second cycle of general secondary education ATB-2nd grade ASO (2012)), which thus addresses only the ontogeny of behaviour. In Flanders, there are various educational networks that each develop their own specific biology curriculum (or learning plans), taking into account the Flemish biology curriculum (= the minimum attainment targets) which has to be achieved. However, also in Flanders, teaching practice is largely determined by the content of biology textbooks, which usually address more learning contents than prescribed by the learning plan objectives of the main educational networks. So, therefore, our first goal was to explore to what extent Tinbergen's four questions (or concepts) are addressed in the chapters about animal behaviour in the most frequently used Flemish biology textbooks and in the students' reasoning after they had been taught about animal behaviour in secondary education. We investigated the latter by examining which of Tinbergen's four concepts students address (1) when asked what they understand about behaviour in general and (2) when asked to give as many explanations as possible for the occurrence of two specific animal behaviours. This second question also falls within the general domain of research on the transfer of knowledge, since we actually asked students to apply knowledge learned in one context (during animal behaviour instruction) to other novel contexts (Marini & Genereux, 1995; Pugh et al., 2014).

This second goal, the study of knowledge transfer, was investigated using two different approaches. First, we compared the extent to which each of Tinbergen's four concepts were used by students in their explanations of specific animal behaviours with the extent to which they were used in their explanations of behaviour in general. In addition, to study the specific ability of students to transfer the concept of evolution to the context of animal behaviour, we sampled not only upper-secondary students but also first-year university students enrolled in biology-related fields of study. As evolution is only taught, albeit in a limited way, in the last (sixth) grade of secondary education in Flanders, the evolution of behaviour is probably completely neglected when students are taught about animal behaviour in the fourth grade. By comparing first-year university students who had completed an extensive course on evolution during the first semester at university with first-year students who had not taken this course, we specifically aimed to investigate whether the first group of students was able to spontaneously transfer the newly learned knowledge about evolution to the concept of animal behaviour, thus whether they were more likely to address the concept of evolution when asked to explain animal behaviours.

Methods

Textbook analysis

We explored the current educational practice for animal behaviour in secondary education in Flanders by investigating the behaviour section in the biology textbooks that were most frequently used by our students' samples (87% of the students reported that their teacher used a biology textbook when teaching about animal behaviour, see below). For both secondary and university students separately, we selected the most frequently used textbooks in such a way that, when combined, they represented more than 90% of all students that reported to have used a textbook. We investigated which topics of animal behaviour were typically emphasised and to what extent Tinbergen's four questions were addressed and explicitly referred to. The 'magnitude' of the section on behaviour was analysed to examine the emphasis on behaviour in each textbook and was determined by counting the relative number of pages of the section on behaviour (see also Bednekoff, 2005). We also examined the general theme in which the part on behaviour was presented. To explore which of Tinbergen's four questions were addressed and emphasised, the second author (MD) compiled a list of all terms printed in a conspicuous way, – as a title or in bold/italic – from the behaviour section in each of these textbooks. Terms that were printed both in a title and in bold or italic in the corresponding text were counted only once. Of the resulting 69 terms, 67 were then classified in the four categories (causation, ontogeny, function and evolution) by the second author and two animal behaviour experts. The terms 'ethology' and 'behavioural biology' could not be classified. There was 100% agreement among the raters, except for the classification of some terms that actually address the function of behaviour (f.e. territorial and mate attraction behaviour) but that were mentioned in the section about the causation of behaviour, in which they were linked to the causal stimulus (f.e. 'hormones motivate *territorial and mate attraction behaviour*'). After discussion, it was agreed to classify these specific terms as function.

Sample

The student population in our research consisted of 70 secondary school students and 149 first-year university students. Of the secondary school students, 31 were males and 39 were females. For the university students these numbers were 61 and 88, respectively.

The 70 secondary school students were drawn from the classes of one specific biology teacher from a high school in Flanders: 24 were 4th grade students (age around 15) enrolled in the Science programme and 46 were 6th grade students (in their final year of secondary education) enrolled in the Science programme ($n = 15$), the Mathematics programme ($n = 10$) or the Human Sciences/Languages programme ($n = 21$).

The 149 first-year university students were enrolled in Biomedical Sciences ($n = 8$), Biology ($n = 38$), Bio-engineer Sciences ($n = 40$), Biochemistry and Biotechnology ($n = 14$) or Veterinary Sciences ($n = 49$) at the University of Antwerp. Eighty percent of the students indicated in the questionnaire (see below) to have followed the Science programme during secondary education. All Biology and Biochemistry students ($n = 52$) had taken an obligatory evolution course (the 'Evolution and Biological Classification' course, with most lectures in this semester-long course being devoted to evolution and natural selection, and which also addressed and described the evolution of animal behaviours) during the first semester, while this was not the case for the other first-year students ($n = 97$).

Research instrument and procedure

As a research tool for examining the understanding/conceptions about behaviour and the extent to which students refer to Tinbergen's four questions, we used a short self-developed questionnaire, which was designed to be completed in 25 minutes or less during class. The questionnaire was distributed at the beginning of class after a short introduction to clarify the purpose of the research. At this point students were also informed that the questionnaire was not obligatory and completely anonymous. Students were asked to complete the questionnaire only if they were prepared to do their best. They were also asked to be 'as thorough as you can'. Secondary school students and first-year university students completed the questionnaire at the end of the second semester on 5 June and 6 June in 2014 and on 6 May and 15 May in 2013, respectively.

The questionnaire consisted of two parts. In the first part, we asked students to report about their secondary school education (specific school, fields of study followed, the specific biology textbook used in the 4th grade when animal behaviour is taught). In the second part, students were asked to answer three open-ended essay questions (Table 1). The first question (the 'Behaviour' question) inquired about students' conceptions about behaviour in general. In each of the two other questions, students were asked to give as many explanations as possible for the occurrence of a specific described animal behaviour, respectively bird song behaviour in springtime (question 2, the 'Bird song' question) and the behaviour of a lion stalking and chasing a zebra (question 3, the 'Hunting' question). The study of bird song is a classic example in modern animal

Table 1. Open-response instrument questions.

Question 1 (Behaviour)	What do you understand by the term 'behaviour'? What do you think about when reading the term 'behaviour'?
Question 2 (Bird song)	Male songbirds like starlings and great tits invest a great amount of time and energy in the production of song, especially during spring. How would you explain this singing behaviour during spring? Try to give as many explanations as possible.
Question 3 (Hunting)	The images below show four fragments from a National Geographic documentary. Describe the behaviour of the lion as accurately as possible and try to give as many explanations as possible for the occurrence of this behaviour.

behaviour textbooks, which illustrates how answers to each of Tinbergen's four questions provide complementary insights (Eens, 1997; Ryan & Wilczynski, 2011). With respect to question 3, the students were also asked to first describe the behaviour of the lion. Students had half a page to answer each of the first two questions and one page for the third question. Validity of the questionnaire was confirmed by a panel of three animal behaviour experts.

Students' answers to each of the three questions were analysed by examining which of Tinbergen's four questions (causation, function, ontogeny, evolution) were addressed. Based on the definition of these four concepts in recent literature (see Bateson & Laland, 2013a; Nesse, 2013; Stamp Dawkins, 2014), a coding rubric was developed and refined (see Table 2). After initial scoring of the answers, based on the rubric that was initially developed (by MD), the coding of several specific answers was discussed with the first author (RP). Based on this, the rubric was adjusted and the following additional rules were applied during coding. When students included specific examples when answering the Behaviour question, these were also scored when containing a specific concept. Additionally, when students used specific words when answering the Bird song and Hunting questions (e.g. 'spring', 'stalking') that imply certain concepts (causation for the first and function for the second) the concept was only scored as being present when the student offered further specification (e.g. 'birds sing during spring because the days are longer', 'the lion stalks his prey to remain unnoticed', …). When students used 'reproductive period', 'specific situation' and 'reaction' in their answer, the former was scored as 'function' (function of behaviour = to reproduce) while the latter two were

Table 2. Scoring criteria for each of Tinbergen's four questions, accompanied with examples from students' responses.

Concept	Criteria	Examples
Causation	Any description indicating a link between cause (stimulus) and consequence (behaviour) within a *short* timespan (i.e. a reaction).	*'How people react to stimuli.'* *'How animals react in specific situations.'* *'… because of changing hormone regulation'.* *'because days become warmer again'.* *'Zebra runs off → lion starts the chase'*
Function	Any description indicating the use/advantage of the specific behaviour *at the time of occurrence.*	*'in order to consciously achieve certain goals'.* *'… which enables organisms to communicate'.* *'Spring is the reproductive period of birds.'* *'The lion is crouching to stay unnoticed.'*
Ontogeny	Any description indicating the development or mechanism, *spanning an individual's lifespan* or the influences of predecessors on the individual that results in the specific behaviour.	*'A person can alter his behaviour consciously or unconsciously.'* 'It is the birds' instinct to reproduce.' *'This is a behaviour he learned from his mother.'*
Evolution	Any description referring to the mechanism, *spanning multiple generations*, resulting in the specific occurrence of the behaviour.	*'Behaviour is also culture-bound in humans.'* *'Behaviour is characteristic of the species.'* *'… how these behaviours evolved'.*

Notes: (1) Evolution should be interpreted broadly: any indication about differences among species as well as cultural evolution. (2) The word 'interaction' as well as references to animals 'knowing' things (e.g. the lion knows he is faster), were not allocated to any concept.

scored as 'causation' (the words referred to reactions to certain stimuli). If a specific concept was used in an answer, independent of how often it was mentioned, this was scored as being present. If students addressed a specific concept when answering the Bird song and Hunting question, but their corresponding explanation was not completely scientifically correct, this concept was also scored as being present since we were mainly interested in the extent in which Tinbergen's four questions were addressed by the students in their explanations of behaviour. Responses of the very few students that clearly had not answered the questionnaire in a serious way were excluded from the analyses.

After initial scoring, students' answers were independently recoded by the second and the last author (ME) using the adjusted coding rubric in order to test its precision and the consistency of the raters. Inter-rater reliability (IRR) was measured using both Cohen's κ and Pearson correlation (the total number of Tinbergen's concepts identified was used in the latter test). The results indicated a high IRR (Cohens's $\kappa = 0.96$, Pearson's $r = 0.97$). Thus the scoring rubric appeared to be sufficiently clear, and the raters sufficiently consistent, for reliable coding of Tinbergen's concepts.

Data analysis

All statistical tests were computed using the QuickCalcs software from the GraphPad website (http://www.GraphPad.com). A significance level of $\alpha = .05$ was employed for all tests. To test whether the use of the four Tinbergen's concepts differed between groups of students or between the different questions, we compared in a pairwise way for each of the four concepts the frequency of use between groups and between questions, by applying Fisher's exact tests. *P*-values were adjusted (p_a) to counteract the problem of multiple statistical pairwise comparisons, using the sequential Bonferroni correction (Holm, 1979). Data for all 6th grade secondary students were pooled since there were no significant differences between students of different fields of study. For each of the three questions we tested whether the proportion of students referring to a specific concept differed significantly among the four concepts using a Chi-squared test. If this was the case, pairwise differences between the frequencies of the four concepts were tested using six Fisher's exact tests. We also analysed the total number of different concepts that were addressed by individual students when answering each of the three questions. For this analysis, all four subgroups of students were eventually pooled because for each of the three questions, the proportion of students referring to a specific number of concepts did not differ significantly between the subgroups ($p_a > .11$ for all comparisons between the two subgroups of secondary and between the two subgroups of university students, and $p_a > .55$ for all comparisons between subsequently pooled secondary and pooled university students).

Results

Animal behaviour in Flemish biology textbooks

Three of the five examined textbooks devoted only between 2% and 4% of their pages to animal behaviour (Table 3). Two textbooks (Biologie 4 and Bio-Skoop 4) were exceptions by devoting 11% and 10% of the pages to animal behaviour, respectively, although the

Table 3. An overview of the most frequently used biology textbooks in the fourth year of secondary education by the sampled secondary and first-year university students, the emphasis on each of Tinbergen's questions (ontogeny, causation, function, evolution) in the section on behaviour as indicated by the number of terms printed in a conspicuous way (as a title (=number between parentheses) or in bold/italic) and the major subjects used to teach those concepts.

	%			Ontogeny		Causation				
Textbook	Secondary students	University students	Pages on behaviour	Innate behaviour	Learned behaviour	Internal stimuli	External stimuli	Function	Evolution	Terms in boldface, italic or as a title
Biogenie (D'Haeninck, Cauwenberghs, & Van Werde, 2009)	43.33	26.00	5 (2%)	4 (1)	9 (8)	3 (3)	6 (6)	7[a] (0)	–	29 (18)
Bio voor Jou (Schuermans et al., 2007)	/	16.00	5 (4%)	1 (1)	8 (2)	4 (1)	2 (2)	2[a] (0)	–	17 (6)
Biologie 4 (De Facq, Degadt, & Soffers, 2004)[b]	38.33	/	16 (11%)	1 (1)	6 (5)	–	2 (2)	(+)	–	9 (6)
Bio-Skoop 4 (De Schutter, Neels, Palmans, & Van der Veken, 2003)	11.67	37.00	18 (10%)	1 (0)	6 (0)	–	–	(+)	–	7 (0)
Macro & Micro in de biologie (Geuns, Casteels, Desfossés, & Vincke, 2002)	/	12.00	4 (2%)	1 (1)	3 (1)	–	1 (0)	(+)	–	5 (2)

Note: All subjects were accompanied by examples in the textbooks. Dashes (–) indicate that the concept is not covered. (+) indicates that the concept is covered but not emphasised using terms printed in a conspicuous way.

[a]Terms referring to the function were mentioned in the section on Causation of behaviour, in which they were linked to the causal stimulus.

[b]Covers the learning plan objectives (LPO) of the educational network 'GO! Education of the Flemish Community'. All other textbooks cover the LPO of the main educational network 'the Catholic schools'.

number of pages that were specifically dedicated to explaining why behaviour occurs (which is the focus of Tinbergen's four questions) was much smaller (slightly more than 1% and 6%, respectively). The other pages described examples of different types of behaviour (aggression, sexual behaviour, …). In all but one textbook (Biogenie), behaviour was part of the larger theme 'Relationships between organisms'. The two other topics that were covered within this theme and that preceded the topic on behaviour were 'Communication', including a description of the different types of communication methods in animals, and 'Different levels of associations between organisms', including associations between species and between conspecifics. The textbook Biogenie had a separate chapter about behaviour.

The ontogeny of behaviour was typically emphasised (in titles or using bold/italic) most in all textbooks (see Table 3). The sections on ontogeny mainly included descriptions of the different types of learned behaviours (trial-and-error learning, conditioning, imitating, imprinting, …) with limited emphasis on innate behaviours (innate behaviour, instinct). Causation was addressed (but to a lesser extent) in four out of five textbooks, focusing on internal and external stimuli. Emphasised terms grouped under 'internal stimuli' referred predominantly to hormonal-related subjects while the terms under 'external stimuli' always included 'external stimuli' or 'sign stimuli'. 'Biogenie' was the only textbook in which different types of external stimuli (temperature, day length, pheromones, …) were emphasised. The function of behaviour was emphasised in only two textbooks but was, as contrasted to ontogeny and causation, not explicitly emphasised in a title (Table 3). Moreover, all terms classified as function (and printed in bold) were all mentioned in the section about the causation of behaviour, in which they were linked to the causal stimulus (f.e. 'pheromones motivate reproductive behaviour and social behaviour'). Although the function of behaviour was not explicitly emphasised in all textbooks, they all contained detailed examples/descriptions of specific behaviours, from which the function of the behaviour could be deduced (e.g. reproductive behaviour, aggressive behaviour, …). Evolution of behaviour was not included and Tinbergen's four questions were never explicitly mentioned as a tool in behavioural research in any of the textbooks. Only one textbook (Bio-Skoop) addressed human behaviour, describing the different types of social behaviour in humans.

Use of Tinbergen's questions in the student populations

We first compared to what extent each of Tinbergen's four concepts was addressed in the answers of the two subgroups of secondary students and the two subgroups of first-year university students.

For each of the three questions, the proportion of 4th and 6th grade secondary students addressing a specific concept in their answer did not differ significantly for all four concepts (Fisher exact tests, $p > .05$), apart from one exception. The proportion of 4th grade secondary students referring to ontogeny when answering the Behaviour question was significantly higher than the proportion of 6th grade secondary students (67% versus 39%, $p = .04$). Given that this was the only significant difference between these two groups, and since we were mainly interested in the general patterns in upper-secondary students, data of all secondary students were pooled for further analyses.

The proportion of university students that had taken the specialised evolution course during the first semester and that addressed the evolution of behaviour was 6%, 0% and 0%, respectively, for the Behaviour, Bird song and Hunting questions. These proportions did not differ significantly from the proportions of students that had not taken this course (8%, 1% and 0%, respectively, Fisher exact tests, $p > .7$ in all cases). Also, both groups did not differ significantly with respect to the proportion of students addressing the three other concepts when answering each of the three questions, apart from one exception. A significantly higher proportion of students having taken the specialised evolution course referred to the function of behaviour when answering the Hunting question (89% versus 59%, $p_a = .0002$). Given that this was the only difference between these two groups, data of all university students were pooled for further analyses.

Student explanations of behaviour in general

For both secondary students and university students answering the Behaviour question, the proportion of students addressing a specific concept differed significantly among the four concepts (X^2-test, $p < .0001$ in all cases, see first 'row of bars' in Figure 1(a) and (b)). In addition, the proportion of secondary students and university students addressing a specific concept did not differ significantly for each of the four concepts (Fisher's exact tests, $p_a > .05$ in all cases), although there was a strong tendency ($p_a = .051$) for secondary students to refer more to ontogeny. As a result, the general pattern of the extent to which each of the four concepts was referred to was comparable

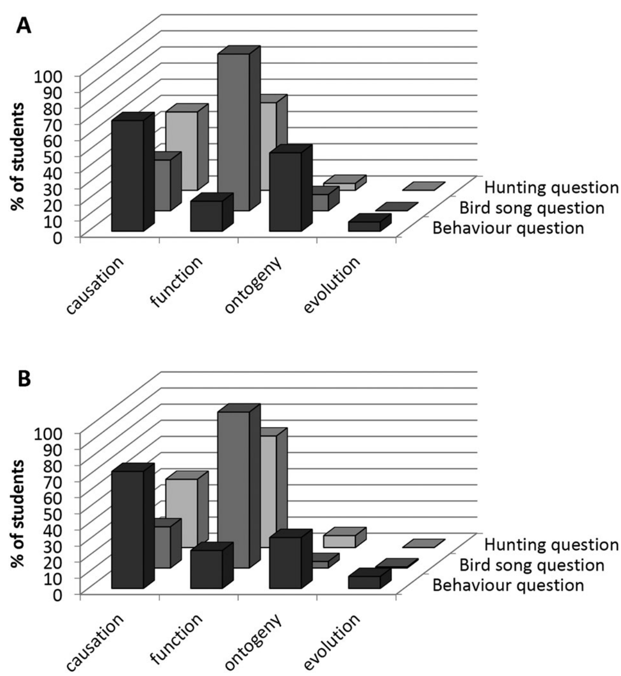

Figure 1. Percentage of secondary school students (a) and first-year university students (b) using a specific Tinbergen's concept (causation, function, ontogeny and evolution) when answering the behaviour, bird song and hunting questions.

in both groups (compare first (front) row of bars in Figure 1(a) and (b)). In both student groups, approximately 70% of the students referred to causation of behaviour, which was referred to significantly more often than all three other concepts. In secondary students, approximately 50% of the students referred to ontogeny, which was significantly higher than both the proportion of students referring to function (18%) and evolution (6%), which were comparable. By contrast, only 31% of the university students referred to ontogeny, which was comparable to the proportion of students referring to function (23%), and significantly higher than the proportion of students referring to the evolution of behaviour, which was only 7%. The latter was referred to significantly less often than all three other concepts.

Student explanations of specific animal behaviours

In both secondary students and university students, the proportion of students referring to a specific concept differed significantly among the four concepts (X^2-test, $p < .0001$ in all cases) for both the Bird song and Hunting questions (see second and third 'row of bars', respectively, in Figure 1(a) and (b)). In addition, for each of these two questions, the proportion of secondary students and university students addressing a specific concept did not differ significantly for each of the four concepts (Fisher's exact test, $p_a > .05$ in all cases), indicating that the overall pattern was highly comparable in both student groups.

Considering the Bird song question, in both student groups, more than 95% of the students addressed the function of this behaviour, which was referred to significantly more often than all three other concepts. The proportion of secondary and university students referring to causation was, respectively, 31% and 25%, which was significantly higher than the proportions of students referring to ontogeny (10% and 4%, respectively) and to evolution (0% and 1%, respectively). The latter was referred to significantly less often than all three other concepts (Figure 1(a) and (b)).

When considering the answers to the Hunting question, both groups of students referred primarily to function (54% of secondary and 69% of university) and causation (49% of secondary and 42% of university), while ontogeny (4% of secondary and 7% of university) was only referred to by a very low proportion of students and evolution was not referred to at all.

For each of the four concepts, the proportion of secondary students referring to it did not differ significantly between the Bird song and the Hunting questions, with the exception that function was referred to significantly less in the Hunting question (Figure 1(a)). The same pattern was found in university students who, in addition, also referred significantly more to causation in the Hunting question (Figure 1(b)). We also compared the proportion of students addressing each of the four concepts between the Bird song and Hunting questions and the Behaviour question. In both groups, students addressed significantly more often the function of behaviour when asked to explain bird song and hunting behaviours (Fisher's exact test, $p < .05$), and also referred significantly less to the ontogeny and the causation of behaviour, compared to when answering the Behaviour question (Figure 1(a) and (b), Fisher's exact test, $p < .05$). The proportion of university students referring to evolution was significantly lower than in the Behaviour question.

Total number of concepts addressed by individual students

Figure 2 shows the number of different concepts that were addressed by *individual* students (all subgroups pooled, see methods) when answering each of the three questions.

For each of the three questions, the majority of the students referred to only one or two concepts, with the proportion of students referring to only one concept (range 47–73%) being significantly higher than the proportion of students referring to two concepts (range 29–31%) (Figure 2). The proportion of students addressing none of the four concepts varied remarkably between the Bird song (0%) and Hunting questions (19%). That 19% of students answering the Hunting question addressed none of Tinbergen's concepts may be explained by the fact that in this question, students were also asked to first describe the behaviour of the lion and have forgotten to subsequently explain the occurrence of this behaviour. Overall, only very few students (range 1–9%) referred to three concepts while, apart from a single university student answering the Behaviour question, none of the students addressed all four concepts.

Specific Tinbergen's concepts addressed by individual students

We also explicitly analysed the specific concepts to which students addressing a specific number of concepts in their answers referred to and compared these between the three questions. The following general patterns emerged (see Table 4 for more detailed information). The specific concepts to which most students addressing only one or two concepts referred to differed between the Behaviour question and the two other questions. When answering the Behaviour question, 72% of students addressing only one concept referred to causation and 90% of students addressing two concepts referred to causation in combination with ontogeny (59%), function (25%) or evolution (6%). By contrast, nearly all students answering the Bird song question referred to function (96%) when using only one concept and to both function and causation (90%) when using two concepts. Likewise, considering the Hunting question, 70% of students referred to function when using only one concept while the majority of students (87%) using two concepts also referred to both function and causation. The very few students addressing three

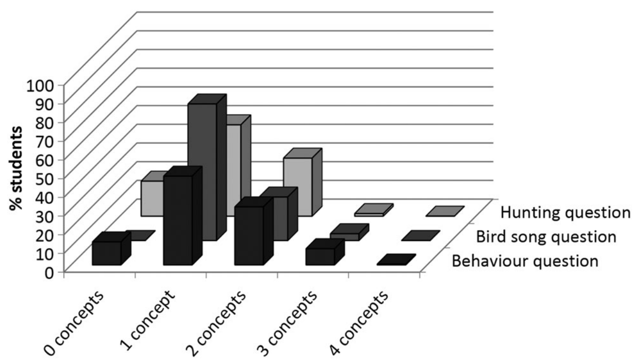

Figure 2. Percentage of students (secondary and first-year university students pooled) using a specific number of Tinbergen's concepts (0, 1, 2, 3 or 4) when answering the behaviour, bird song and hunting questions.

Table 4. The specific (combinations of) Tinbergen's concepts (C = Causation, F = Function, O = Ontogeny, E = Evolution) addressed by individual students using respectively one, two or three concepts when answering the behaviour, bird song and hunting questions.

	Behaviour question	Bird song question	Hunting question
1 concept	*N* = 104	*N* = 160	*N* = 107
Causation	72	4	28
Function	11	96	70
Ontogeny	17	0	2
Evolution	0	0	0
2 concepts	*N* = 68	*N* = 51	*N* = 68
C + O	59	2	7
F + O	7	8	6
C + F	25	90	87
O + E	3	0	0
C + E	6	0	0
F + E	0	0	0
3 concepts	*N* = 19	*N* = 8	*N* = 3
C + F + E	21	0	0
C + F + O	53	100	100
C + O + E	26	0	0
F + O + E	0	0	0

Notes: Values given are the percentage of students. *N* denotes the number of students. Secondary and first-year university students were pooled.

concepts all referred to causation in combination with function and ontogeny when explaining specific behaviours. This was also the case for about half (53%) of these students when answering the general behaviour question (Table 4).

Discussion

Educational practice for animal behaviour

Our explorative analysis of the treatment of animal behaviour in biology textbooks in upper-secondary education in Flanders, Belgium, clearly illustrates that animal behaviour accounts for only a small fraction of biology textbooks and that the practice of teaching animal behaviour does not reflect the current practice of research in the field of animal behaviour (see Fulmer & Hauber, 2013). In none of the investigated textbooks was there an explicit reference to Tinbergen's framework of four questions (causation, ontogeny, function, evolution) as a tool for studying and explaining animal behaviour, although some of his questions were addressed. As prescribed by the single attainment target about animal behaviour, the ontogeny of behaviour was indeed typically addressed and emphasised most in all textbooks, focusing mainly on the different types of learned behaviour. In addition, most textbooks also explicitly addressed and emphasised the causation of behaviour. Hence, current teaching practice in Flanders appears to focus almost exclusively on proximate explanations (ontogeny and causation) of animal behaviour. In addition, it should also be noted that some of the ethological terms that were emphasised in most textbooks, such as 'fixed action pattern' and 'sign stimulus', were important in the past but have not been central to research in animal behaviour for decades (see Alcock, 2013). The latter was also concluded by Bednekoff (2005) when analysing the treatment of animal behaviour in introductory biology textbooks in higher education in the USA. Our recent results, unfortunately, still confirm the conclusion of Van Moolenbroek et al. (2005), after investigating the educational practice in the Netherlands more than 10 years ago, that behavioural biology in secondary education should be innovated.

To what extent do students address Tinbergen's four concepts?

Considering students' responses to the questionnaire, we can draw some general conclusions about the extent to which Tinbergen's concepts are present in students' general conceptions about behaviour and in their explanations of specific animal behaviours, after they experienced the specific educational practice in Flanders.

The typical pattern, in secondary school as well as in first-year university students, is that the majority of students address only one or two of Tinbergen's concepts, but that the specific concepts that are referred to differ markedly between the behaviour question and the two other questions. When asked to explain what they understand by the term behaviour and what they think about when reading this term, the majority of students referred to causation when addressing one concept and to causation in combination with ontogeny when addressing two concepts. By contrast, when students were explaining specific animal behaviours, the majority referred to function (and not to causation) when addressing only one concept and to function in combination with causation when addressing two concepts. These results strongly suggest that only when answering the general behaviour question did students write down what they remember from having learned in secondary school about animal behaviour, where the emphasis is mainly on the ontogeny and the causation of behaviour.

When considering the extent to which each of Tinbergen's four questions was addressed at the student population level, the general patterns were comparable to those typically found in the concepts of individual students, which is of course not surprising. However, this analysis, in addition, also revealed some other interesting patterns and conclusions.

When answering the general behaviour question, the majority (70%) of the students in both student groups referred to the causation of behaviour. Our analyses, both at the individual and population levels, thus revealed that the causation of behaviour, which was emphasised in some, but not all, of the textbooks, was addressed most in the students' explanations of behaviour in general. Hence, although in the educational practice of teaching animal behaviour in Flanders, there is a very strong emphasis on the ontogeny of behaviour, this concept is not represented most in students' general conceptions about behaviour (although it was addressed the second most). Our analyses also revealed that there was a strong tendency ($p = .051$) for secondary students to refer more to ontogeny when answering the general behaviour question than university students did. This may have been due to the fact that the population of secondary students also included 4th grade students who did refer significantly more to ontogeny than 6th grade students. This most likely results from the fact that they had recently learned about animal behaviour, while the other student groups probably had largely forgotten what they had learned in the 4th grade. Georghiades (2000) noted that limited research in science education addresses the issue of durability. Although durability should preferentially be investigated using a longitudinal study (see Pugh et al., 2014), our results, based on a cross-sectional comparison, strongly suggest a decrease of learned knowledge over time. However, it was striking that our analyses of students' explanations of behaviour in general (with a prevalence of causation and ontogeny) only revealed a decrease in memory over time for ontogeny, but not for causation. The latter may be due to the fact that causation is a concept that is also emphasised in formal biology education in general, where most issues are presented through cause and effect (Wilke & Straits, 2005), while this is less the case for ontogeny (so students may more likely forget this concept). In addition, cognitive psychologists have shown that our minds are strongly biased towards causal explanations (e.g. Sloman, 2005; Kahneman, 2012), which may also have contributed to the fact that most students explaining behaviour in general addressed causation.

By contrast, when secondary and first-year university students are asked to give as many explanations as possible for the occurrence of bird song and hunting behaviour, the majority of the students addressed the function of behaviour and, although to a much lesser extent, the causation of behaviour. It could be argued that our results may not be generalised since students only had to explain two specific animal behaviours and results, therefore, may have been different if we had selected other behaviours. However, the general pattern was highly comparable for both behaviours, except that function was referred to significantly less and causation significantly more in the hunting question in both student groups. The latter was most likely due to the more obvious presence of a stimulus causing the behaviour (i.e. the zebra) in the hunting question, suggesting there may have been item feature effects on knowledge retrieval (see also Nehm & Ha, 2011).

Our result that the majority of students trying to explain specific behaviours always referred, at a minimum, to the function of these behaviours, although this concept was hardly emphasised in the biology textbooks and probably also not by the biology teacher, is however not surprising. The first question that children or students usually ask when observing animal behaviour is: 'Why is this animal behaving this way?' (Bolhuis, 2002). Hence, this concept is probably already present in their precognition before they are taught about animal behaviour. In fact, cognitive science research indeed has demonstrated that humans naturally and intuitively reason about biological entities, structures, processes and phenomena in a predictable way (e.g. Coley, Solomon, & Shafto, 2002; Coley & Tanner, 2012, 2015). One of these so-called cognitive construals, teleological thinking, may explain why the majority of students addressed the function of behaviour when explaining specific animal behaviours. Teleological thinking is a common type of causal reasoning based on the assumption of a goal, purpose or function (Kelemen, 1999; Kelemen & Rossett, 2009). Biology education researchers have indeed documented the existence of teleological thinking among both high school and university students (Nehm & Ridgway, 2011). Moreover, Coley and Tanner (2015) compared the use of construal-based reasoning in discipline-based biology problems between biology majors (first semester undergraduates) and nonmajors, and found no differences between both student groups. Likewise, we also found no differences between responses of secondary and first-year university students, despite the two student groups differing in several aspects. The group of secondary students was more heterogeneous with respect to age, their interest in biology in general and probably also their study performance (not all secondary students eventually enrol in university education) than the university students who were all enrolled in biology-related fields of study. On the other hand, secondary students all were taught by the same teacher, which decreased the variability among students' background and implies that students' knowledge in the topic as a result of formal animal behaviour (or biology in general) instruction was constructed based on these two main sources (the teacher and the textbook). By contrast, the university students may have been highly variable regarding these two sources. Hence, the high similarity between the secondary school and university samples' patterns of responses may not result from formal education in animal behaviour, but may largely be due to the presence of intuitive teleological thinking. This is also supported by the lack of differences between 4th grade and 6th grade secondary students, although the latter experienced more formal biology education. However, functional approaches are also common in formal biology education in general (Lahiri, 1977; Thornton, Todd, Milburn, Borkakoti, & Orengo, 2000), which may also have contributed to the results.

Likewise, the fact that that our minds are apparently strongly biased towards causal explanations (Sloman, 2005) may also explain to some extent the prevalence of causation in both student groups when explaining specific behaviours. Van Moolenbroek, Boersma, and Waarlo (2007) studied the precognition of Dutch secondary school students who had not yet been taught about animal behaviour using interviews instead of an open-ended questionnaire. They reported that the concepts of function and causation (but also ontogeny) were indeed represented in the answers, while the concept of evolution was considered as absent. However, given that causation was emphasised during animal behaviour teaching and also in biology education in general (Wilke & Straits, 2005), formal education may also have contributed to some extent to these results.

Our results also revealed that evolution was generally not addressed in both secondary and university students' explanations of animal behaviour. Considering secondary students, this is as expected, given that (1) the evolution of behaviour is completely neglected when students are taught about animal behaviour in the fourth grade, (2) the general concept of evolution is only taught in the last (sixth) grade of secondary education in Flanders, with only a few lessons being dedicated to this concept and (3) there is also no explicit reference to the evolution of behaviour in the biology textbooks of the 6th grade (pers. obs.). This suggests that students graduating from secondary school and enrolling in university education have no deep understanding of this concept. The latter is supported by our result that first-year university students that had not taken a specialised evolution course during the first semester also generally completely neglected the evolution of behaviour in their explanations.

To what extent do students transfer knowledge?

An important goal in science education is to strive for students to progress to deep understanding of concepts, which includes the ability to apply knowledge learned in one context to a different one (Anderson & Schönborn, 2008). In the present study, we investigated knowledge transfer in the domain of animal behaviour.

First, our results showed that even first-year university students that had recently completed a semester-long course on evolution did not address evolution when explaining specific behaviours and hence did not spontaneously apply this knowledge to the domain of animal behaviour. Given that in Flanders, people in general do not believe in creationism, it is highly unlikely that students' lack of belief in evolution may have affected transfer of the concept of evolution. Our results are in line with the results of Pugh et al. (2014) investigating the abilities of 3th and 4th grade secondary students to transfer the concept of natural selection. They concluded that transfer and duration of transfer were fairly limited and that only a few students seemed prepared to use the concept of natural selection in a generative way to understand phenomena in other knowledge domains.

Second, our results also revealed that while most secondary and university students address causation and ontogeny when asked what they understand about behaviour in general, they apparently did not spontaneously apply or transfer the concept of ontogeny when asked to explain specific animal behaviours, since only a very low proportion of students addressed this concept. Hence, as contrasted to the concept of causation, there appeared to be limited transfer of the concept of ontogeny.

Based on our results, we recommend that teachers should more explicitly focus on fostering transfer of the concepts of ontogeny and evolution and use specific teaching for transfer strategies.

Conclusions and educational implications

The results of this study indicate that in the practice of teaching animal behaviour in secondary education in Flanders, Belgium, there is clearly no explicit reference to Tinbergen's framework of four questions (causation, function, ontogeny and evolution) as a tool to study animal behaviour. As a result, most upper-secondary and even first-year university students in Flanders most likely are not aware of all four different sorts of questions that scientists currently ask about animal behaviour. It should be noted that, in the present study, we have, unfortunately, not explicitly asked students whether or not they are familiar with Tinbergen's framework. Therefore, we additionally inquired third-year university biology students ($n = 38$) entering a behavioural biology course and all confirmed that they indeed were not yet aware of this framework. If students do not understand the sort of questions that scientists ask about animal behaviour, it may be difficult for them to understand how scientists test hypotheses about animal behaviour. Given the strong focus on scientific inquiry-based learning in the attainment goals of secondary biology education (Kremer et al., 2014), we highly recommend that Tinbergen's conceptual framework should be explicitly addressed in biology textbooks, or that, at least, teachers should explicitly focus on it when teaching animal behaviour. While explaining that four different questions need to be answered for a complete understanding of animal behaviour, teachers can emphasise the importance of asking the right question in scientific research and of having a clear idea of what would count as an answer.

Although Tinbergen's framework emphasises the need for an integrated understanding, it should be admitted that, generally, his four questions are still mainly studied independently in (current) animal behaviour research, although functional and evolutionary questions are often combined together, and likewise so too are mechanistic and developmental questions (Bateson & Laland, 2013a). In relatively few cases have all four of Tinbergen's questions been answered for a single characteristic. At present, communication, and in particular bird song, is probably the area of animal behaviour that best illustrates how answers to all four questions come together to provide more complete explanations (Eens, Pinxten, & Verheyen, 1991, 1993; Eens, 1997; McGregor, 2005; Pinxten, De Ridder, Balthazart, & Eens, 2002; see Figure 1 in Bateson & Laland, 2013a, for answers to all four questions with respect to bird song). Given that most students are very familiar with bird song and that communication is addressed in the section about animal behaviour in most biology textbooks in secondary education (at least in Flanders) and hence should be taught anyway, this provides a great opportunity to illustrate the importance of Tinbergen's conceptual framework for an integrated understanding. Given that evolution is normally only taught in the 6th grade, the evolution of bird song could be treated in a simplified way in the 4th grade when animal behaviour is taught, and treated again, but more thoroughly, in the 6th grade when evolution is taught.

In addition, although Tinbergen's four questions' were framed for behaviour, it has been recently emphasised that they are equally useful for other traits in living systems and thus can be extended to the full range of biology (Bateson & Laland, 2013a; Nesse, 2013). Indeed, all traits in living organisms need all four explanations. We need to know how they work, how they develop, their phylogeny and how past variations have influenced fitness in ways that help to explain current forms. Hence, given the broad applicability of Tinbergen's framework to explain the occurrence of specific characteristics in living creatures, it could also be regarded as a tool to further develop 'biological thinking' in students (Boersma & Schermer, 2001). In approaching a trait from these different perspectives, students are encouraged to employ a more elaborate way of thinking and will develop more accurate mental models of particular phenomena in Biology. It could therefore be argued that also for this reason Tinbergen's four questions should be an integral part of any biology curriculum in secondary education. Likewise, Nehm et al. (2009) already stressed that, given that every topic in biology is related to and dependent on evolutionary analyses, there should be an active integration of evolutionary concepts at all levels and across all domains of introductory biology (see also Hillis, 2007).

As emphasised by Strassmann (2014), the challenge for the future is to apply concepts from animal behaviour across biology with tools that would have amazed Niko Tinbergen.

Acknowledgements

We are grateful to all the participating students and to the student biology teachers who administered the open-response questionnaires. We also wish to thank three anonymous reviewers for their constructive suggestions and Josie Meany-Ward for contributing with language suggestions.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported financially by the Institute of Instructional and Educational Sciences, University of Antwerp.

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References

Alcock, J. (2013). *Animal behaviour: An evolutionary approach*. Sunderland: Sinauer Associates.

Anderson, T. R., & Schönborn, K. J. (2008). Bridging the educational research-teaching gap. Conceptual understanding, part 1: The multifaceted nature of expert knowledge. *Biochemistry and Molecular Biology Education*, *36*, 309–315.

ATB-2nd grade ASO. (2012). *Attainment targets for biology for the second grade of general secondary education*. Flemish Ministry of Education. Brussels.

Bateson, P., & Laland, K. N. (2013a). Tinbergen's four questions: An appreciation and an update. *Trends in Ecology & Evolution*, *28*, 712–718.

Bateson, P., & Laland, K. N. (2013b). On current utility and adaptive significance. A response to Nesse. *Trends in Ecology & Evolution*, *28*, 682–683.

Bednekoff, P. A. (2005). Animal behavior in introductory textbooks: Consensus on topics, confusion over terms. *BioScience*, *55*(3), 2–6.

Bell, R., Smetana, L., & Binns, I. (2005). Simplifying inquiry instruction: Assessing the inquiry level of classroom activities. *The Science Teacher*, *72*(7), 30–33.

Boersma, K. T., & Schermer, A. (2001). Ontwikkeling van een nieuw biologieprogramma in de 21e eeuw [Development of a new Biology programme in the 21th century]. *Tijdschrift voor Didactiek der β-wetenschappen*, *18*, 19–41.

Bolhuis, J. J. (2002). *De Evolutie van de Gedragsbiologie*. Oratie bij de aanvaarding van het ambt als hoogleraar gedragsbiologie aan de Universiteit van Utrecht [The Evolution of Behavioural Biology. Inaugural lecture at the acception of the position as Professor of Behavioral Biology at the University of Utrecht]. Retrieved from http://web.science.uu.nl/behaviour/bolhuis/BolhuisOratie.

Bolhuis, J. J., & Giraldeau, L.-A. (2005). *The behaviour of animals. Mechanisms, function, and evolution*. Oxford: Blackwell.

Chiappetta, E. E., Ganesh, T. G., Lee, Y., & Phillips, M. C. (2006). *Examination of science textbook analysis research conducted on textbooks published over the past 100 years in the United States*. Paper presented at the annual meeting of the National Association for Research in Science Teaching, San Francisco, CA.

Chiappetta, E. L., & Koballa, T. R. (2002). *Science instruction in the middle and secondary schools* (5th ed.). Upper Saddle River, NJ: Merrill/Prentice Hall.

Coley, J. D., Solomon, G. E. A., & Shafto, P. (2002). The development of Folk biology: A cognitive science perspective on children's understanding of the biological world. In P. Kahn & S. Keller (Eds.), *Children and nature: Psychological, sociocultural and evolutionary investigations* (pp. 65–91). Cambridge, MA: MIT Press.

Coley, J. D., & Tanner, K. (2012). Common origins of diverse misconceptions: Cognitive principles and the development of biology thinking. *CBE-Life Sciences Education*, *11*, 209–215.

Coley, J. D., & Tanner, K. (2015). Relations between intuitive biological thinking and biological misconceptions in biology majors and nonmajors. *CBE-Life Sciences Education*, *14*, 1–19.

De Facq, F., Degadt, D., & Soffers, R. (2004). *Biologie 4*. Malle: de Sikkel.

De Schutter, P., Neels, L., Palmans, R., & Van der Veken, M. (2003). *Bioskoop 4*. Kapellen: Pelckmans.

D'Haeninck, L., Cauwenberghs, P., & Van Werde, K. (2009). *Biogenie 4.1*. Antwerpen: De Boeck nv.

DiGiuseppe, M. (2014). Representing nature of science in a science textbook: Exploring author–editor–publisher interactions. *International Journal of Science Education*, *36*(7), 1061–1082. doi:10.1080/09500693.2013.840405

Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, *35*, 125–129.

Dugatkin, L. A. (2014). *Principles of animal behaviour*. New York, NY: W.W. Norton & Company.

Eens, M. (1997). Understanding the complex song of the European starling: An integrated ethological approach. *Advances in the Study of Behavior*, *26*, 355–434.

Eens, M., Pinxten, R., & Verheyen, R. F. (1991). Male song as a Cue for Mate choice in the European starling. *Behaviour*, *116*, 210–238.

Eens, M., Pinxten, R., & Verheyen, R. F. (1993). Function of song and song repertoire in the European starling (Sturnus vulgaris): An aviary experiment. *Behaviour*, *125*, 51–66.
Fulmer, A. G., & Hauber, M. E. (2013). A celebration of a true milestone of ethology: 50 years of Tinbergen (1963). *Ethology*, foreword of Special Virtual Issue.
Georghiades, P. (2000). Beyond conceptual change learning in science education: Focusing on transfer, durability and metacognition. *Educational Research*, *42*, 119–139. doi:10.1080/001318800363773
Geuns, J., Casteels, V., Desfossés, F., & Vincke, J. (2002). *Macro micro in de biologie*. Wolters Plant.
Hillis, D. M. (2007). Making evolution relevant and exciting to biology students. *Evolution*, *61*(6), 1261–1264.
Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*, 65–70.
Kahneman, D. (2012). *Thinking fast and slow*. New York, NY: Farrar, Strauss & Giroux.
Kelemen, D. (1999). The scope of teleological thinking in preschool children. *Cognition*, *70*, 241–272.
Kelemen, D., & Rossett, E. (2009). The human function compunction: Teleological explanations in adults. *Cognition*, *111*, 138–143.
Kremer, K., Specht, C., Urhahne, D., & Mayer, J. (2014). The relationship in biology between the nature of science and scientific inquiry. *Journal of Biological Education*, *48*(1), 1–8. doi:10.1080/00219266.2013.788541
Lahiri, A. (1977). The functional approach in biology. *Biosystems*, *9*, 57–68.
Levitis, D.A., Lidicker, W. Z.Jr., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, *78*, 103–110.
Marini, A., & Genereux, R. (1995). The challenge of teaching for transfer. In A. McKeough, J. Lupart, & A. Marini (Eds.), *Teaching for transfer: Fostering generalization in learning* (pp. 1–19). Mahwah, NJ: Lawrence Erlbaum.
Martin, P., & Bateson, P. (2007). *Measuring behaviour. An introductory guide*. Cambridge: University Press.
Mayer, R. E. (2002). Rote versus meaningful learning. *Theory Practice*, *41*, 226–232.
McGregor, P. K. (2005). Communication. In J.J. Bolhuis, & L-A. Giraldeau (Eds.), *The behaviour of animals. Mechanisms, function, and evolution* (pp. 226–250). Oxford: Blackwell.
Nehm, R. H., & Ha, M. (2011). Item feature effects in evolution assessment. *Journal of Research in Science Teaching*, *48*, 237–256.
Nehm, R. H., Poole, T. M., Lyford, M. E., Hoskins, S. G., Carruth, L., Brent, E. E., & Colberg, P. J. S. (2009). Does the segregation of evolution in biology textbooks and introductory courses reinforce students' faulty mental models of biology and evolution? *Evolution Education Outreach*, *2*, 527–532. doi:10.1007/s12052-008-0100-5
Nehm, R. H., & Ridgway, J. (2011). What do experts and novices "see" in evolutionary problems? *Evolution Education Outreach*, *4*, 666–679.
Nesse, R. M. (2013). Tinbergen's four questions, organized: A response to Bateson and Laland. *Trends in Ecology & Evolution*, *28*, 681–682.
NRC. (2010). *Research at the intersection of the physical and life sciences* (p. 106). Washington, DC: National Academics Press.
NSF Workshop. (2012). 2012 animal behavior workshop report. *National Science Foundation*, 1–21. Retrieved from the National Science Foundation website: http://nsf.gov/pubs/2012/bio12008/bio12008.pdf
Pinxten, R., De Ridder, E., Balthazart, J., & Eens, M. (2002). Context-dependent effects of castration and testosterone treatment on song in male European starlings. *Hormones and Behavior*, *42*, 307–318.
Pugh, K. J., Koskey, K. L. K., & Linnenbrink-Garcia, L. (2014). High school biology students' transfer of the concept of natural selection: A mixed methods approach. *Journal of Biological Education*, *48*, 23–33.
Ryan, M. J., & Wilczynski, W. (2011). *An introduction to animal behavior. An integrative approach*. New York, NY: Cold Spring Harbor Laboratory Press.

Schuermans, G., Barbez, D., Covens, M., Crauwels, M., Nerinckx, I., & Schotsaert, P. (2007). *BIO voor JOU*. Wommelgem: Van In.

Schwartz, R. S., Lederman, N. G., & Crawford, B. A. (2004). Developing views of nature of science in an authentic context: An explicit approach to bridging the gap between nature of science and scientific inquiry. *Science Education*, *88*(4), 610–645.

Sloman, S. A. (2005). *Causal models: How we think about the world and its alternatives*. New York, NY: Oxford University Press.

Stamp Dawkins, M. (2014). Tribute to Tinbergen: Questions and how to answer them. *Ethology*, *120*, 120–122.

Stern, L., & Roseman, J. E. (2004). Can middle-school science textbooks help students learn important ideas? Findings from project 2061's curriculum evaluation study: Life science. *Journal of Research in Science Teaching*, *41*(6), 538–568.

Strassmann, J. E. (2014). Tribute to Tinbergen: The place of animal behavior in biology. *Ethology*, *120*, 123–126.

Taborsky, M. (2014). Tribute to Tinbergen: The four problems of biology. *A Critical Appraisal. Ethology*, *120*, 224–227.

Thornton, J. M., Todd, A. E., Milburn, D., Borkakoti, N., & Orengo, C. A. (2000). From structure to function: Approaches and limitations. *Nature Structural & Molecular Biology*, *7*, 991–994. doi:10.1038/80784

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433.

Van Moolenbroek, A. (2012). *Be aware of behaviour. Learning and teaching behavioural biology in secondary education* (Unpublished doctoral dissertation). Utrecht University, Utrecht.

Van Moolenbroek, A., Boersma, K. T., & Waarlo, A. J. (2005). Gedrag in de biologiemethoden achterhaald [Behaviour is outdated in biology textbooks]. *Niche*, *36*, 16–20.

Van Moolenbroek, A., Boersma, K. T., & Waarlo, A. J. (2007). Denkbeelden van leerlingen over gedrag van mens en dier en het onderzoeken daarvan [Conceptions of students about behaviour of humans and animals and investigating these conceptions]. *Tijdschrift voor Didactiek der β-wetenschappen*, *24*, 5–30.

Weiss, I. R., Pasley, J. D., Smith, P. S., Banilower, E. R., & Heck, D. J. (2003). *Looking inside the classroom: A study of K-12 mathematics and science education in the United States*. Chapel Hill, NC: Horizon Research, Inc.

Wilke, R., & Straits, W. J. (2005). Practical advice for teaching inquiry-based science process skills in the biological sciences. *American Biology Teacher*, *67*(9), 534–540. doi:10.1662/0002-7685(2005)067[0534:PAFTIS]2.0.CO;2