EDITORIAL

Ethology into a new era

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What's in the news?

As of this issue, Ethology sports a new attire. Those who prefer to hold a printed copy in hand instead of being contented with a computer screen presentation will recognize an increase in size, in all dimensions. This became necessary because of the growing popularity of the journal. Probably the major reason for this increase in attractiveness is Ethology's rapid submission to publication times (on average less than 2 months between submission and decision, and 2.9 months between final acceptance and print publication; source: electronic editorial office database, year 2004). With the steady increase in manuscript submissions (17% annual increase in recent years), speed as a major quality of *Ethology* would be at risk if the acceptance rates were to remain at appropriate levels (nearly 40% in recent years). Therefore, the publisher and editors decided to increase the number of pages published. We took this opportunity to change the layout and appearance, hopefully to the reader's liking.

Also new is that manuscripts will now be published online as soon as proof reading has been completed, that is within a few days of receipt of corrected proofs from authors. This too will accelerate dissemination of scientific progress to our readers. OnlineEarly articles are fully peer reviewed, edited and complete - only lacking page numbers and volume/issue details - and are considered fully published from the date they first appear online. This date is shown with the article in the online of contents (see http://www.blackwelltable synergy.com/loi/eth). The articles are available as full text HTML or PDF and can be cited as references by using their Digital Object Identifier (DOI) number. OnlineEarly is automatically available to those with a subscription to Synergy, the online journals service from Blackwell Publishing. Once allocated to an issue, the article is removed from the OnlineEarly area and appears instead in the relevant online issue prior to going to print.

Recent developments

Six years have passed since the last major changes took place with Ethology. This is an opportunity to contemplate the journal's development: what have we achieved, where are we heading? Our strategy set forth in 2000 has been simple from the start: an active team of editors going all out for high speed of handling, proficiency and transparency. At a time when many journals conceal from their authors their procedures, the logic of their decisions and even the identity of their editors, our policy strives for the opposite: in our view the scientific process should be as open and intelligible as possible, from generating ideas and data collection right through to the discussion and publication of results. Anonymous editors is not our style. Personally, I believe that even peer reviews should not be anonymous; if critique is based on arguments, its instigator does not need to hide from the appraised. If it is not based on arguments, it should not be uttered. However, as this view is not indisputable, we leave it to our reviewers, of course, whether they wish to reveal their identity. In any case, publication statistics prove us right in general, and are corroborated by an increase in the journal's impact factor by about 45% over four years (mean 1998-2000 = 1.1; mean 2002-2004 = 1.6; source: ISI data base).

A feature introduced in 2000 has been our "Current Issues – Perspectives and Reviews" section. Leading ethologists contribute novel insights and personal syntheses about hot topics and particularly active fields of research. This has become a very popular section of the journal, as derived from its heavy use and citation (mean impact factor of these

articles 8.24 over 2001-2005). We shall intensify our emphasis on this section in the future. Another feature introduced in January 2000 was online access to the journal, which has clearly contributed to the journal's success: yearly increase of online access >>30%, e.g. 44,755 downloads of online articles in 2004 (latest year for which a complete data set is available). About 10% of articles published in Ethology are downloaded >200 times already within the same year as publication. An example may illustrate this high throughput: the online version of a recent paper on behavioural causes and consequences of sexual size dimorphism (Blanckenhorn 2005, published in November 2005) was accessed 283 times already within two weeks of publication. Prime recognition of the journal by behavioural scientists corresponds to Ethology's good distribution: it is currently subscribed by 2844 consortia, institutions and databases worldwide, with tendency still rising.

One feature suggested in my Editorial in January 2000 has not been used as strongly as anticipated: the possibility to write 'Commentaries', for instance on controversial issues. I regret this because we view scientific discussion as a crucial (and rather underrepresented) component of scientific progress. Therefore, I renew herewith my encouragement to submit such papers to *Ethology* and assure priority treatment, i.e. very speedy handling.

What is the development of ethology as a field?

To answer this question, we should first clarify: what in fact is ethology? What may seem like a strange question is in fact timely to ask due to the dynamics of behavioural science. Ethology deals with the study of behaviour at four different levels, evolution, function, development and causation. These four main questions in behavioural research were identified by Niko Tinbergen (1963) in his seminal paper "On aims and methods of ethology" (published in this very journal, then called "Zeitschrift für Tierpsychology"). Tinbergen thought that a comprehensive, coherent science of ethology has to give equal attention to each level and to their integration. What has come of this pious hope? Is there a balance in research between Tinbergen's famous four questions, or is ethology a "four-legged animal hopping around on one big leg, with the other three dangling somewhat ineffectively", as caricatured by Marian Dawkins in 1989? Her allusion to the dominance of behavioural ecology among the subdisciplines of ethology was certainly justified during its hype period in the late eighties. In the meanwhile, however,

ethology has somewhat regained its balance, as a brief look through our latest volume (Ethology 111) demonstrates: questions of evolution (e.g. Andersson 2005, Blanckenhorn 2005, Fieder et al. 2005, Handley & Nelson 2005, Leoncini & Rivault 2005), development (e.g. Amorim & Hawkins 2005, Brännäs et al. 2005, Creer 2005, Hager & Johnstone 2005, King et al. 2005) and causation (e.g. Freake & Phillips 2005, Holland et al. 2005, Jandt & Jeanne 2005, Neff & Sherman 2005, Poisbleau et al. 2005, Sumana et al. 2005) have come on stage again, even if the study of "function" may still be the favourite target of the field (e.g. Aisenberg & Costa 2005, Kopisch et al. 2005, Woodcock et al. 2005, Loyau et al. 2005, O'Brien et al. 2005, Prokop & Vaclav 2005). This is an important step forward.

Ethology is less characterized by a common theory than by an approach (Bateson & Klopfer 1989), namely to address Tinbergen's four questions in such a way that they mutually inform one another. A critical survey may reveal that this aim has been fulfilled only rarely. Yet there is growing awareness among researchers of animal behaviour that this is indeed an aim worth pursuing. In some model systems considerable distance has been covered towards this end. For example, a target species popular since the early days of ethology is the honeybee. Whilst in the times of Karl von Frisch it was mainly communication and orientation that topped the research agenda (v. Frisch 1923, 1940, 1962, 1965), more recently much interest has been expressed in the origin of bee sociality (Michener 1974), which spawned excellent data on behavioural function (Schmickl & Crailsheim 2002, Tarpy et al. 2004, Pastor & Seeley 2005), causation (Robinson 2002, Land & Seeley 2004, Schneider et al. 2004), development (Sullivan et al. 2000, Rueppell et al. 2004, Elekonich & Roberts 2005) and evolution (Gadau et al. 2000, Tarpy & Page 2002, Linksvayer & Wade 2005). Among behavioural studies of vertebrates, successful examples of a comprehensive approach include vocal communication in birds (Catchpole & Slater 1995, Slater 2003, Marler & Slabbekoorn 2004), especially the learned songs of passerine birds, which have been adopted as model system by the behavioural, cognitive and neurosciences alike (Brainard & Doupe 2002). Glancing through recent volumes of *Ethology* shows that studies of the neurobiological and molecular bases of song learning and adult singing are complemented by studies on behavioural development (Soha & Marler 2001, King et al. 2005), geographic variation in song as one of the consequences of vocal learning (Runciman et al. 2005), the functions of song as territorial signal and in mate choice and mate stimulation (Beebee 2004, Martin-Vivaldi et al. 2004, Mota & Depraz 2004, Hile et al. 2005, Hyman 2005), and by comparative studies concerned with the evolution of vocal learning, song type repertoires and dialects (Handley & Nelson 2005, Nelson et al. 2004). Both the mechanistic and functionally oriented approaches keep on generating hypotheses addressed by the respective other field, which demonstrates the strength of an integrated approach. Studies of songbird behaviour generate new insights in themes as general and diverse as interactions between the genome and learning (Haesler et al. 2004), the separation of gonadal from genetic effects on sexual brain differences (Agate et al. 2003), the functional significance of variety in song learning strategies (Beecher & Brenowitz 2005), the function and development of female song and duetting (Langmore 1998, Riebel 2003, Hall 2004), and the importance of gene-culture co-evolution in bird song learning (Lynch et al. 1989, Lachlan & Servedio 2004).

Despite the enormous popularity and success of behavioural research, there is a certain scepticism among contributors to this field about ethology as a (timely) discipline. These reservations, however, concern the term, not the science. Many "ethologists" of the seventies have now turned into "evolutionary biologists", following an extended period as "behavioural ecologists" in the eighties and nineties. Research fields with a history appear old fashioned after a change in paradigm, which may suggest that a change of name is appropriate, like in the fashion industry. But it is the change of paradigm that we should consider when musing about scientific progress. For example, was the advent of "behavioural ecology" in the seventies a significant step forward? Clearly it was. The consequent application of evolutionary theory to the study of behaviour greatly improved its scientific value (Krebs & Davies 1978). Rigorous hypothesis testing succeeded the all too frequent habit of collecting descriptive data, which were often interpreted by more or less arbitrary post-hoc explanations. But clearly, casting one's eyes on the study of evolutionary mechanisms alone did not go far enough. Trying to understand the adaptive value of a trait without understanding the underlying mechanisms is like trying to construct a turning wheel without understanding the function of ball-bearings; it won't work well. In behavioural ecology, all too often coincidence with a prediction has been misinterpreted as its proof. Even if such practice still happens, the general thrust of behavioural research has fortunately turned towards a more comprehensive approach. Ethology has regained its balance to a considerable extent since behavioural ecology, the study of adaptive function and arguably ethology's most successful branch in the recent past, is more and more complemented by profound research on mechanisms.

If this is true, why do behavioural scientists often still hesitate to speak of "ethology" when referring to their research? "Behavioural biology" is a term that emerged a few years ago to cover behavioural research going beyond the study of just one of Tinbergen's "four legs". When ethologists in Europe recently decided to combine their local meetings on a European level, they named the resulting conference series "European Conferences on 'Behavioural Biology''' (ECBB), not on 'Ethology'. The reason is probably that ethology is often mixed up with the Lorenzian approach, which in fact had little concern for how evolution works (see Burkhardt 2005). "Classical ethology" is indeed a field that largely has lost its practical significance, which in no way hampers its historical importance. No matter, this is all semantics. Ethology, behavioural biology what's in a word? The important - and indeed highly appreciated - development is the recalling of the integrative nature of behavioural research, ethology's true forte.

Ethology - the journal

What is the role of *Ethology* as a journal in this development? The "Zeitschrift für Tierpsychologie", this journal's original title, was founded in 1937 as the first international journal for the scientific study of animal behaviour. It has published original work from all branches of behavioural research and on all major animal taxa ever since. A brief look through the latest volumes demonstrates the breadth of topics and approaches, including basic research on the function, causation, development and evolution of behaviour (majority of papers; see examples given above), animal breeding and husbandry (Illmann et al. 2005), conservation (Blumstein et al. 2004), methodology (Baker & Logue 2003), cognition (Heinrich & Bugnyar 2005), comparative analyses (Iwaniuk & Arnold 2004) and theoretical models (Jeschke & Tollrian 2005). A wide range of animal taxa is represented: Volume 111 contains behavioural studies of molluscs (in total 1.4% of empirical papers; Soto et al. 2005), crustacea (2.7% of total; e.g. Gherardi & Atema 2005), spiders (10.8%; e.g. Futami & Akimoto 2005), insects (16.2%;

e.g. Saeki et al. 2005), fish (10.8%; e.g. Wilson & Stevens 2005), anurans (9.5%; e.g. Smith & Hunter 2005), reptiles (4%; e.g. Martin & Lopez 2005), birds (24.3%; e.g. Quader 2005) and mammals (20.3%; e.g. Jennings et al. 2005; this includes also nonhuman primates (10.8% of total; e.g. Wittig & Boesch 2005) and humans (1.4% of total; Fieder et al. 2005)). Field and lab research is reported in a representative mix and authoritative reviews complement the journal's contents (e.g. Johnstone 2000, Penn 2002, Blanckenhorn 2005). For the future, we should attempt to keep this balance. It is the breadth of topics and approaches, the integration of studies on ultimate and proximate mechanisms, that is and should remain *Ethology's* objective. Our authors, reviewers and our editorial team will strive to contribute towards this end.

Literature Cited

Agate, R. J., Grisham, W., Wade, J., Mann, S., Wingfield, J., Schanen, C., Palotie, A. & Arnold, A. P. 2003: Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. Proc. Natl. Acad. Sci. USA **100**, 4873–4878.

Aisenberg, A. & Costa, F. G. 2005: Females mated without sperm transfer maintain high sexual receptivity in the wolf spider *Schizocosa malitiosa*. Ethology **111**, 545—558.

Amorim, M. C. & Hawkins, A. D. 2005: Ontogeny of acoustic and feeding behaviour in the grey gurnard, *Eutrigla gurnardus*. Ethology **111**, 255–269.

Andersson, M. 2005: Evolution of classical polyandry: three steps to female emancipation. Ethology **111**, 1—23.

Baker, M. C. & Logue, D. M. 2003: Population differentiation in a complex bird sound: A comparison of three bioacoustical analysis procedures. Ethology **109**, 223—242.

Bateson, P. P. G. & Klopfer, P. H. 1989: Whither ethology? Perspectives in Ethology 8. Plenum Press, New York.

Beebee, M. D. 2004: Variation in vocal performance in the songs of a Wood-Warbler: Evidence for the Function of Distinct Singing Modes. Ethology **110**, 531–542.

Beecher, M. D. & Brenowitz, E. A. 2005: Functional aspects of song learning in songbirds. Trends Ecol. Evol. 20, 143—149.

Blanckenhorn, W. U. 2005: Behavioral causes and consequences of sexual size dimorphism. Ethology 111, 977—1016.

Blumstein, D. T., Daniel, J. C. & Springett, B. P. 2004: A test of the multi-predator hypothesis: rapid loss of

antipredator behavior after 130 years of isolation. Ethology **110**, 919–934.

- Brainard, M. S. & Doupe, A. J. 2002: What songbirds teach us about learning. Nature **417**, 351—358.
- Brännäs, E., Berglund, U. & Eriksson, L. O. 2005: Time learning and anticipatory activity in groups of arctic charr. Ethology **111**, 681–692.
- Burkhardt, R. W. Jr 2005: Patterns of Behavior: Konrad Lorenz, Niko Tinbergen and the Founding of Ethology. University of Chicago Press, Chicago.
- Catchpole, C. K. & Slater, P. J. B. 1995: Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge.

Creer, D. A. 2005: Correlations between ontogenetic change in color pattern and antipredator behavior in the racer, *coluber constrictor*. Ethology **111**, 287—300.

- Elekonich, M. M. & Roberts, S. P. 2005: Honey bees as a model for understanding mechanisms of life history transitions. Comp. Biochem. Physiol., Part A Mol. Integr. Physiol. **141**, 362–371.
- Fieder, M., Huber, S., Bookstein, F. L., Iber, K., Schafer, K., Winckler, G. & Wallner, B. 2005: Status and Reproduction in Humans: New evidence for the validity of evolutionary explanations on basis of a university sample. Ethology **111**, 940—950.
- Freake, M. J. & Phillips, J. B. 2005: Light-dependent shift in bullfrog tadpole magnetic compass orientation: evidence for a common magnetoreception mechanism in anuran and urodele amphibians. Ethology **111**, 241—254.
- Frisch, K. v. 1923: Über die "Sprache" der Bienen. Eine tierpsychologische Untersuchung. Zoologische Jahrbücher (Physiologie) **40**, 1–186.

Frisch, K. v. 1940: The language and recal ability of bees in contrast. Naturwissenschaften **28**, 65–69.

Frisch, K. v. 1962: Dialects in language of bees. Sci. Am. **207**, 79.

- Frisch, K. v. 1965: Tanzsprache und Orientierung der Bienen. Springer-Verlag, Berlin.
- Futami, K. & Akimoto, S. 2005: Facultative second oviposition as an adaptation to egg loss in a semelparous crab spider. Ethology **111**, 1126—1138.

Gadau, J., Page, R. E., Werren, J. H. & Schmid-Hempel,P. 2000: Genome organization and social evolution in hymenoptera. Naturwissenschaften 87, 87–89.

Gherardi, F. & Atema, J. 2005: Memory of social partners in hermit crab dominance. Ethology **111**, 271–285.

Haesler, S., Wada, K., Nshdejan, A., Morrisey, E. E., Lints, T., Jarvis, E. D. & Scharff, C. 2004: FoxP2 expression in avian vocal learners and non-learners. J. Neurosci. 24, 3164—3175.

Hager, R. & Johnstone, R. A. 2005: Differential growth of own and alien pups in mixed litters of mice: a role for genomic imprinting? Ethology 111, 705–714.

Hall, M. L. 2004: A review of hypotheses for the functions of avian duetting. Behav. Ecol. Sociobiol. 55, 415–430.

Handley, H. G. & Nelson, D. A. 2005: Ecological and phylogenetic effects on song sharing in songbirds. Ethology **111**, 221–238.

Heinrich, B. & Bugnyar, T. 2005: Testing problem solving in ravens: string-pulling to reach food. Ethology 111, 962—976.

Hile, A. G., Burley, N. T., Coopersmith, C. B., Foster, V. S. & Striedter, G. F. 2005: Effects of male vocal learning on female behavior in the Budgerigar, *Melopsittacus undulatus*. Ethology **111**, 901—923.

Holland, R. A., Winter, P. & Waters, D. A. 2005: Sensory systems and spatial memory in the fruit bat *Rousettus aegyptiacus*. Ethology **111**, 715–725.

Hyman, J. 2005: Seasonal variation in response to neighbors and strangers by a territorial songbird. Ethology **111**, 951–961.

Illmann, G., Pokorna, Z. & Spinka, M. 2005: Nursing synchronization and milk ejection failure as maternal strategies to reduce allosuckling in pair-housed sows (*Sus scrofa domestica*). Ethology **111**, 652–668.

Iwaniuk, A. N. & Arnold, K. E. 2004: Is cooperative breeding associated with bigger brains? a comparative test in the corvida (Passeriformes). Ethology 110, 203—220.

Jandt, J. M. & Jeanne, R. L. 2005: German yellowjacket (*Vespula germanica*) foragers use odors inside the nest to find carbohydrate food sources. Ethology **111**, 641–651.

Jennings, D. J., Gammell, M. P., Payne, R. J. H. & Hayden, T. J. 2005: An investigation of assessment games during fallow deer fights. Ethology **111**, 511—525.

Jeschke, J. M. & Tollrian, R. 2005: Predicting herbivore feeding times. Ethology **111**, 187–206.

Johnstone, R. A. 2000: Models of reproductive skew: A review and synthesis. Ethology **106**, 5–26.

King, A. P., West, M. J. & Goldstein, M. H. 2005: Non-vocal shaping of avian song development: parallels to human speech development. Ethology 111, 101—117.

Kopisch, A. D., Schwagmeyer, P. L. & Mock, D. W. 2005: Individual consistency in parental effort across multiple stages of care in the house sparrow, *Passer domesticus*. Ethology **111**, 1062—1070.

Krebs, J. R. & Davies, N. B. 1978: Behavioural Ecology: An Evolutionary Approach. Blackwell Scient. Publ., Oxford.

Lachlan, R. F. & Servedio, M. R. 2004: Song learning accelerates allopatric speciation. Evolution **58**, 2049—2063.

Land, B. B. & Seeley, T. D. 2004: The Grooming invitation dance of the honey bee. Ethology **110**, 1–10.

Langmore, N. E. 1998: Functions of duet and solo songs of female birds. Trends Ecol. Evol. **13**, 136–140.

Leoncini, I. & Rivault, C. 2005: Could species segregation be a consequence of aggregation processes? example of Periplaneta americana (L.) and P. fuliginosa (Serville). Ethology 111, 527—540.

Linksvayer, T. A. & Wade, M. J. 2005: The evolutionary origin and elaboration of sociality in the aculeate hymenoptera: maternal effects, sib-social effects, and heterochrony. Q. Rev. Biol. **80**, 317–336.

Loyau, A., Jalme, M. S. & Sorci, G. 2005: Intra- and Intersexual Selection for Multiple Traits in the Peacock (*Pavo cristatus*). Ethology **111**, 810–820.

Lynch, A., Plunkett, G. M., Baker, A. J. & Jenkins, P. F. 1989: A model of cultural evolution of chaffinch song derived with the meme concept. Am. Nat. **133**, 634–653.

Marler, P. & Slabbekoorn, H. 2004: Nature's Music: The Science of Birdsong. Elsevier Academic Press, San Diego.

Martin-Vivaldi, M., Palomino, J. J. & Soler, M. 2004: Strophe length in spontaneous songs predicts male response to playback in the Hoopoe *Upupa epops*. Ethology **110**, 351—362.

Martin, J. & Lopez, P. 2005: Wall lizards modulate refuge use through continuous assessment of predation risk level. Ethology **111**, 207–219.

Michener, C. D. 1974: The Social Behavior of the Bees: A Comparative Study. Belknap Press, Cambridge (Mass.).

Mota, P. G. & Depraz, V. 2004: A test of the effect of male song on female nesting behaviour in the serin (*Serinus serinus*): a field playback experiment. Ethology 110, 841—850.

Neff, B. D. & Sherman, P. W. 2005: In vitro fertilization reveals offspring recognition via self-referencing in a fish with paternal care and cuckoldry. Ethology **111**, 425–438.

Nelson, D. A., Hallberg, K. I. & Soha, J. A. 2004: Cultural evolution of puget sound white-crowned sparrow song dialects. Ethology **110**, 879–908.

O'Brien, E. L., Burger, A. E. & Dawson, R. D. 2005: Foraging decision rules and prey species preferences of northwestern crows (*Corvus caurinus*). Ethology **111**, 77–87.

Pastor, K. A. & Seeley, T. D. 2005: The brief piping signal of the honey bee: begging call or stop signal? Ethology **111**, 775–784.

Penn, D. J. 2002: The scent of genetic compatibility: sexual selection and the major histocompatibility complex. Ethology **108**, 1—21.

Poisbleau, M., Fritz, H., Guillemain, M. & Lacroix, A. 2005: Testosterone and linear social dominance status in captive male dabbling ducks in winter. Ethology 111, 493—509.

Prokop, P. & Vaclav, R. 2005: Males respond to the risk of sperm competition in the sexually cannibalistic praying mantis, *Mantis religiosa*. Ethology **111**, 836–848. Quader, S. 2005: Elaborate nests in a weaverbird: a role for female choice? Ethology **111**, 1073—1088.

Riebel, K. 2003: The 'mute' sex revisited: vocal production and perception learning in female songbirds. Adv. Study Behav. **33**, 49—86.

Robinson, G. E. 2002: Genomics and integrative analyses of division of labor in honeybee colonies. Am. Nat. 160, \$160—\$172.

Rueppell, O., Pankiw, T., Nielsen, D. I., Fondrk, M. K., Beye, M. & Page, R. E. 2004: The genetic architecture of the behavioral ontogeny of foraging in honeybee workers. Genetics **167**, 1767—1779.

Runciman, D., Zann, R. A. & Murray, N. D. 2005: Geographic and temporal variation of the male zebra finch distance call. Ethology **111**, 367–379.

Saeki, Y., Kruse, K. C. & Switzer, P. V. 2005: Physiological costs of mate guarding in the japanese beetle (*Popillia japonica* Newman). Ethology **111**, 863—877.

Schmickl, T. & Crailsheim, K. 2002: How honeybees (*Apis mellifera* L.) change their broodcare behaviour in response to non-foraging conditions and poor pollen conditions. Behav. Ecol. Sociobiol. **51**, 415–425.

Schneider, S. S., Lewis, L. A. & Huang, Z. Y. 2004: The vibration signal and juvenile hormone titers in worker honeybees, *Apis mellifera*. Ethology **110**, 977–985.

Slater, P. J. B. 2003: Fifty years of bird song research: a case study in animal behaviour. Anim. Behav. **65**, 633–639.

Smith, M. J. & Hunter, D. 2005: Temporal and geographic variation in the advertisement call of the booroolong frog (*Litoria booroolongensis*: Anura: Hylidae). Ethology **111**, 1103—1115.

Soha, J. A. & Marler, P. 2001: Cues for early discrimination of conspecific song in the white- crowned sparrow (*Zonotrichia leucophrys*). Ethology **107**, 813–826.

- Soto, R. E., Castilla, J. C. & Bozinovic, F. 2005: The impact of physiological demands on foraging decisions under predation risk: a test with the whelk *acanthina monodon*. Ethology **111**, 1044–1049.
- Sullivan, J. P., Jassim, O., Fahrbach, S. E. & Robinson, G. E. 2000: Juvenile hormone paces behavioral development in the adult worker honey bee. Horm. Behav. 37, 1—14.

Sumana, A., Liebert, A. E., Berry, A. S., Switz, G. T., Orians, C. M. & Starks, P. T. 2005: Nest hydrocarbons as cues for philopatry in a paper wasp. Ethology 111, 469—477.

Tarpy, D. R. & Page, R. E. 2002: Sex determination and the evolution of polyandry in honey bees (*Apis mellifera*). Behav. Ecol. Sociobiol. **52**, 143–150.

Tarpy, D. R., Gilley, D. C. & Seeley, T. D. 2004: Levels of selection in a social insect: a review of conflict and cooperation during honey bee (*Apis mellifera*) queen replacement. Behav. Ecol. Sociobiol. 55, 513—523.

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

Wilson, A. D. M. & Stevens, E. D. 2005: Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. Ethology 111, 849—862.

Wittig, R. M. & Boesch, C. 2005: How to Repair Relationships - Reconciliation in Wild Chimpanzees (*Pan troglodytes*). Ethology **111**, 736–763.

Woodcock, E. A., Rathburn, M. K. & Ratcliffe, L. M. 2005: Achromatic plumage reflectance, social dominance and female mate preference in black-capped chickadees (*Poecile atricapillus*). Ethology **111**, 891—900.