

die Säugetiere eine andere Grundstrategie verfolgen. Nur auf einer solchen Grundlage könnten jene Fälle richtig bewertet werden, die vom Typus abweichen. Solche Mängel verraten eine Mißachtung des überragenden Wertes, der der spezifischen Nomenklatur auf der integrativen, 'oberen' Ebene zukommt, wenn man die Lebenserscheinungen aus öko-evolutiver Perspektive analysiert, also aus jener Blickweise, für deren Entwicklung gerade Ernst Mayr, einem der Lehrer des Verfassers, ein besonderes Verdienst zukommt.

3. Das Auslassen des Gesamtbildes und damit der Verzicht auf eine niveaudäquate Betrachtung (im ersten Forschungsschritt 'Beobachtung' = 'Beachtung schenken'!!!) gilt auch für das Verhalten insgesamt. Gewiß sind es immer wieder einzelne Verhaltensweisen, die zur Analyse reizen und in völlig korrekter Weise dazu isoliert werden. Wenn aber die Resultate nicht in das Gesamtbild eingefügt werden, dann wird die Grundfrage 'Was *ist* denn Verhalten?' nicht mehr zu beantworten sein. Zwar läßt sich so noch gut forschen. Wer nur spezielle Fragestellungen im Blick hat, mag damit zufrieden sein. Aber die Ethologie verliert dabei ihre Kompetenz, über das *Verhalten des Menschen* mitzureden. Daß dieses Thema uns alle angeht, macht Verf. im letzten Kapitel zwar deutlich (z.B. Thema Kriege), aber seine konkreten Aussagen sind allzu begrenzt, und menschliches Verhalten aus der auf Soziobiologie eingeeengten Sicht verständlich zu machen, ist in keiner Weise mehr ausreichend möglich.

4. Eine letzte Bemerkung betrifft die Literatur. Wir wissen, daß amerikanische Forscher sich im allgemeinen darauf beschränken können, die englischsprachige Literatur aufzunehmen. Trotzdem wird man bedauern, daß sich unter den Quellen nur ganz wenige finden, die in deutscher Sprache publiziert worden sind. Die fehlende Kenntnis der deutschen Literatur zeigt sich in der viele Mängel aufweisenden Diskussion des Instinktproblems. In der Übersetzung sind bei mehreren Werken die deutschen Ausgaben genannt (etwa bei den Büchern von Lorenz, allerdings nicht bei 'King Salomon's Ring', im Original: 'Er redete mit dem Vieh, den Vögeln und den Fischen').

Der Autor betont den subjektiven Charakter seiner Auswahl. Dies grundsätzlich zugestanden, wundert man sich doch, daß nicht nur Erich von Holst, sondern auch John Crook, George Schaller und John T. Emlen, also Pioniere der integralen ökologischen Betrachtung, nicht oder nur unzureichend Berücksichtigung fanden.

Parrish, J. K. & Hamner, W. M. (eds) 1997: Animal Groups in Three Dimensions. Cambridge University Press, Cambridge. 378 pp., numerous figs. £60.00, US\$ 90.00. ISBN 0-521-46024-7.

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Animal groups can be spectacular, as anyone knows who has witnessed the synchronised flash as a flock of waders in flight coherently switches direction. Other graphic examples in this book include swarms of army ants, and schools of mullet so large and dense that oxygen is depleted and fish at the rear must come to the surface to breathe (McFarland & Okubo). Grouping is not an uncommon phenomenon – 50% of fish species school as juveniles. And nor is it without important ecological and commercial consequences – for instance we are told that it is only the aggregated distribution of zooplankton that allows many of their predators to feed at a sufficient rate to meet metabolic costs, and maybe the same is true of some human fisheries.

This book is an edited multiauthored collection of 20 chapters. These are grouped into four sections: 'Imaging and Measurement', 'Analysis', 'Behavioural Ecology and Evolution', and 'Models'. Each section is introduced with a review, but generally the topic of each chapter has been chosen by the authors themselves, so that half a chapter may properly belong in one section and half in another. Different authors have aimed to cover the topic with very different breadths of brush. For instance Osborn's wide-ranging 24-page comparison of different methods of photogrammetry, is followed by a 7-page account of just two days' data from an acoustic survey of marine zooplankton. Several chapters begin with a moderately thorough review, but then head into more detailed coverage of the authors' own research. This can flow awkwardly but works particularly successfully in Heppner's chapter on the structure of bird flocks.

In this sort of book I find it stimulating and healthy if some chapters criticise the approach taken in others. Although some chapters discuss the disadvantages of various techniques of data collection and analysis, generally in the book any disagreements are restricted to bland differences of emphasis. So I did cheer Dill et al.'s critical comments on the lack of appropriate null hypotheses in this field, particularly having just read some of the earlier contributions (e.g. Parrish & Turchin's analyses of acceleration in response to the position of neighbours). Dill et al. are also refreshingly critical of ad hoc descriptive models of aggregations, for instance those based on inverse-square attractive forces.

Warburton's chapter concentrates on such models but is at pains to emphasise the biological justifications.

Perhaps the lack of overt disagreement is partly a result of every author refereeing at least one other chapter. Generally the standard of editing has been high, for instance with very few typographic errors (but please abbreviate second to s, not sec). The index is useful, but not fully comprehensive.

When I read the title of the book I immediately thought of Hamilton's paper on 'Geometry for the selfish herd' (1971), a citation classic that has inspired an enormous body of empirical work aiming to explain why animals group. In fact this paper is rarely mentioned in the book, but the reader need not feel the loss because it turns out that there are so many other issues to address. The editors organised the book and the preceding workshop because they sensed a lack of communication between workers in the field, and I suspect that everybody will find here many ideas new to them. One fact that I soon learnt was that there were relevant areas of research of which I was totally unaware. A measure of the diversity is the 34 pages of references. Work cited has been published as late as 1995 (later for self-citations).

Unfortunately the breadth of the subject makes it impossible to cover evenly and completely in this format of independently written chapters. However, the book gives a far better overview than the normal themed collection of research papers, and the editing has successfully minimised areas of repetition between chapters. The editors admit that 'no subject is covered exhaustively and many topics are untouched' so perhaps it is rather mean of me now to consider how much is omitted.

I can only judge this from a limited set of topics that I happen to know something about. The first section is on techniques, and what I have experience with here is passive acoustic localisation, which, for instance, can utilise the calls of cetaceans to reveal their positions (e.g. Spiesburger & Fristrup 1990). This technique is not mentioned, in spite of Jaffe's review chapter covering a wide range of other three-dimensional sensing techniques, some more relevant to anatomical studies than to distinguishing individuals. Radar is another technique that Jaffe fails to consider, although there is a brief paragraph in the chapter on bird flocks. What a shame not to mention one of the most striking images of flock structure, the 'ring angels' on radar screens that reveal the pulsed dispersal of starlings from the roost (Eastwood 1967).

From my perspective as a theoretical behavioural ecologist, other gaps and some errors are glaring. For instance no reference is made to the small body of theoretical work that has developed Hamilton's idea of the selfish herd (e.g. Cannings & Cruz Orive 1975; Morton et al. 1994). Nor is an obvious review of empirical tests of this theory cited (Mooring & Hart 1992). Hamner & Parrish's chapter on 'The conflict between individuality and group membership' contains some fundamental theoretical misunderstandings, for instance of when we expect groups to break apart. It is not when the 'proximal cost/benefit ratio swings negative for the majority of the group'. They should be considering net benefits rather than cost/benefit ratios, but the more important point is that each single individual should leave if its expected benefits from group membership outweigh its expected costs. Hamner & Parrish are also wrong that an uneven spatial distribution of 'cost/benefit ratios' within a group is necessarily a reason to mutiny or continuously cycle positions: if some individuals are more able or willing to defend the best positions, other positions can still be worth occupying. The correct game-theoretic analysis is the same as used to predict the distribution of animals between food patches, developed from the ideal free distribution (Milinski & Parker 1991). This literature is briefly mentioned in Ritz's later chapter. Some of the best empirical work testing theoretical ideas about grouping has been performed on fish schools by workers such as Milinski and Krause; both these authors are cited, but more than two of Krause's papers deserve mention.

I found no consideration of empirical or theoretical work on avian and mammalian leks, or amphibian and orthopteran mating aggregations. These are some of the most studied of animal groups, and theory applied to them makes an interesting contrast with that used to explain herds and shoals: if grouping of prey makes each less likely to attract a predator, is it not remarkable that grouping of males can make each more likely to attract a female? I sympathise more with the exclusion from the book of social mammals, co-operatively breeding birds, and social insects (although one chapter models trail-following in ants).

Another worrying aspect of the coverage is the geographic bias: out of 27 authors, 21 were based in North America, 3 in Japan, 3 in Australia, and 0 in Europe. So in summary it is easy to identify gaps, not just between chapters, but also within chapters that attempt to review an area. Or should they more fairly be judged as merely having attempted to introduce an area, as perhaps too little space was available to do more, especially if authors were encouraged to include details of their own research?

At least one review chapter does deserve to become a standard citation (although the steep price cannot help in this). That is the first chapter, by Parrish et al. which identifies some of the key features of animal groups, and the most important questions that we should be asking about them, both

mechanistic and functional. It would be desirable if their definitions of various levels of aggregation and congregation became widely adopted, but probably these words are already too widely used in a looser sense. I also found high-quality research amongst the chapters that concentrated on more specific ideas. Three studies that I think particularly neat are: Dill et al.'s model of how individuals should position themselves to optimise the detection of change in a neighbour's behaviour; Grünbaum's demonstration that by copying their neighbours fish could amplify the weak gradients from distant odour sources; and Turchin & Simmon's thoughtful analysis of bark-beetle swarms (unusually in this book, based on measuring fluxes past fixed points, not on following individuals).

Continuing this positive note, I would like to draw from the book some take-home messages, particularly of themes common to several chapters. The diversity of taxa considered in the book is impressive, and often the groups formed in unrelated taxa share similarities of structure. While Ritz mentions evidence that the function of grouping may be the same in aquatic crustaceans as in fish, other authors here emphasise that grouping in different taxa may well be a consequence of quite different sorts of selection pressure. The same holds for the mechanisms of group formation in different taxa, which may vary widely in their sensory modalities and their mobility (e.g. see Yen & Bundock's chapter on aggregation in zooplankton). Variety is not just taxonomic: the distribution of the zooplankton exhibits clustering at several different spatial scales, and whereas individual behaviour may be responsible at the fine scale, physical forces such as currents are more likely causes for broader-scale patchiness.

Although it might seem easier to answer questions about how groups form than questions about their adaptive value, biologists have been much more interested in functional questions, so that mechanistic explanations actually lag behind. For all groups we can ask how group members locate each other and about the cues used to decide whether to join a group. But biologists have been more intrigued to understand how dense rapidly moving aggregations of birds and fish can co-ordinate sudden turns so smoothly. In this respect I enjoyed a brief allusion to the traffic rules that humans use on the motorway to avoid collisions. In particular I remembered the police advice to keep an eye on the brake lights of the car two in front, because this is reminiscent of both the way that real birds copy nonadjacent neighbours (Potts 1984), and the way that the flocking of 'boids' has been computer simulated (Reynolds 1987). There is also the interesting question of whether flock members are adapted to 'indicate' before or during a turn (Denton & Rowe 1994); and do they check the rear-view mirror first?

Several authors stress the technological problems facing us in mapping the position of individuals in a three-dimensional flock, and then the extra problems associated with following these individuals over a period of time. Often there is a conflict between a fine enough spatial resolution to pick out individuals and a wide enough field of view or depth of focus to follow individuals for a reasonable period. The solution that this book emphasises is to embrace technology and collaborate with non-biologists. Certainly advances in computer technology will assist. However, although I realise that the title of the book directs it towards three-dimensional studies, my own preferred line of attack would be to work with two-dimensional systems where possible. Thus even here Romey is not ashamed to report his work on whirligig beetles that move mostly on the water surface. Logically we do predict differences between three dimensions and two (e.g. Cannings & Cruz Orive 1975), but practically I suspect that the same principles are similarly important in both.

With some of the new automated techniques it is possible to generate enormous quantities of data. Dill et al. make the point that it is then more important than ever to have an explicit hypothesis to test against a meaningful null hypothesis. Often the most appropriate way in which to compare data on spatial distributions within a herd will be through Monte-Carlo simulations and randomisation tests, because statistics such as nearest-neighbour distances are neither normally distributed nor independent between group members. Having prior hypotheses also has the advantage of suggesting experimental manipulations that disentangle competing hypotheses. We often have a surfeit of functions and mechanisms that theoretical modelling has shown could explain the patterns observed, but a lack of experimental evidence that might confirm which processes actually are important.

In summary this is an overpriced but worthwhile book with something in it for everyone who is interested in animal groups. But let us hope that it acts as a stimulus for a single-author book reviewing far more comprehensively and consistently the widely scattered research already existing on this topic.

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Aitkin, L. 1998: *Hearing—the Brain and Auditory Communication in Marsupials*. *Zoophysiology* Vol. 36; Springer Verlag, Berlin, Heidelberg. 117 pp., 43 figs. ISBN 3-540-62946-7.

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Marsupials have long been a group neglected by science, because the overwhelming majority of them lives in the southern hemisphere, far away from the old centers of research. Fortunately this situation has changed, so that there is now much more work directed at these primitive mammals. Lindsay Aitkin, from the Monash University in Melbourne, focused his research on the central part of the auditory system as well as on vocalization of marsupials. He now combines his own work with the results of others in the form of this monograph. The contents are presented in nine chapters, from the design of the mammalian auditory system to hearing and vocalization in marsupials, and then from the outer ear, through the middle ear and the cochlea on to the central part of the auditory system, all the way to the auditory cortex. It is predominantly a discussion based on a collection of special articles, and thus a pretty technical affair, interesting for those already working in the field of auditory research, but certainly very hard to read for people who are not actively involved with this sensory system. Hidden in the text are insights that are based on an experience of more than a quarter century of work on marsupials, but they are not apparent to the casual reader.

The structure of the auditory system in marsupials is very similar to that in eutherians. They normally have a mobile outer ear with a very specific inner surface, mostly free of hairs. In the middle ear marsupials also have the typical chain of the three ossicles, along with the muscles. However, both outer and middle ear are marginal to the authors own work, and are thus covered only in a cursory way. In the inner ear marsupials are also fitted out with an Organ of Cortic, complete with the usual set of inner and outer hair cells. The central portion of the auditory pathway is not exactly identical, but very similar to the situation in eutherians. It also involves the inferior colliculus of the mid-brain as well as the medial geniculate body of the diencephalon. As in man or eutherians, the basic question is the same for marsupials: How is the auditory system receiving and analysing acoustic signals? Most of the work has been devoted to these problems, and because it is difficult to determine the auditory capabilities, especially in wild and exotic animals, a lot of data are presented related to the various methods, as well as their shortcomings and technical problems. Recordings of cochlear microphonics and of single units in the periphery are presented, as well as results of microelectrode penetrations in various locations of the brain stem, or recordings of the auditory cortex. All this is compared to behavioural thresholds, as strenuously determined in some marsupials, making it usually hard to decide what the animals really hear. These laboratory findings are compared to the few field observations related to hearing and vocalization in marsupials. One of the difficulties is that marsupials are generally relatively quiet animals that do not vocalize that much, making it even more difficult to evaluate the biological effects of their sense of hearing. In one aspect marsupials are a much easier target for research than eutherians. They are born more or less as embryos, making it especially easy to study their structural and functional ontogeny, including the hearing system, as well as vocalization. A number of studies and their findings are presented. To summarize, this book can be said to be a solid base for research in this field, and it will give an easy start to newcomers.