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Title Some Field Notes
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Abbreviations

CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CEMP	CCAMLR Ecosystem Monitoring Program
DEB	Dynamic Energy Budget
HH	The author of this paper

1. Introduction

This paper is about additional information and speculation. The essay consists of two sections. In the first section comments are made on parts of the textbook for reasons which will be explained in the regarding paragraph. In the second section an attempt will be made to link the DEB-theory with two topics in the study of animal behavior: 1) parental investment and 2) hibernation. The theory of DEB presents simple mechanistic rules that describe the uptake and use of energy and nutrients and the consequences for physiological organization throughout an organism's life cycle. The aim of this essay is to reflect on alternative ideas and approaches in the study of animal behavior using the above mentioned mechanistic rules in general and the so-called K-rule for allocation {p.86} in particular. Before I put some of my thoughts in writing, I have to stress that the text below not only can be complete nonsense but also outdated. Due to time constraints, it was not possible to carry out an adequate literature search. So, maybe the points made are already a subject of investigation or have been sorted out and published.

2. Comments

2.1 Diving behavior

{p.274}: Maximum diving depth for auks and penguins tends to be proportional to volumetric length. The author: 'This can be understood if diving depth is proportional to the duration of the dive; the later is proportional to length, cf. {71} by the argument that the respiration rate of these endotherms is about proportional to surface area and oxygen reserves to volume'.

<u>Comment</u>

Ponganis and Kooyman (2000): 'Increased oxygen stores and body size, although important factors in diving capacity, do not fully explain the observed differences in diving behavior of these birds'. A relatively small brain (the advantage of being stupid), tolerance of anaerobic metabolism, and changes in stroke frequency and buoyance to decrease metabolic demands are possible factors extending the diving capacity of the deep-divers among these birds. For a good review on the behavioral and physiological ecology of diving see Boyd (1997).

2.2 Delayed implantation in true seals (*Phocidea*)

{p.104} last paragraph: 'The long delay for the grey seal *Halichoerus* (= 145 days Table 3.2) probably relate to timing with the seasons to ensure adequate food supply for the developing juvenile'.

<u>Comment</u>

This statement is not untrue. Bowen (1991) p.68: 'It is also possible that autumn pupping of grey seals in the UK is a response to the strong autumn peak in primary productivity in the North Sea'. However, some interesting considerations on delayed implantation in true seals can be made keeping the so-called K-rule for allocation {p.86} and the below-described facts in mind:

1. True seals, *Phocidae*, reproduce synchronized to the annual cycle. Female phocids come ashore or on ice to give birth and lactate. Copulation takes place towards or at the end of lactation. Pregnancy usually lasts 7-9 months and synchronization with the annual cycle is achieved through delayed implantation (King, in Trillmich 1996: p.536).
2. Mothers come onto the breeding substrate with all the resources for maintenance and milk production during the period of lactation (4-60 days) stored in their body. Males do not

contribute to parental care. Weaning is abrupt at the end of the nursing period and pups often fast for considerable time after weaning, living off their accumulated fat reserves.

3. Phocids continue to grow throughout their adult lives.
4. Phocids experience an annual molt in which they shed all their fur and, in some species (*fi.* elephant seals) portions of their epidermis. Molt demands high peripheral temperatures and molting pinnipeds typically fast or eat little when hauled-out. In elephant seals attachment of the blastocyst occurs at the end of the summer molt, female gray seals molt just before the time of implantation.
5. In seals reproductive success is positive correlated with size [HH: I still have to check this statement!].

Keeping the K-rule for allocation in mind I can also argue something else. In some phocid species the long duration of the delayed implantation enables a mother to recover the body resources following lactation (and molt) in order to produce a large pup as possible at birth and weaning for the present breeding season and the subsequent ones.

2.3 The reconstruction of food intake in penguins
The method displayed in Figure 7.6 has potential interesting features to be applied in an ecosystem-monitoring program, for example the CCAMLR Ecosystem Monitoring Program (http://www.ccamlr.org). When a reliable reconstruction of food intake by a chick or a pup during its nursing period can be realized, it is an elegant method to increase the sample sizes of so-called indictor species. The CEMP uses for instance growth parameters among other things of predator species as shags, penguins, petrels, albatrosses and fur seals to detect changes in the Antarctic marine ecosystem

2.4 The hereditability of size and growth
Growth curves are a main topic in the textbook. Surprisingly little is said about the genetics of size and growth {p.266 bottom line}. The hereditability of size and growth (including the timing of a growth spurt) might give us a better understanding of life-history strategies and reproductive tactics. I even wonder if data on genetics of size and growth is available for non-domestic animals anyway?

3. A mechanistic approach in behavioral ecology
Krebs & Davies ((1991) p.IX: 'Mechanisms. Behavioural Ecology was spawned as a wayward offspring of ethology, focusing on just one of Tinbergen's (1963) 'four questions' (function) and eschewing the other three (mechanism, ontogeny, evolutionary history). Inexorably behavioural ecologists are being drawn back into the study of mechanisms'. So, behavioral ecologists need to embrace mechanisms to make progress. Is the DEB-theory an appropriate tool to get these scientists out of their quack-mire?

3.1 Parental investment
First some terms. Parental investment is the extent to which parental care of individual offspring reduces the parent's residual reproductive value. Parental care is any form of parental behavior that appears likely to increase the fitness of a parent's offspring. Parental expenditure is the expenditure of parental resources (including time and energy) on parental care of one or more offspring (Clutton-Brock 1991).

Studies of brood size manipulations in birds report significant reductions in local survival and/or reductions in later fecundity in the case of brood size enlargement. Manipulation of brood size and daily work schedules reduces the effectiveness of the immune system. In these situations there seems to be a physiological allocation of energy to reproductive effort versus repair and maintenance, and a corresponding trade-off between current offspring and future reproduction.

Here, I wish to discuss the reduction in fecundity (*fi*. a smaller clutch size in the subsequent season). {p.116}: 'Clutch size in birds typically relates to food supply during a two-month period prior to egg laying and tends to decrease if breeding is postponed in the season [618]. The laying date is determined by a rapid increase in food supply. Since feeding conditions tend to improve during the season internal factors must contribute to the regulation of clutch size'. Furthermore {p.116}: 'Under conditions of prolonged starvation, organisms can deviate from the standard reproduction allocation'. The issue here is whether it is possible to understand such a reduced clutch in the framework of the DEB-theory. I do not know how long it will take for an effected immune system to recover. So, let us assume that the immune system has fully recovered before the breeding season and the dynamics of the food supply is the same for subsequent breeding seasons. Then, if the laying date is not postponed one can predict that the bird has to eat less, because the internal factors regulating clutch size are the same as in the previous season.

3.2 The mystery of periodic arousal in hibernation

Hypothermia during mammalian hibernation is not continuous. Periodically hibernators increase their body temperature from near 0° C to 36-38° C during so-called arousals. The functional significance of these periods remains unknown. It is proposed that arousals are required to eliminate metabolic waste products, replenish blood glucose levels, restore cellular electrolyte balance or to restore sleep. To my knowledge, with the exception of sleep (Daan *et al.* 1991), the hypotheses have not been properly tested (Willis 1982). An interesting problem is whether the DEB equations for energy acquisition and use, and the balances for the uptake and use of essential compounds can be used 1) to predict the timing and duration of arousal periods; and 2) to design experiments to test the non-sleep hypotheses?

4. References

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