
Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders

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(c) Dynamic model

We assumed that fitness is a direct function of the total net energy gained, which is reasonable given that we are considering a relatively short period (a single tide cycle), far away from the breeding season in the middle of the arctic winter, where strong winds (greater than 60 km h^{-1}) and low temperatures (less than -40°C) commonly occur.

We considered two state variables in the analysis, stomach contents s and energy stores e . Stomach contents s could range from 0 to 30 kJ (see §3), discretized for model implementation into 100 categories. Energy reserves e ranged between 0 and 10 000 kJ, which was well above the range that could be acquired or depleted in a single tidal cycle under even the most intensive foraging regime. This range was discretized into 1000 categories.

The model considered an entire tidal cycle (372 min) in

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of foraging behaviour, instead incorrectly predicting that eiders should concentrate their foraging effort in slack currents (Heath *et al.* 2007). Static approaches employ classic economic theory (e.g. Charnov 1976), and base their predictions on maximizing a currency such as the rate or efficiency of energy intake. However, these currencies do not necessarily represent longer term fitness (Ydenberg 1998), which is often assumed, but rarely tested. The appropriate currency can depend on whether time or energy constraints are limiting (Ydenberg & Hurd 1998) and as demonstrated here, both time (tide cycle) and energy (digestive bottleneck) constraints can act together in a dynamic manner.

Maximizing rate or efficiency over the long term in the wild can be a complex process. For example, animals cannot run indefinitely at a constant maximum dash speed, and similarly may optimize energy intake at different timescales (Ydenberg 1998; Fortin *et al.* 2002; Heath *et al.* 2007). In some situations, long-term rewards may be best achieved by a short-term reduction in effort so that the best strategies involve intermittent bouts of inactivity

(Williams *et al.* 2000; Kramer & McLaughlin 2001; Wienstein 2001; Heath *et al.* 2008), or more complex temporal structuring of activity patterns (Cole 1994). Investigating behavioural patterns therefore requires simultaneous consideration of the trade-offs that can occur between multiple overlapping physiological and abiotic rate processes in a dynamic multi-scale framework.

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food availability and prey or host selection. The present study focused exclusively on temporal activity patterns, and demonstrates the importance of considering trade-offs between short-term and long-term processes in an otherwise constant ecological context. Behaviour can be understood as the means by which an organism negotiates a coupling between its internal physiological processes and processes in its environment. Particularly when these processes are nonlinear (such as many components of diving activities), it should not be surprising that an understanding of behavioural patterns can vary as a function of the scale of the investigation (Schneider 2001). Dynamic modelling provides an approach in which the grain and extent of observation can be changed and mul-

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