Understanding diet choices in changing environments: optimisation modelling and experiments with free-living blue tits

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Background and Motivation: Foraging animals have to make complex decisions about diet taking into account multiple constraints. Much of the theoretical and empirical work on foraging is based on the assumption that foraging animals pursue a single currency, typically energy. More recently, models of optimal diet composition have sought to explore how animals regulate the intake of different currencies that are essential to survival and reproduction (Houston et al 2011 Ecol Lett 14,1101). This project will focus on developing an improved understanding of how foraging animals deal with complex decisions about diet, taking into account multiple constraints, which have rarely been considered in diet selection models. The student will build on existing models of optimal diet composition by combining energetic, ecological and micronutrient considerations and develop new models to predict an individual's diet choice under different ecological conditions. A system of diet-choice experiments will then be used to test and refine the predictions in the field using the blue tit *Cyanistes caeruleus*. The results of the project are intended to improve understanding of how organisms respond to changes in their environment. With future environmental change likely to push local environmental conditions beyond those that species have evolved to deal with, it is hard for ecologists to predict how animals will respond to complex new ecological conditions. One potential solution is to seek to understand how animals deal with complex decisions in their current environments, in particular by focusing on how priorities and choices alter as environmental conditions vary. Assuming that animals' underlying decision rules are likely to remain generally similar, a better understanding of their decisions can then be used to improve predictions of how species might respond to novel future environmental conditions.

Study System: The project will use the foraging choices of wild blue tits as a model system for investigating complex diet choice under changing environmental conditions. Research will focus on the conflict between satisfying energy demands and ensuring sufficient intake of a specific type of nutrients. We will focus on antioxidants as they are important for health, survival and reproduction in a wide range of organisms and we have a good understanding of this nutrient for the local blue tit population. During the breeding season, parents and offspring have a high demand for both energy and antioxidants. Parents forage mainly on caterpillars and face a conflict because their two main prey items differ in nutrient content and camouflage, the latter affecting energy intake rate: *Operophtera*, green caterpillars that are harder to detect against a green foliage but rich in many antioxidants, vs. *Erranis*, a less camouflaged brown caterpillars with lower contents of many antioxidants (Arnold et al 2010 Biol J Linn Soc 99,708). This raises many interesting questions about how the prey's camouflage affects its predator's hunting efficiency, and therefore its intake of energy and nutrients. Similarly during winter foraging, birds require to maintain a balance between energy and antioxidant intake, but food items will differ in energy and antioxidant content. Blue tits therefore have to make these types of diet choices under widely varying environmental conditions (which change their energy expenditure requirements) so they make an ideal system in which to study questions about the relative importance of energy and antioxidants.

Objectives: The project will initially focus on the following key objectives but the student will be able to build on these and develop further research questions.

1) Develop state-dependent dynamic optimisation models to generate specific predictions of diet choices as a function of environmental conditions and the individual's physiological state
2) Use diet choice field tests to test the model's predictions on how prey camouflage effects diet choice
3) Use diet choice field tests to test the model's predictions on how diet choice varies with energy requirements (reflected by for example breeding effort, ambient temperature and length of the overnight fasting period)
4) Use diet choice field tests to explore whether characteristics of the birds (including physiological condition) or its territory influence its diet choices and how such choices are linked to measures of fitness

Research Environment, Supervisory Team & Training Opportunities: The student will be joining a growing research grouping carrying out fieldwork in the oak woodland ecosystem of the Scottish Centre for Ecology and the Natural Environment (SCENE). SCENE is the University of Glasgow's unique field station situated on the shores of Loch Lomond in the southern Scottish Highlands and is within one of the UK's largest national parks. SCENE has a state of the art research building providing world class research facilities to support fieldwork in the surrounding woodlands with a large population of individually-marked blue tits using the field station's 450 nest boxes. The studentship will be supervised by a team with experience in modelling and field work on foraging tits. Ross MacLeod focuses on behavioural responses to environmental change and pioneered the application of ring mounted PIT tags to behavioural monitoring (Macleod et al. 2005 J Anim Ecol 74,956, Macleod & Gosler 2006 Anim Behav 71,1081). Ruedi Nager focuses on factors influencing reproductive strategies in bird. Together they have over 10 years of research experience using tits as model species to understand key challenges in ecology and conservation and have or are supervising 18 PhD students. Graeme Ruxton's expertise is in modelling applied to behavioural ecology and with an interest in how foragers evaluate the attractiveness of potential food. He will provide support for the mathematical modelling and deriving the appropriate experiments to test the models. The student will receive training in a range of approaches and fields, including experimental design and data analysis, modelling in behavioural ecology, avian ecology fieldwork skills and gain significant expertise in the application of cutting edge behavioural monitoring tools using PIT tags to record behaviour of free-living individuals in the field.

Methodological approach: The project will explore the diet choice under conflicting constraints combining modelling and experimental approaches. The initial focus will be on prey that differ in camouflage and contain varying levels of antioxidants as tits can discriminate between prey with different antioxidant contents even without visual clues (Senar et al 2010 PLoS One 5). This approach will then be expanded to other situations. A forager may selectively feed on antioxidant-rich camouflaged prey to maximise antioxidant intake, but may have to feed on less camouflaged prey that is poor in antioxidants when energy intake needs to be maximised. The constraint of energy maximisation may shift with the individual's state, the relative abundance of the different food types and changes in environmental conditions. Modelling of this problem using a state-dependent dynamic optimisation approach will generate specific predictions about the diet choices of birds as a function of environmental conditions and physiological state. Specifically, we will develop models that allow diet choice at any given instant to be dependent on the bird's current state of reserves in terms of both antioxidants and energy. This is a relatively novel approach as almost all existing theory assumes that foragers have a single currency to maximise, rather than a need to balance two. The model will make predictions about diet choice as a function of three types of factor all of which can be controlled in our empirical work: the relative qualities and abundances of the food types available; the physiological state of the animal (body mass) and the environment (e.g. temperature, with lower temperatures increasing the relative need for energy intake over anti-oxidants). This will allow very specific testing of model predictions in the field using an experimental set-up based on a classic choice chamber (see supplementary information). This will allow wild birds to enter an enclosed feeding area to which the birds are habituated (the basic set-up was successfully trialled in 2010). Birds will be able to choose between feeding stations with different food types. Suitable food types can be created artificially so ensuring that they differ only in the required characteristics. Food types will be regularly switched between sides to avoid biases by individual side preferences. Access to the experimental feeding chamber and how long each individual bird feeds on each food will be recorded by PIT tag technology. The relationship between feeding time and food intake rate will be calibrated using video cameras at the start of fieldwork and at regular intervals throughout experiments. It will therefore be possible to record longitudinal series of foraging decisions for many individual birds in relation to each diet choice test. The automated recording of the diet choices also makes it simple to repeat choice test experiments at different times within each season and under different levels of energy requirements that vary through the year (e.g. greater energy requirements mid-winter and when provisioning nestlings). Thus, food choice priorities (energy vs. antioxidant maximisation) will change with season. Further models on optimal diet choice could also include predation risk (McLeod et al 2007 Ecol. Lett 10,945; Cresswell et al 2009 Proc R Soc B 276,3553) and empirically testing the model using different levels of perceived predation risk (altered by play back of alarm calls). This will give us a better understanding of under what environmental conditions energy or antioxidants are prioritised and when food choices will alter.