UNDERSTANDING MULTIMODALITY IN ANIMAL SIZE DISTRIBUTIONS

INTRODUCTION

Body size is arguably the single most descriptive aspect of organismal form and function (e.g., Peters 1983; Calder 1984). Because of this, distributions of body size of species and individuals have been used to make inferences regarding the processes structuring ecological communities (Holling 1992; Ernest 2005), to make predictions regarding future dynamics of ecological systems (Condit *et al.* 1998; Feeley *et al.* 2007), and to scale up individual level processes to understand ecosystem level patterns (Enquist *et al.* 2003; White *et al.* 2004). This work relies on a general understanding either of the distribution of species-level average sizes (the species size distribution or SSD) or the distribution of individual body sizes (the individual size distribution or ISD). The general form of these distributions is often considered to be relatively simple, exhibiting either a monotonic decline (Morse *et al.* 1985; Enquist & Niklas 2001; Kerr & Dickie 2001; Coomes & Allen 2007) or a single interior mode (Hutchinson & MacArthur 1959; Siemann *et al.* 1996; Gaston & Blackburn 2000). However, it has also been suggested that both species and individual size distributions may exhibit more complex, multimodal patterns in some systems and taxonomic groups (Griffiths 1986; Holling 1992; Ernest 2005; Allen *et al.* 2006). While demonstrating the presence of this multimodality has proven controversial (Manly 1996; Siemann & Brown 1999), we have recently found convincing evidence for multimodality in the ISDs of bird communities that requires mechanistic exploration (see Report of Fellowship Activities; White et al. In prep).

Interestingly, despite the recognition that the SSD and the ISD are inherently linked (Harvey & Lawton 1986; Siemann *et al.* 1996; White *et al.* 2007), the study of the two patterns has occurred primarily in isolation of one another. Because the processes proposed to generate these distributions can often be made to produce predictions for both sets of distributions, it should be more productive to study them in concert (e.g., Figure 1). The few studies that have directly compared SSDs and ISDs have yielded equivocal results, with some communities exhibiting similar ISDs and SSDs and others showing very different distributions (e.g., Siemann *et al.* 1996; Ernest 2005; Figure 1). The processes proposed to explain multimodality can be divided into two groups: those that predict high overlap between the two distributions (i.e., they require high species richness at body sizes where there are large numbers of individuals; Holling 1992; Siemann *et al.* 1999) and those that allow for different, even offset, distributions of species and individuals (Ernest 2005). Thus determining how the

Figure 1. Relationship between ISD and SSD for a bird community

ISD and the SSD are actually related will provide important information about the processes structuring communities. We propose an in-depth integration of the individual and species-size distributions combining macroecological/ecoinformatics approaches with statistical and mechanistic modeling to understand the observed multimodality in the ISD and the processes structuring ecological communities.
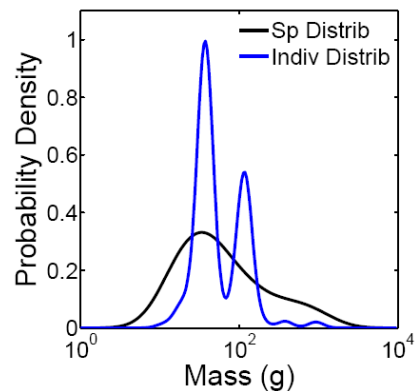
PRELIMINARY RESULTS

As part of my postdoctoral research I evaluated the general form of the individual size distribution in birds throughout North America. This was done by fitting monotonic, unimodal (with one interior mode), and multimodal distributions (Gaussian mixture models fit using

expectation maximization) to 1295 bird communities and evaluating which model fit each community best using AIC and BIC based model selection (Burnham & Anderson 2002). Most bird community data does not include individual masses, so we used the normal distribution of body size within a species and the strong mean-variance scaling relationship between species to generate realistic size distribution data. These analyses revealed that all 1295 communities were characterized by multiple modes with most communities having 3-5 modes. This multimodal form deviates substantially from the shape observed in aquatic systems and tree assemblages, where the individual size distribution is typically well described by a decreasing monotonic function (Kerr & Dickie 2001; White *et al.* 2007). This rigorous demonstration of multimodality in the ISD requires mechanistic exploration. In addition, the tools that I developed can be used to re-examine the controversy over the general form of the SSD.

RESEARCH PLAN

Objective (1) Is the species size distribution multimodal? While this question has been a contentious issue for over a decade, it has yet to be fully addressed using either the rigorous tools of quantitative ecology or the weight of the large database approaches of ecoinformatics and macroecology. We will develop a large database of terrestrial SSDs for multiple taxonomic groups (e.g., birds and mammals). By combining data from broad scale coordinated sampling efforts (e.g., Breeding Bird Survey & Christmas Bird Count), literature compilations (Brown & Kurzius 1987), LTER data, and species lists extracted from the literature, we anticipate a database of >3000 bird communities and >300 mammal communities. When data on abundance and individual body sizes are available they will be collected for use in addressing objectives (2) and (3). These community species lists will be combined with published body size data (Smith *et al.* 2003; Dunning 2007; Lislevand *et al.* 2007) to generate the SSD database. We will use the methods developed by EPW for determining the number of modes in the individual size distribution in combination with empirically motivated Monte Carlo analysis to determine how frequently SSDs exhibit multimodality and the confidence with which this multimodality can be established. We will also evaluate the influence of spatial scale, a factor known to influence the form of the distribution (Brown & Nicoletto 1991; Allen *et al.* 2006) on the occurrence of multimodality. The database will be published in Ecological Archives to facilitate additional research on SSDs and other community patterns. Code for advanced multimodality detection will also be published to facilitate the use of these methods by other researchers.

Objective (2) What is the relationship between the species and individual size distributions and what structuring processes does the observed relationship support? To improve our understanding of the processes generating multimodality in size distributions we will evaluate the relationships between species-size distributions and individual-size distributions. Several studies have compared species and individual size distributions to one another (Siemann *et al.* 1996, 1999; McClain 2004; Ernest 2005). However, these studies (totaling < 20 communities) offer conflicting results regarding whether or not the SSD and ISD are multimodal and whether the peaks in species richness occur at the same body sizes as the peaks in abundance. In addition, the methods used in these studies fail to account for the fact that some degree of overlap between the SSD and ISD must occur because by definition a species and the individuals that compose it must have the same average size. We will use a null modeling approach to overcome this inherent relationship. For each community we will randomly assign abundances to species from the empirical abundance distribution, effectively decoupling any meaningful relationships between body size and individual species abundance. For each randomization we will calculate the observed overlap between the ISD and SSD and we will compare the resulting distribution of overlap values to that for the observed data. If the overlap is greater than expected by chance this suggests that ISDs and

SSDs are meaningfully related to one another, supporting hypotheses based on division rules (Siemann et al. 1999) or differences in resource availability to different size classes (Holling 1992). If it is less than expected this will support hypotheses based on community interactions such as competition (Ernest 2005). These analyses will be conducted using both raw abundance and estimates of resource use derived using allometric relationships.

Objective (3) Modeling multimodal size distributions using self-organized similarity models and guild based mixing models. It has been suggested that multimodal SSDs may result from self-organizing mechanisms creating clusters of species of similar size that can coexist through equalizing mechanisms (sensu Chesson 2000), while stabilizing mechanisms allow the coexistence of different clusters (Scheffer & van Nes 2006). Thus multimodality can be produced without patchiness in resource availability along the size axis. We will build on Scheffer and van Nes (2006) to determine if their model can produce the patterns observed in Objectives (1) and (2). Modifications of their model that include zero-sum constraints, size-dependent resource availability, and asymmetric competition, will also be studied.

Alternatively multi-modal size distributions may result from a simple assembly process based on combining different guilds which differ in their species-size distributions (Figure 2). While continental scale SSDs are often unimodal, if the relative representation of guilds in a local community differs from the continental pool either in regard to species presence or in the relative abundance of individuals, this could result in multi-modal distributions of species or individual size. To evaluate this possibility we will fit Gaussian mixture models to empirical distributions using parameters derived from the pool's SSD. If the mixture models replicate the observed size distributions and produce realistic proportional representations of different guilds, this will support a guild-based assembly process. The results of both modeling approaches will be compared to the behavior of the empirical size distributions in our database

Fig. 2. Species size distributions for avian trophic guilds.

based on the general patterns occurring within single communities (e.g., overlap between the SSD and ISD) and based on geographic variation in the size distributions (e.g., can the models predict the observed variation in the number and position of the modes across space).
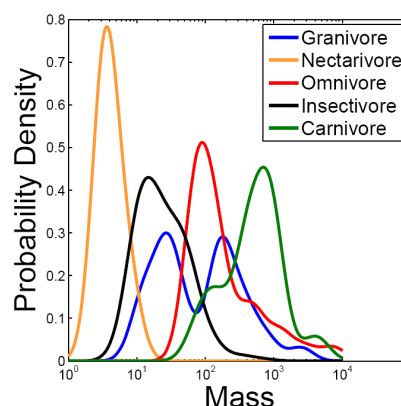
COLLABORATIVE ACTION PLAN

This project involves two senior personnel in addition to the PI, and a postdoctoral researcher. Drs. Morgan Ernest and Allen Hurlbert will be responsible for the acquisition of mammalian (Ernest) and avian (Hurlbert) community data, and providing expert guidance on model development for mammal (Ernest) and bird (Hurlbert) communities. In addition Dr. Ernest will help with data publication and Dr. Hurlbert with GIS work. The PI will be responsible for data management, analysis, and modeling. The postdoc will participate in all aspects of the project under the guidance of the appropriate personnel and will travel to interact with Dr. Hurlbert.

BROADER IMPACTS

This research will train one post-doctoral researcher and two graduate students. In addition, we will be developing the use of Web 2.0 tools to facilitate remote collaboration, including the use of a project wiki equipped with text and voice chat features to allow on-line meetings, the storage and manipulation of all data on a remotely accessible database server, and a group blog to keep all collaborators up-to-date on the progress of various aspects of the project.