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# Modelling the prey detection performance of *Rhinonicteris aurantia* (Chiroptera: Hipposideridae) in different atmospheric conditions discounts the notional role of relative humidity in adaptive evolution

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ABSTRACT

We examined a recent notion that differences in echolocation call frequency amongst geographic groups of constant frequency (CF)-emitting bats is the result of a trade-off between maximising prey detection range at lower frequencies and enhancing small-prey resolution at higher frequencies in different atmospheric (relative humidity; RH) environments. Isolated populations of the endemic Australian orange leaf-nosed bat *Rhinonicteris aurantia* were used as an example since geographic isolation in different environments has been a precursor to differences in their characteristic echolocation call frequencies (mean difference c. 6 kHz; means of 114.64 and 120.99 kHz). The influence of both atmospheric temperature and RH on maximum prey detection range was explored through mathematical modelling. This revealed that temperature was of similar importance to relative humidity and that under certain circumstances, each could reduce the effect of the other on ultrasound attenuation rates. The newly developed models contain significant conceptual improvements in method compared to other recent approaches, and can be applied to the situation of any other species of bat. For a given set of atmospheric conditions, the prey detection range of *R. aurantia* was reduced slightly when call frequency increased by 6 kHz, but an increase in RH, temperature or both reduced detection range significantly. A similar trend was also evident in prey detection volume ratios calculated for the same conditions. Spatial volume ratios were applied to assess the impact of changed atmospheric conditions and prey size on foraging ecology. Reductions in detection range associated with increases in RH and/or temperature also varied in relation to the size (cross sectional area) of insect prey. Modelling demonstrated that small (6 kHz) movements in call frequency could not compensate for the changes in prey detection range and spatial detection volumes that result from significant changes in atmospheric temperature or RH. The notion that differences in RH are the primary cause leading to adaptive evolution and speciation in CF-emitting bats by precipitating intraspecific differences in the mean call frequency of geographically isolated bat populations was not supported by the results of this case study.

## 1. Introduction

Intraspecific differences in the characteristic frequency of bat echolocation calls among geographically isolated groups have yet to be fully explained (reviews in Francis and Habersetzer, 1998; Guillén et al., 2000; Armstrong and Coles, 2007). Most studies that examine echolocation call frequency variation have focused on the families Hipposideridae and Rhinolophidae. These bats emit calls with a narrowband constant frequency (CF) component, accompanied by a terminating, and often preceding, frequency modulated (FM) sweep (Griffin, 1958). Here we also concentrate on these CF–FM species. It is intuitive that the differences in characteristic echolocation frequency among isolated groups have resulted from adaptation to different local environmental conditions, which if it were the case, could be the basis for their future 'ecological speciation' (review in Schluter, 2001). Although an alternative and equally feasible explanation is that differences between groups come about through a process of drift (Jones and Barlow, 2004), in the present study we examined call frequency differences in the context of testing a hypothesis implicating adaptation. Understanding how these geographic patterns come about will give an insight into both the adaptive evolution of echolocation systems and the process of ecological speciation in

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bats. Examination of factors apparently responsible for differences between closely related sympatric species has previously provided insights into dietary niche specialisation and species evolution (e.g. Heller and von Helversen, 1989; Kingston et al., 2000; Kingston and Rossiter, 2004).

We consider an allopatric scenario that precedes reinforcement of species boundaries in sympatry, according to the ecological mode of speciation (Schluter, 2001). Under this mode, divergent natural selection according to some environmental factor gives rise to differences in population average characteristic call frequency. Reproductive isolation (pre-mating) would then be derived from the function of echolocation calls in a social context that allows species and preferred-mate recognition. The dual function of echolocation calls in resource acquisition and communication was expounded by Kingston et al. (2001) and Kingston and Rossiter (2004). However, although vocalisations not involved in echolocation have been demonstrated to function in social interactions (e.g. Barlow and Jones, 1997), this has yet to be demonstrated empirically for echolocation signals. Nevertheless, we acknowledge that echolocation calls allow recognition of conspecifics (e.g. Matsumura, 1981). Given that bats in these two families have an acoustic fovea of limited bandwidth (discussed in Kingston et al., 2001), any differences in call frequency that result from adaptation to local environments might also initiate pre-mating isolation among geographic isolates if calls from immigrants are detected towards the margins of this fovea.

Candidate environmental factors have so far proved elusive. Call frequency varies to a relatively small degree within species according to a range of factors such as season (Long and Schnitzler, 1975: 215; Jones and Ransome, 1993), body temperature (Huffman and Henson, 1991), maternal and age-related influences (Jones and Ransome, 1993) and ontogenetic effects (Pedersen 1996, 2000). However, none of these influences have been used to explain the development of geographic differences in the call frequency of CF bats, especially in the context of adaptive evolution. It is well known that body size can change relatively quickly in small populations such as those on islands (review in Lomolino, 2005), which could be used to explain geographic differences in call frequency. Indeed, many studies have highlighted the negative correlations between call frequency and various morphological features (Guppy and Coles, 1988; Heller and von Helversen, 1989; Jones 1995, 1996; Robinson, 1996; Francis and Habersetzer, 1998; Kingston et al., 2000; Zhao et al., 2003), but these features are not directly involved in the production or modification of the emitted signal (see discussion in Armstrong and Coles, 2007), and many of the known examples of geographic differences in call frequency do not derive from small island populations. Furthermore, this general negative correlation seen among members of *Hipposideros* and *Rhinolophus* does not hold within species (review in Francis and Habersetzer, 1998; Armstrong and Coles, 2007), and of importance here, does not point to mechanisms that produce geographic differences in frequency.

Perhaps the most feasible ecological factor involved in disruptive ecological selection was proposed by Guillén et al. (2000). They suggested that CF-emitting bats adapt call frequency to the relative humidity (RH) conditions of their particular region, making a very fine adjustment in the trade-off point between increasing frequency to enhance prey resolution (i.e. detection or recognition of the object) and decreasing it to maximise prey detection range. Although we are unaware of any empirical studies that demonstrate the ecological or evolutionary consequences of RH on bat echolocation call frequency, it is often stated that increases in RH result in increased signal attenuation, and that its effect is heightened with increased signal frequency (e.g. Griffin, 1971; Bazley, 1976; Lawrence and Simmons, 1982; Hartley, 1989). Well-supported situations of ecological speciation are difficult to obtain (Schluter, 2001), and likewise it is difficult to study the effect of RH in producing geographic differences in call frequency by direct experimentation. An alternative approach adopted in the present study involves mathematically modelling the effect of different humidity atmospheres on the detection range and spatial detection volume of volant prey for different echolocation frequencies. To test the hypothesis of Guillén et al. (2000), we used methods similar to Houston et al. (2004), who measured the amplitude of echoes reflected from ensonified insects of different sizes and calculated the maximum detection distance for each at different ultrasonic frequencies. As CF emitting bats are highly sensitive to the brief amplitude glints and spectral broadening of echoes produced when the wings of fluttering insects are momentarily perpendicular to the bat (reviewed in Schnitzler, 1987; Kober and Schnitzler, 1990; von der Emde and Schnitzler, 1990), we used the planar disc-equivalent cross-sectional area of insect wings to characterise the size of prey.

We used a dataset collected from the Australian endemic *Rhinonicteris aurantia* (Chiroptera: Hipposideridae; Armstrong and Coles, 2007). The situation of *R. aurantia* was particularly suitable since echolocation call frequency differences exist between two geographic isolates that occupy quite different environments. This species occupies a relatively continuous range across the north of Australia including the Kimberley region of Western Australia and the Top End of the Northern Territory. An isolated population also occurs in the Pilbara region of Western Australia separated from the Kimberley by the 500 km expanse of the Great Sandy Desert (Fig. 1). The average difference in call frequency between the two isolates is c. 6 kHz (Armstrong and Coles, 2007), which is typical in terms of the magnitude of intraspecific differences between geographic groups in other species. Given that the size of most morphological features are similar between isolates (Armstrong, 2002), and that there are significant climatic differences between the Pilbara (“where tropical-cyclonic and ‘Mediterranean’ influences act on essentially arid climates”; Gentilli, 1972; Tinley, 1991) and Kimberley/Northern Territory (tropical and monsoonal; Gentilli, 1972), we expected our models to suggest significantly reduced maximum prey detection range if the higher call frequencies of the Pilbara population were theoretically applied to the population further north. If correct, this would implicate RH as a potential factor in adaptive evolution, and suggest the basis for a general mechanism that initiates the allopatric component of ecological speciation in CF-emitting bats. The methods we used for calculating maximum prey detection range represent a significant improvement over

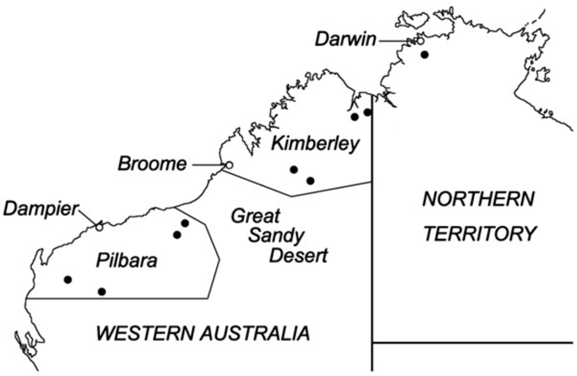

**Fig. 1.** Locations in northern Australia from which echolocation calls were collected in the study of Armstrong and Coles (2007) (closed circles; key towns/cities indicated by open circles).