Clark Lab Research Vision

The Biomechanics of Courtship Displays

Animal courtship displays can include remarkable athletic performances. Current research in animal behavior seeks to understand animal courtship behaviors in terms of multiple/complex signaling theory and receiver neurobiology. The Clark Lab will pursue a complementary approach: the comparative biomechanics of courtship displays. Our hypothesis is that dynamic courtship behaviors become exaggerated through directional female preference, a behavioral analog to well-studied exaggerated ornaments such as elongated tails of birds or fish (Clark 2009, Clark submitted). The resulting locomotor feats are in some ways similar to human sporting events such as gymnastics or the 100 meter dash.

Why such courtship behaviors arise is not well understood. Our approach to understanding their evolutionary origin and function is to examine the biomechanics of courtship displays through two complementary research foci. First, courtship displays can be stereotyped and easily elicited, and thus are ideal for the study of the physiology of extreme performance (Clark 2009). Second, we examine how the physiological underpinnings of such ‘behavioral ornaments’ bears on their function and evolution (Clark submitted). The Clark lab will pursue the mechanics of display performances using flight displays as a model system, particularly (though not exclusively) on hummingbirds, through integrated lab studies on mechanism and field studies of function, within a phylogenetic comparative perspective.

Courtship in the lab. Courtship displays of many taxa are athletic feats. The Clark lab will study the physiology and biomechanics of these displays. Hummingbird flight is an especially tractable system for the study flight biomechanics, due to the ease with which they are kept in captivity and fly within wind tunnels (Clark & Dudley 2009). Previous analyses of hummingbird flight have mostly focused on hovering or forward flight (the equivalent of human walking or light running); more impressive behaviors have barely been tested. Their remarkable courtship displays are easy to elicit under certain conditions (e.g. Clark & Feo 2008, Clark & Feo 2010, Feo & Clark 2010). The Clark lab will study such ‘animal gymnastics’ by eliciting courtship displays in a controlled (aviary) setting that allows testing of specific physiological and biomechanical hypotheses of performance. For example, what mechanisms allow hummingbirds to double the wingbeat frequency during courtship displays? Courtship displays of other flying taxa, e.g. butterflies, are also of interest.

Aeroacoustics of animal flight. As the footfalls of runners on a racetrack tells us, locomotion produces incidental sound and can contain information about performance. Many birds have evolved initially-incidental flight sounds into communication signals that are showcased during dynamic courtship displays (e.g. hummingbirds, snipe, honeyguides, manakins). Many of these sounds are produced by aeroelastic flutter of flight feathers (Clark et al. 2011). Flutter-induced sounds are a highly tractable bioacoustic system with some inherent advantages over analogous vocal sound systems: feathers are easily obtained and their sounds re-produced in simple wind tunnel experiments. There are intrinsic links between the production of these sounds and flight performance. For example, sound loudness increases with airspeed (Clark et al. 2011), and wingbeat frequency is directly encoded by the wing trill rate. Females that prefer acrobatic displays may therefore use display sounds to measure display performance. The Clark lab studies the aeroacoustics of flight in order to understand how these sounds are produced, with an eye to understand how they evolve and what information about flight performance they contain. I am also interested in another ecological and behavioral interface of flight aeroacoustics: the silent flight of owls, which has potential technological application as aeronautical engineers strive to build stealthy Micro-air Vehicles.

Field biomechanics. The Clark lab will pursue field experiments on wild populations that test hypotheses of courtship display function. One potential project entails measurement of male mating success (e.g. via paternity analysis on nestlings) as a function of male ability to produce communicative flight sounds. Lab experiments suggest it is feasible to subtly tune the acoustic frequency of a wild bird's courtship display sounds, by trimming or adding a small amount of mass, allowing subtle experimental tests of acoustic function. Of particular interest is the hypothesis that flight displays are visually hard but acoustically easy for a female to assess, thus females are selected to use acoustic cues as proxies for male flight performance.

Phylogenetic inference. The Clark lab incorporates interspecific, phylogenetic comparisons of courtship displays in order to make inferences of evolutionary processes, and as a source of hypotheses to test in the lab or field. For example each of the ~35 species of the 'bee' hummingbird clade has unique tail morphology and display behaviors that together produce the courtship sounds (Clark unpublished). Phylogenetic comparative analysis will allow inference of the nuanced evolutionary interplay between feather morphology and courtship behavior that together generate feather-songs (Clark in prep). Another unexpected pattern in the 'bee' clade are multiple, phylogenetically independent instances of apparent self-mimicry, in which the same animal produces similar sounds both vocally and with feathers (Clark & Feo 2010). Are they mimicking themselves? If so, why? Such patterns, made apparent by phylogenetic comparative analysis, suggest hypotheses straightforwardly tested in lab and field experiments on focal taxa.

These four approaches examine how and why flying animals perform courtship displays at levels ranging from proximate aeroacoustics to ultimate phylogenetic approaches. Courtship displays offer a veritable Olympics of extreme animal athletic performances, and seem underappreciated in animal behavior relative to morphological ornaments. This is perhaps because morphology is easy to appreciate in photos or museum specimens, while behaviors are not. The Clark Lab's pursuit of the comparative mechanics of courtship will further our understanding of animal flight, and how animals use these displays to showcase their athletic performance to conspecifics.

Chris Clark's Ph.D. Research

1. Physiological costs of elongated tails

The elongated tails of many birds are a classic example of a trait enlarged by sexual selection. Aerodynamic theory predicts these elongated tails pose aerodynamic costs such as drag and impaired maneuverability. I explored the consequences of evolving elongated tails, using hummingbirds as a model system. This project had three components:

a. phylogenetic analyses

I quantified evolution of tail shape, allometry, and dimorphism in 330 species of hummingbirds. Patterns of hummingbird tail morphology are inconsistent with aerodynamic theories predicting that forked tails are aerodynamically optimal (Clark 2010, Auk). Moreover, I test Lande's (1980) hypothesis that sexually-selected traits arise first in both sexes, and are then lost in females (MS in prep, target: Evolution)

b. elongated tails' effects on forward flight (collaborator: R. Dudley)

Using a wind-tunnel, we measured the metabolic costs to linear flight of elongated tail-streamers, finding that they increase drag, but that the costs appear to be lower than previously thought (Clark & Dudley 2009, PRSB). Our methods include mask respirometry, and we also document that the hummingbird metabolic power-curve is U-shaped, not J-shaped as previously reported (Clark & Dudley 2010, PBZ).

c. Effects of an elongated tail on maneuverability

Elongated tails may affect maneuvers. In Jamaica, I experimentally manipulated tail length of the Red-billed Streamertail to test whether their elongated tail streamers affect maneuverability. Individuals were filmed with synchronized high-speed cameras to measure linear and angular position, velocity, and acceleration during an escape maneuver (Clark 2010 J. Orn.)

2. Duck functional morphology (Collaborators: Patricia Brennan, Rick Prum)

I collaborated with Dr. Patricia Brennan to study the functional morphology of the explosive eversions of the muscovy duck penis (Brennan et al. 2010, PRSB). We are also working on a project to describe the bioacoustics of Ruddy Duck display sound that are produced when males strike their breast with their bill (in prep).