Coping with uncertainty
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The increase in biological diversity from the poles toward the equator is one of the most fundamental patterns of life on earth. Opposite of the pattern of increased diversity as you approach the equator, the occurrence and amplitude in seasonality reduce from highly predictable seasons at the poles to aseasonal environments at the equator. In predictable seasonal environments, organisms have often evolved adaptive physiological programs and use reliable cues to respond to anticipated variation in environmental conditions; this is generally highly synchronized with life history stage demands. But how can equatorial afro-tropical birds adjust their phenotype or time their nesting to coincide with environmental conditions that increase nest survival when the environment is constantly changing in an unpredictable stochastic way? Understanding how birds adjust their phenotype in these unpredictable near-equatorial areas provides an important step towards a better understanding of life history strategies in these unpredictable stochastic environments that are suggested to have differences in cue-use and responses to environmental drivers as compared with their much studied high latitude counterparts.

In this thesis, we investigate if/how the stochastic environment influences temporal variation in nest success of Red-capped larks, and whether Red-capped larks adjust their phenotype through behavioral space use and physiological adjustments of body mass and immune function to adapt to the stochastic environment. I also test whether variation in body mass and immune function follows the historical seasonal or a stochastic pattern reminiscent of current environmental variation. Our model species, the red-capped lark is a small gregarious bird found in short-grass and bare-ground habitats widely distributed across Africa. Males and females form pairs during breeding but interact in mixed-sex flocks when not breeding. Pairs build ground-level open-cup nests and typically lay two eggs per clutch. Clutch size is usually two eggs but 1–3 egg clutches occur occasionally.

In chapter 2, we show that despite breeding year-round, nesting success is not consistent but rather varies in an inconsistent fashion both among months and years. Birds breeding when most conspecifics are also breeding have a higher nesting success than their counterparts breeding when nesting intensity is low. Although nest predation was the single most significant cause of nest failure, the negative correlation of nest success with flying invertebrates and rainfall pointed to incidental depredation. Incidental depredation occurs when nest contents are depredated as secondary prey encountered by predators searching for different primary prey. Presumably, these incidental nest predators were more abundant or active with more rain and flying invertebrates.

Our objective in chapter 3 was to understand year-round variation in home-range size in the context of the highly aseasonal and unpredictable variation in weather and resources typical of many equatorial habitats, in addition to the birds’ changing social structure and year-round breeding. The intensity of nesting (total number of nests found per month) was the main factor influencing the home range of Red-capped larks, which applied to both the combined composite home ranges of breeding and non-breeding birds and to the home ranges of non-breeding birds only. Red-capped larks had larger home ranges when few individuals were breeding but the home ranges decreased as the number of breeding pairs increased. Also linked to breeding, Red-capped
larks differed in social organization between breeding and non-breeding individuals through fusion of pairs to large groups when not in breeding and fission during breeding. During breeding, nesting birds are confined to areas near their nest which may explain the smaller home ranges when nesting. For the non-breeding birds, exclusion by the breeding pairs which become territorial may limit access of some areas to non-breeding birds and similarly lead to smaller home ranges.

In chapter 4 of this thesis, we aimed to investigate (1) if body mass variation in Red-capped larks is better explained by evolutionary adaptation to long term weather patterns or by phenotypically plastic responses to current weather conditions? (2). How strong of a cue are weather patterns in predicting future food availability or does food vary in an unpredictable manner, and if so, (3). Do Red-capped Larks’ body masses vary dependent on life history stage or increase with higher food availability to buffer against unanticipated harsh times in the stochastic environment, independent of life history stage? Our results in this chapter attest to the stochasticity and unpredictability of food availability in the equatorial afro-tropical environments and the unreliability of weather as a cue for future food availability. Despite the change in weather patterns from a historical seasonal to a current non-seasonal environment, body mass of Red-capped Larks was only partly explained by phenotypically plastic responses to current weather conditions, and also to some extent appeared evolutionarily adapted to long term weather patterns. Although food availability was unpredictable, we did not find evidence that birds accumulate extra reserves for use during breeding but on the contrary body mass in Red-capped larks decreased with increased food availability independent of life history stage which suggests year-round food availability. However, molting birds decreased mass with higher ambient temperatures and favourable environmental condition to even lower levels than birds in quiescence. With food sufficient year-round, Red-capped larks may opt for a lean mass under good conditions to counter associated negative costs of higher body mass that include increased locomotory costs and higher vulnerability to predation, more so during molting when flight efficiency is reduced due to missing feathers and reduced wing area.

Although temporal variation in immune function in animals, and in particular vertebrates, has been explained proposed to reflect a trade-off with energetically or nutritionally expensive life-history events such as reproduction and molt, in chapter 5 of this thesis, we found no evidence that immune function in Red-capped larks was reduced during breeding. Instead, consistent with the alternative proposal that immune function reflects adjustment to changing environmental factors that influence resource availability and disease threat; all four immune indexes were explained by at least one or more of the socio-environmental factors, while life history stage played a minor role. The immune system plays an important role as the body's natural defence against infection and disease. The stronger influence of social-environmental factors may, therefore, be due to the hypothesized higher parasite diversity and pathogen pressures in tropical areas compared to temperate regions. In addition to variation of immune indices with favourable social-environmental factors, immune function in Red-capped larks was also influenced by variation in temperature and rain. With the level of immune indices suggested to be reflective of the threat of infection, variation of immune indices with temperature and rainfall may reflect increased disease risk and/or pathogen pressure in the environment.

To conclude, our study underlines the relevance of conducting more studies in aseasonal tropical areas in order to disentangle effects of weather, food availability and breeding that vary in an unpredictable and unsynchronized manner, but that peak simultaneously in most seasonal areas, coupled with the high diversity of life history strategies observed in the tropics.