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Report on the dissertation of Javier Oňate-Casado, M.Sc.
"Patterns of song variation in migratory and sedentary birds: A comparison of two sister pipit species"

This is a well-presented and academically strong thesis, which presents results from a series of field-based studies on within and between-species variation in vocal signals. Two of the chapters have already been published in internationally respected peer-reviewed journals, and have already garnered several citations each. Overall, the work reflects the outcome of a very ambitious and determined approach to test hypotheses related to individual acoustic monitoring, impacts of more traditional monitoring techniques and different levels of vocal diversity across two related taxa. These results are likely to have positive conservation impacts not only for these threatened species, but more broadly. The work is of sufficient quality and rigour and I recommend it be awarded the degree of Ph.D.

Below I discuss each chapter and some of the strengths and remaining questions arising from each of the chapters in the dissertation.

General Introduction –

The introduction reflects a fairly through review of the background literature, setting up a logical contextual framework for the studies presented in the following chapters. It is helpful here that the study organism and study sites are carefully described and the decision to base the work on these species is properly justified.

I have a broad question here about whether we should consider individual vocal signatures to be signals or cues. For example, on page 13 the author mentions that Myotis myotis (bats) have individual-specific acoustic features "… in echolocation calls to recognize conspecifics and maintain social bonds within their colonies". The way this is written suggests that the inclusion of these features is a communicative "decision", i.e. that these features are signals, rather than cues which conspecifics could use to extract information about the vocaliser's identity. This leads to a bigger question about your own research presented throughout the thesis – are the acoustic features underlying individual vocal signatures in the pipits actually "signals" (i.e. produced intentionally or selected for communication) or are they simply cues – i.e. passive features that are linked to body size or vocal tract shape?

Page 14 states "these insights suggest that the primary evolutionary drivers of individuality in …acoustic signals. is not fully understood"

I would go one step further and ask if there is any evidence (in non-vocal learners particularly) that this is a trait under selection?

What are the proximate mechanisms that can lead to vocal individuality in animals generally? And in songbirds? To what extent are these heritable (or likely to be)?

What do you know about the frequency of occurrence of new birds into these populations? In the introduction it mentions "limited gene flow", what does that mean in terms of frequency of new birds with different song types in the population?

Chapter 1 –

In this study you show that individuals of both sexes in tawny pipit can be acoustically identified. This first relied on having a set of recordings that came from known individuals, mostly birds with uniquely identifiable colour rings. As this chapter concludes that IAM would be a viable alternative to more invasive traditional methods of monitoring populations. Is this actually practical without having a marked population? How would this method suit a population of unknown size, or how would one be confident that unmarked birds were truly different individuals?

Does the method depend on knowing (a) how many different individuals there are in the set of recordings and/or (b) knowing which vocalisation belongs to which individual?

For migratory species the temporal stability of song only considers song across a short period of the year, and a period where birds are likely to be in peak singing condition hormonally for much of the time. How would you predict this to vary in a resident species? We know from birds with strong seasonality that songs can become very "plastic" outside of the breeding season even in close-ended learners, and recrystalise with the onset of reproductive cycle (e.g. (Smith, Brenowitz, Beecher, & Wingfield, 1997)). This suggests that IAM may only be useful in a limited time of year?

Chapter 2 –

It is not entirely clear to me if the goal here is to understand whether the use of playback as a lure to catch and ring birds would impact the response of birds in a behavioural playback experiment testing aggression to a simulated territorial intrusion, or if it would impact the efficacy of re-trapping individuals during ringing/monitoring activities, or both?

I could imagine that many ringers might be more interested in trapping naïve or new (unringed birds or birds ringed elsewhere) than re-trapping birds. Researchers might rather want to monitor which birds are still around or returning, and then colour rings might be a less invasive way to check that.

Finally, just to play the devil's advocate – the number of people out there wanting to do playback experiments investigating behavioural responses is likely extremely small in the grand scheme of things? This is all not exactly a question, but would like to hear the candidate's thoughts on the relevance of this study to future ringers and researchers in light of these different goals they may have.

In this chapter, were males identified by their songs just by visually comparing spectrograms (e.g. at start of "behavioural assessment and data analysis" paragraph, pg. 21)

In the discussion, there is some mention of age and personality being potential contributors to variation in response to playback. In a paper by (LaRocque et al., 2023), they used RFID readers on feeders with PIT-tagged ringed population to investigate recapture rates by sex, personality traits (e.g. exploration, handling aggression, sampling behaviour) and found that males less likely to be recaptured than females, support for feeding rate and latency to resume feeding after simulated predation risk as being linked to recapture rates. Here they conclude that energetic needs may drive birds to increased likelihood of recapture, despite perception of risks. What would be an analogous driving force for your study? Is defense of territory less evolutionarily compelling?

How many pipits do you estimate are in the population that are never caught?

Chapter 3 –

Page 2 of introduction: I am not sure what is meant by " …juveniles learn from most males singing around…" does it mean that juveniles learn the most from the males nearby them? Or does it mean that they learn songs from males that sing the most? Neither of these?

Do they never learn from singing females?

What would you predict that the lack of congeners would do to the need for interspecific identification? I mean that if there are no similar species singing anywhere nearby, would you predict this might have an impact on the amount of individual variation? Or the amount of colony-level variation? In which direction?

Although you did not find acoustic signatures that predict population/location, how confident are you that there really are not acoustic signatures (e.g. comprising features you did not measure)?

For one, there are instances in the literature where human researchers could not find statistical differences between songs/vocalisations but the birds behaviourally can tell the difference. Examples that come to mind:

> Reichard and Price (2008) showed that mockingbird and thrashers could tell species apart immediately, regardless of temporal pattern that humans use to tell the two apart.
>
> Adam et al (2023) found that zebra finch females can tell unpractised from practiced song, despite the researchers finding no acoustically significant differences between the songs

How can one be sure that one is investigating the "correct" or biologically-relevant aspects of the songs? How could one test this?

Which aspects of the pipit songs are inherited vs. learned? (e.g. Lewis, Kwong, Soma, de Kort, & Gilman, 2023)

What could be learned by cross-fostering between islands? Between species?

In the first paragraph of the discussion Ch 3, it states "This pattern was, however, not primarily driven by further song divergence of dissimilar songs but rather by the lack of closely similar song types". I am not sure that I understand the difference between the two, in terms of functionality?

This study suggests that the songs of both species are consistent over time. However on the time that they are sampled (only one song bout of a few minutes at some point in the day, and then again in a different year the same way?), I think you could easily miss more short term and also seasonal changes in song consistency. For example blue tits and Eurasian blackbirds we know change over the course of a day in the quality of songs, including in consistency (e.g. Sierro, de Kort, & Hartley, 2023). Does this limit the usefulness of IAM in these populations, or make a difference in the outcome of your dialects analyses?

Considering that there are only about 3 minutes of song recorded from many of these males, how do you know that males used only a single song type (mostly)?

One big final question – why is this interesting or surprising? One might argue that of course individuals of any species are all somehow unique in their morphology and behaviour, even if in small ways. I would think any species that has any kind of social interaction at all (just finding a mate, for example) would need to tell individuals apart. Shouldn't the null hypothesis be that the animals do differ rather than that they do not? It would be much more surprising to find that there are NOT individual differences, wouldn't it?

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