



Vocal diversity patterns

In the March issue of *Frontiers*, Laiolo and Tella (*Front Ecol Environ* 2007; 5[2]: 68–72) summarize aspects of their ongoing research into determinants of vocal diversity in the shrub–steppe dependent Dupont’s lark, *Chersophilus duponti*. Studies of cultural elements have rarely been conducted in fragmented landscapes, and this study has the potential to yield insight into these patterns and the mechanisms driving them. Unfortunately, their discussion was speculative and tenuous, extending beyond the scope of the data presented; while the patterns were clear, the underlying processes were not. We were surprised by the lack of reference to studies of vocal variation in widespread species, dialects in naturally fragmented systems, and demographic drivers of cultural and genetic diversity, all of which are well established in the literature (eg Tack *et al.* 2005). In addition to this issue of context, four specific shortcomings of their work warrant discussion.

There was insufficient information provided regarding the historic pattern and spatial extent of habitat loss that led to the current arrangement of habitat patches. The effects of habitat fragmentation are modified greatly by time, such that fragments and islands converge in many ecological properties over thousands of generations (Watson 2002). Even within recently modified landscapes, the influences of habitat loss and habitat fragmentation are divergent (Fahrig 2003). The authors seemed unclear on which processes were driving the observed patterns, and neglected to evaluate two alternate hypotheses to explain their findings. The vocal differentiation noted between habitat patches may have been influenced by pre-existing variation within the historic range of the lark, as noted by Westcott and Kroon (2002) in *Prionodura newtonia*. Or vocal behavior may have been influenced by differences in vegetation between patches, consistent with the acoustic adaptation hypothesis (Morton 1975). Rather, they

restricted their discussion to the third possibility, that the differences were driven by demographic factors operating within patches of different size and, presumably, different carrying capacity. By emphasising analyses consistent with this conclusion and downplaying or excluding other analyses, these alternative explanations could not be rigorously dismissed.

Aside from the purported influence of patch size on song repertoire size, Laiolo and Tella noted an effect of isolation on call repertoire, with fewer call types recorded from the more isolated patches. This association (Laiolo and Tella’s Figure 5b) was greatly influenced by one outlying patch – this single data point having great leverage. This hypothesis must be regarded as provisional, and the role of isolation remains to be clarified.

Given known dispersal abilities of this species, it is equally likely that smaller repertoires in outlying fragments result from small founding populations, as opposed to eroded populations of birds that lived there prior to habitat fragmentation. Again, evaluation of these competing explanations is hampered by the lack of detail regarding the extent and nature of habitat loss in the study area.

Finally, and most importantly, there is no direct evidence, either for this species or birds generally, that changes in repertoire size have any effect on individual or population fitness (Kroodsma 2004). While reasonable, the empirical data required to back up such an assertion simply aren’t there.

We regard Laiolo and Tella’s article as an important step toward recognizing the importance of cultural elements in animal populations, and the effects (both direct and indirect) of habitat fragmentation on those elements. However, the data presented do not back up the assertions made, and the influence of habitat fragmentation on vocal diversity in this species remains unclear.

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The authors reply

We thank Watson and Tack for their interest in our work and for giving us further opportunity to discuss birdsong in human-altered landscapes. We believe that Watson and Tack misinterpreted the scope of the paper, as well as the patterns we documented (namely, song diversity reduction and *not* reduction in variability of birdsong acoustics). The three processes they propose to explain cultural erosion as an alternative to human-driven habitat transformation are extensions of this erroneous belief.

We excluded a priori the *acoustic adaptation hypothesis* because signal attenuation and/or degradation are not considered to be major determinants of song repertoire size, although the structure of the habitat, ambient noise, and abiotic factors may influence birdsong acoustics (eg duration, pitch, amplitude; see Slabbekoom [2004]). Even if vegetation structure is rather similar among patches due to the restrictive habitat selection of the species (Laiolo and Tella 2006 a,b), we cannot exclude that differences in

humidity, temperature, and wind could account for variation in the spectral characteristics of Dupont's lark song (as larks are aerial singers). However, no prior hypothesis has suggested that these could cause shifts in *song-call-type abundance*, the focus of our paper, and such abiotic factors are even less likely to covary with habitat fragmentation. We are aware of the studies on natural vocal variation within bird species and we cited those that treated birdsong repertoires from a *qualitative* point of view (occurrence of song/syllable types rather than *quantitative* switches in acoustics), as these better matched the scope of our paper. We also cited studies on bird communication systems in fragmented landscapes (Laiolo and Tella 2005).

Watson and Tack also addressed the possibility of *founder effect*, one of the hypotheses we considered. This hypothesis was discarded because there is published evidence of historically large population sizes and steppeland cover in the study area (Aragües 1992), in addition to the personal observations of one of us (JLT), who born there. For readers interested in the fate of Iberian steppe-lands, information on past and present changes can be found in Tella *et al.* (2005), which notes recent Dupont's lark range restriction and local extinctions, and in Laiolo and Tella (2006a), which documents the loss of the species' habitat throughout the Iberian peninsula. We stress that two populations went extinct during our study, and one uttered song types that were not recorded at any other Spanish site; these unique tunes were lost with the last male in the area.

We did not consider the hypothesis of *pre-existing historic variation* because we found no evidence of dialect boundaries in a large and less fragmented geographic zone comparable in size to our study area (see Laiolo and Tella 2006b for a comparison of the Iberian Mountains and Ebro Valley). Notably, Westcott and Kroon's (2002) study cannot be cited as an example of song dialects pre-dating isolation, as the authors themselves hypothesize a link be-

tween *Prionodura newtonia* song variation and recent forest clearance.

Finally, Watson and Tack question the relationship between call diversity and isolation due to the influence of a supposedly outlying point (see figure). However, the relationship remains significant after this point is removed ($r = -0.17$, $F_{1,21} = 4.33$; $P = 0.049$; which, in the interest of clarity, is not a statistical outlier. We also stress that the key role of isolation was previously addressed in detail in Laiolo and Tella (2006b), where we analyzed call diversification with respect to the composition of the habitat matrix and alternative isolation indices. Finally, the relationship between repertoire and fitness was not within the scope of this paper.

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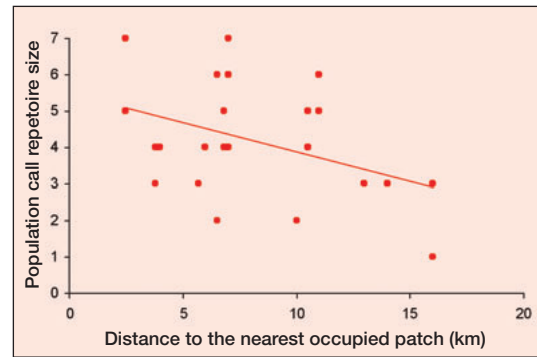


Figure 5b, (Front Ecol Environ 2007; **5**[2]: 68–72) excluding data from the most isolated patch.



Compensatory mitigation

In the August issue of *Frontiers*, Wilcox and Donlan (*Front Ecol Environ* 2007; **5**[6]: 325–31) proposed economically based compensatory mitigation for marine bycatch. The example they used to demonstrate their case was the flesh-footed shearwater, *Puffinus carneipes*, on Lord Howe Island, Australia. The compensatory action proposed was the eradication of ship rats, *Rattus rattus*, to be funded by the local long-line fishing industry.

As I have studied flesh-footed shearwaters on Lord Howe Island and am currently overseeing the planning phase for eradicating introduced rodents from this island, the article immediately grabbed my attention. Upon reading it, I saw the model as flawed and dismissed it outright. The model is based on the assumption that the current loss of 50% of eggs and chicks (50% of eggs produce flying young; Priddel *et al.* 2006) can be eliminated entirely by removing rats. This, of course, is biological nonsense. I presumed the article, and the issue of compensatory mitigation on Lord Howe Island, would die a quick death. Not so – I have received numerous communications about it. To inform the debate as to whether this type of compensatory approach is a panacea for island conservation or harmful (as suggested by Doak *et al.* [*Front Ecol Environ* 2007; **5**(7): 350–51]), I summarize the comments I received.

First, because data that I published

was used in the model (albeit incorrectly), and because I am a strong advocate for rat eradication on Lord Howe Island, there was a presumption that I would support this particular example of compensatory mitigation. This is not the case. I have major concerns with both the concept and the model, and was disappointed that the authors had apparently used our data without having actually read the manuscript (Priddel *et al.* 2006), as nowhere in it do we claim rats to be an issue for flesh-footed shearwaters. In fact, we dismiss them as a threat. We demonstrate that clearing and urbanization are the prime threats on land, while plastics and long-lining are the potential threats at sea.

Second, readers who recognized the flaws in the Wilcox and Donlan model, but who are unfamiliar with Lord Howe Island, are now skeptical of the need to eradicate rats from the island. I point out that the impact of rats on flesh-footed shearwaters has never been cited as justification for the eradication of rodents from this island. Lord Howe

Island is a World Heritage Area of immense ecological importance, with a high degree of endemism. Rats have been implicated in the extinction of at least five land birds and an unknown number of invertebrates and plants. They continue to threaten the survival of numerous species (DEC 2006), and rat predation on Lord Howe Island has been listed as a key threatening process under the *New South Wales Threatened Species Conservation Act 1995*.

Third, now that the lucrative long-line fishing industry has been fingered as a potential cash cow, the various agencies with statutory responsibilities for biodiversity conservation on Lord Howe Island will have to reassess the need to commit funds to any future rodent eradication program. Other potential funding bodies are also likely to question whether they would be better served by diverting their hard-earned cash to projects where no alternative funding source has been identified.

The eradication of introduced rodents from Lord Howe Island is

arguably one of the most noteworthy conservation actions that could be undertaken in the South Pacific. Introduction into the public arena of the concept of compensatory mitigation of bycatch has so far done little to promote our cause. Indeed, it has given us another hurdle to overcome in securing the necessary funding from conventional sources. It would be terrific if the fishing industry were to provide the US\$2 million or so needed to complete the eradication, but I, for one, will not be waiting.

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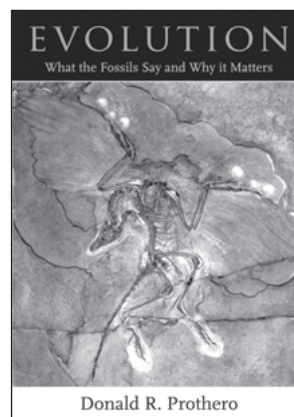
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