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OPINION PAPER

Comparing disturbance and generalism in birds and mammals: A hump-shaped pattern

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Abstract

Using indices as proxies, we observed that comparing a large number of common birds and mammals, the level of generalism peaks in species inhabiting habitats at intermediate disturbance levels. This pattern might be universal, at least in these homeothermic vertebrates. Birds show nonetheless some differences in pattern from mammals, where specialization at intermediate levels of disturbance is not present. Differences in ecological and evolutionary traits between birds and mammals might determine different adaptive responses to historical anthropogenic changes, explaining these taxa-specific hump-shaped patterns.

Keywords: Hemeroby; Disturbance; Land use; Birds; Mammals

Measuring disturbance and generalism

It is commonly believed that species of disturbed habitats are generalists, whereas species of undisturbed habitats are specialists (Devictor et al. 2008). Regarding the measurement of disturbance, many different approaches are available (Sousa 1984; Battisti, Poeta, & Fanelli 2016) both at species- and community-level (review in Magurran & McGill 2011). A very useful concept is that of hemeroby, which represents the quantification of the gradient from pristine to heavily disturbed habitats (Kowarik 1989; Kowarik 2006; Schleupner & Schenider 2013). Similarly, the generalism may be measured in many different ways (Devictor et al. 2008).

Recently, we developed two new indices: the hemerobic score (HS), which is already in use in plant ecology and is used here to represent the average level of hemeroby at which a species occurs, and the hemerobiotic entropy (HH) representing the range of habitats where a species lives (Battisti & Fanelli 2015; Battisti, Fanelli, Mariani, & Capizzi 2017).

These indices allow to measure the level of generalism of species along gradients of disturbance using hemeroby as a proxy. We calculated these indices for a large number of common birds and mammals in a Mediterranean region: HS was calculated as the barycentre of the distribution of frequencies of the i-th species in each habitat type characterized by a different value of hemeroby. Applying the Shannon index

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to the distribution of frequencies of the i-th species in different habitats, we obtained an index of niche breadth of the species along the gradients of disturbance (HH; see supplementary data Appendix A). Indicating respectively the mean position along two gradients (disturbance and generalism), these indices might have interesting implications (for example, to monitor whether the environmental state of the habitats has altered; Albuquerque, Assunção-Albuquerque, Cayuela, Zamora, & Benito 2013; Santana et al. 2014). Here, we report on a comparison between generalism/specialization of species and the level of disturbance where they occur using two indices never applied in birds and mammals (homeothermic vertebrates) before.

A surprising emerging pattern

When we compared HS and HH across different species of common birds and mammals a surprising pattern appeared: the generalism of species is not maximum at the highest levels of disturbance, as expected (Marvier et al. 2004), but peaks at intermediate levels of disturbance (Fig. 1). In other words, we observed a high value of HH (highest generalism) in species inhabiting habitats at intermediate levels of hemeroby, and lower values both in undisturbed and heavily disturbed (urban) habitats. We believe that this hump-shaped generalism pattern, which is consistent for both mammals and birds (curves showed similar AIC scores: mammals: 7.482, birds: 7.516; Akaike Information Criterion approach; Akaike 1983), is general and it is closely related to the well-known intermediate disturbance hypothesis (Roxburgh et al. 2004).

More specifically, among mammals it is possible to distinguish: (i) species with low HS (<3) and increasing HH (from 0.3 to 1.4) including specialized interior species of forests and other pristine habitats; (ii) species with intermediate HS (3–6) and high HH (about 1.1–1.6) of open and edge/mosaic habitats; (iii) species with the highest HS (>6) and decreasing HH (from about 1.5 to 1), linked to disturbed and dynamic habitats (e.g. croplands, anthropized habitats: see check-list in Table 2, Supplementary materials). Species inhabiting pristine habitats not surprisingly occur only in a small range of habitats with low HS and are specialized, but also synanthropic species are restricted to only anthropized habitats ("disturbance specialists").

In birds we identified: (i) specialized species strictly linked to pristine habitats (forest interior species) showing the lowest HS and the highest specialization; (ii) a large set of intermediate-generalist species of mosaic landscapes including species of progressively more disturbed habitats (e.g. croplands, patchy mosaics, etc.); (iii) species typical of highly disturbed habitats (highest HS) showing a progressive increase in specialization (decrease in HH; check-list in Appendix A: Table 2).

Species inhabiting habitats with an intermediate level of disturbance could be more adaptable to a broader range of environmental conditions. The fact that species inhabiting pristine habitats are also ecologically specialized is a cornerstone in ecology (specialization-disturbance hypothesis; Vàsquez & Simberloff 2002). Nevertheless, the fact that species occurring in urbanized habitats (high HS) are also specialized is counter-intuitive and apparently discordant with the common sense (and literature) where synanthropic species have been considered generalists (Bonier et al. 2007).

Analyzing the pattern in detail, we observed that birds, differently from mammals, showed a complex pattern. Indeed the polynomial curve fitting bird species points could be further divided through a bifurcation into two sub-curves: (i) a first hump-shaped curve (HS ranging between 2 and 6) including species ranging from generalist of mosaic landscapes (Le Cœur 2002) to progressively more specialized species inhabiting moderately disturbed habitats (e.g. farmlands: Gregory et al. 2004); (ii) a second linear curve (on the extreme right; HS > 7), including a peculiar set of species linked to progressively even more disturbed habitats (strictly synanthropic species: Faeth et al. 2011).

Therefore, with low level of disturbance (pristine habitats) bird species progressively increase their generalism (HH) moving from pristine to intermediately disturbed habitats up to a modal value (about 4 in HS). After this peak, with the increase of the level of disturbance, the pattern for birds shows a progressive decrease of level of generalism with the increase of disturbance. In birds, this pattern shows a bifurcation with two tails on the right (Fig. 1).

Therefore, we observed in birds three groups of species occurring respectively in: (i) pristine habitats (left tail), (ii) habitats showing an intermediate level of disturbance (first tail on the right), and (iii) highly (irreversibly) disturbed habitats (second tail on the right). Although we also observed a progressive differentiation in the HH-HS pattern in mammal species occurring in differently disturbed habitats (see Appendix A: Table 2), did not observe a progressive specialization at intermediate levels of disturbance (the 'first-tail') as in birds (Fig. 1).

Searching processes behind the patterns

We hypothesize different causal drivers for these different patterns. Birds differ from terrestrial mammals in terms of ecological and evolutionary traits (e.g. higher dispersal and colonization ability) that make the former more adaptable and specialized to ephemeral habitats: for example, there are many more birds specialized for wetlands (high HS) than mammals (Croonquist & Brooks 1991). As opposed to mammals, which are largely represented by generalist species in agricultural landscapes (Pita et al. 2009), there are many farmland specialist birds of high conservation concern (Gregory et al. 2004).

Biological attributes and ecological traits predispose species to disturbance sensitivity and related risk of local extinction (Cardillo et al. 2008), with a taxonomic selectivity making birds different from mammals (Russell et al. 1998).