



Trophic requirements beyond foraging habitats: The importance of prey source habitats in bat conservation



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ARTICLE INFO

Article history:

Received 29 April 2015

Received in revised form 27 July 2015

Accepted 31 July 2015

Available online 15 August 2015

Keywords:

Ontogenetic habitat shift

Trophic requirements

Predator–prey interactions

DNA metabarcoding

Landscape

ABSTRACT

Conservation efforts for endangered animals commonly focus on the protection of foraging habitats, aiming to ensure sufficient food availability. However, the diet of many species is based on animals that undergo habitat shifts across ontogenetic life stages, yielding considerable differences between the lifelong habitat requirements of both predator and prey. Consequently, prey availability may not only depend on the suitability of the foraging grounds where predator and prey coincide, but also on habitats where the ecological requirements of the non-prey stages are fulfilled. In this study we test to what extent prey of the insectivorous bat *Rhinolophus euryale* (Blasius 1853) originate either from the grounds where they are consumed, or in areas/habitats outside the bat's foraging sites. We analyzed the diet of *R. euryale*, by identifying its prey to the species level using DNA metabarcoding, and by searching for its prey's larval feeding requirements in the literature. We found that the larvae of the moth prey grow both inside and outside the grounds where they are hunted by the bats once the moths reach their adult stage. The importance of prey that originated from outside the bat's foraging grounds varied considerably across seasons. As a result, *R. euryale* does not only rely on the landscape elements where it hunts, but also on other source areas/habitats that supply it with food. This study shows that conservation measures that aim to address the foraging requirements of predatory species should not be limited to merely protecting their foraging grounds, but should also take into account the ecological requirements of their prey throughout their life stages.

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1. Introduction

Ensuring prey availability and suitable foraging areas are key factors in the successful conservation of endangered species (Sinclair et al., 2006). As such, they are two of the main topics addressed in conservation scientific studies (e.g. Agosta, 2002; Fenton, 1997; Shuterland and Green, 2004; Russo and Jones, 2003). It is generally assumed that by conserving foraging areas, prey availability is also ensured. However, this assumption is not adequate when the ecological needs of the prey exceed the foraging ground of the predator. Furthermore, predator–prey interactions and food web studies are commonly defined in terms of fixed communities, despite the temporal and spatial heterogeneity of trophic relationships (Miller and Rudolf, 2011; Polis and Strong, 1996). Niche shifts across ontogenetic life stages are commonplace in

animals with complex life cycles (Rudolf and Lafferty, 2011; Rudolf and Rasmussen, 2013), so the lifelong habitat requirements of predators and prey may differ considerably despite the fact that they need to coincide in time and space (Ryall and Fahrig, 2006).

Holometabolous insects are one of the main exponents of ontogenetic habitat shifts, owing to the sheer difference in requirements of larvae and imagoes (Gullan and Cranston, 2000; Miller and Rudolf, 2011). Holometabolous insects such as lepidopterans, coleopterans and dipterans are the main prey of many insectivore vertebrates at different stages of their life cycle, including caterpillars for birds (Barbaro and Battisti, 2011; Busby and Sealy, 1979; Hogstad, 1988), moths for bats (Dietz et al., 2009), and both larvae and imago for rodents and lizards (Bellows et al., 1982; Brown et al., 2014). Consequently, insectivores' prey availability may not only depend on the suitability of the grounds where predators and their insect prey forage, but also on habitats and areas where the ecological requirements of the non-prey stages are fulfilled, i.e. the places and habitats where the larvae that will become prey at the adult stage develop. Any change in these habitats can alter population source-sink dynamics of the prey (Pulliam, 1988; Schreiber and Rudolf, 2008). In addition, the predator–prey interactions could also

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be affected, leading to changes in ecosystem structure and processes (Rudolf and Rasmussen, 2013).

To date the ecological requirements of prey have not been investigated. This is most likely due to the lack of species-level information on the consumed prey, especially in the case of insectivorous and elusive animals. Visual analyses of stomach and fecal contents have seldom provided taxonomic resolution beyond the order or family level (Whitaker et al., 2009). However, the implementation of molecular tools for diet analysis has triggered an important step forward in the last few years (Clare, 2014; Pompanon et al., 2011). The species-level identification of prey items provided by molecular tools has allowed researchers to unveil ecological information hidden in the food items. For instance, Alberdi et al. (2012) inferred foraging habitats based on consumed species, Clare et al. (2013) used dietary information to assess the quality of aquatic habitats, and McCracken et al. (2012) reported bats foraging on and tracking pest moths on a regional scale. Accordingly, we are now able to broaden the scope of conservation studies, to go in more depth into prey–predator relationships, as well as to assess the finer ecological requirements of prey species.

Semi-natural landscapes, created by traditional land use and composed of grasslands, hedgerows and forest patches, are of paramount importance for the conservation of many elusive vertebrate and invertebrate species. These include birds, rodents, bats, butterflies and moths that interact as predators and prey (Dover and Sparks, 2000; Marshall and Moonen, 2002; Merckx et al., 2012; Millán de la Peña et al., 2003; Tschardt et al., 2008; Slade et al., 2013). In particular, this mixture of vegetation structures enhances foraging opportunities for the Mediterranean Horseshoe bat (*Rhinolophus euryale*, Blasius 1853; Goiti et al., 2008; Hutson et al., 2008), a moth-specialist bat with declining populations throughout the Mediterranean Basin (Andreas et al., 2012; Goiti et al., 2004; Hutson et al., 2008). Changes in agriculture and land use policies have led to the alteration of this landscape type (EEA, 2005), resulting, for example, in the decline of many bird and lepidopteran species (EEA, 2005, 2013; SEO/BirdLife, 2014; Söderström et al., 2001). We argue that predators such as the Mediterranean Horseshoe bat may not only lose foraging grounds (as well as nesting sites in birds) through direct removal of hedgerows or woodland patches. They may also be affected by the transformation of *non-used* landscape elements that act as prey-source habitats that are essential for the other life-stages of their insect prey. As such, the extent to which a habitat and prey-specialist predator is dependent on the habitat requirements of the non-prey stages of consumed prey has direct implications for conservation. For instance, conservation guidelines for *R. euryale*—and other bat species—have so far focused mainly on the conservation of their feeding and roosting areas (Eurobats, 2014), under the assumption that these portions of the landscape fulfill the functional needs of the species. However, the precise ecological requirements of the consumed prey throughout their entire life cycle, and thus the implications for the foraging requirements of *R. euryale*, remain unknown.

In particular, we aim to test whether the foraging habitats of an insectivorous bat also cover the habitat requirements of the other life-stages of the consumed prey. Or whether the prey require sites outside the foraging range of bats to complete their lifecycle, which should therefore be considered as part of the predators' foraging requirements (both spatial and ecological) in order to achieve effective conservation management. Considering the ontogenetic niche shift of insects, adult prey's flying behavior, and the high level of landscape heterogeneity where *R. euryale* inhabits, we predicted that the habitat needs of consumed prey are not fulfilled by the ecological characteristics found in the foraging grounds of bats. The entire landscape could be acting as a prey source, where the relevance of different habitats would temporally and spatially vary due to larvae–host plant specificity and phenology. This study aims to gain insight into the complex predator–prey relationships between bats and insects. It also advocates a global vision that encompasses elements beyond first-level relationships for the conservation of threatened species.

2. Material and methods

2.1. Study area

The study was located in the Karrantza Valley, in the westernmost part of the Basque Country (northern Iberian Peninsula). It is a hilly valley with elevations ranging 200–855 m a.s.l., characterized by an Atlantic temperate oceanic climate. Rainfall occurs throughout the year (annual mean 1400 mm). The predominant land use of the site is devoted to dairy cattle breeding, along with small *Pinus radiata* and *Eucalyptus globulus* plantations. Thus, the landscape consists of a mosaic of small meadows and pastures, surrounded by an important hedgerow network consisting mainly of *Salix atrocinerea*, *Corylus avellana*, *Rubus ulmifolia*, *Acer campestre*, *Quercus robur* and *Crataegus monogyna*, interspersed with tree plantations and deciduous and holm oak woodland patches. The deciduous woodlands consist mainly of *Quercus robur*, *Fraxinus excelsior*, *Castanea sativa* and *Corylus avellana*. A limestone mountain range borders the northwest part of the valley, which provides abundant natural cavities and dense *Q. ilex* woods with limestone outcrops.

2.2. Sample collection

Bats were captured in one of the largest known breeding colonies in the northern Iberian Peninsula (Goiti et al., 2006) during May, July and September of 2012, coinciding with *R. euryale*'s pre-breeding, breeding and post-breeding seasons respectively. The colony roosts in a limestone cave situated at 334 m a.s.l. This cave is used by a few dozen individuals as a hibernaculum during winter, but 400–600 individuals congregate between mid-April and mid-June to breed (own data). The cave is also used by other species through the year: *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros*, *Myotis emarginatus* and *Miniopterus schreibersii*. Previous studies (Goiti et al., 2006, 2008) showed that *R. euryale*'s individuals of this colony forage within a 10 km radius from their roost on native deciduous woodlands, woodland edges and hedgerows, showing fairly similar behavior to other populations in Italy and Spain (Russo et al., 2002, 2005; Salsamendi et al., 2012). Bats were captured with a 2 × 2 m harp trap (Tuttle, 1974) located in the entrance of the colony roost from 00.30 a.m. onwards, as bats returned to the cave. Captures were conducted in a single night for each season (the 14th of May, the 3th of July and the 9th of September) in order to minimize disturbance. Each captured bat was held individually in a clean cloth bag until it defecated (a maximum of 40 min). Bats were sexed and aged, their weight and forearm length measured and their fecal material was collected. Feces were frozen within 6 h from the moment of collection. Bats were immediately released into the cave after handling.

2.2.1. Ethics statement

Capture and handling protocols followed published guidelines for treatment of animals in research and teaching (Sherwin, 2006) and were approved by the Ethics Committee at the University of the Basque Country (Ref. CEBA/219/2012/GARIN ATORRASAGASTI). Captures were performed under license from the Regional Council of Biscay.

2.3. DNA extraction, PCR amplification and sequencing

We considered the individual bat as the sampling unit (Whitaker et al., 1996), and 10–30 mg of feces per bat were used for DNA extraction with the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA), following the manufacturer's instructions with some modifications (Zeale et al., 2011). We extracted DNA from a total of 20 fecal samples per season. A 157 bp length fragment of the mitochondrial DNA cytochrome c oxidase subunit I barcode region (COI) was PCR amplified from each DNA extract using modified ZBJ-ArtF1c and ZBJ-ArtR2c primers (Zeale et al., 2011). Sample tagging, PCR conditions, cycle programs and

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