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Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: Research frontiers and management implications

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ABSTRACT

Bats are major consumers of arthropods, and there is ever growing evidence that they play a pivotal role in the fight against agricultural pests. However, relatively little research has addressed explicitly this important topic, and studies in temperate regions (especially European case studies) are infrequent. In the last few years, state-of-art molecular methods to identify prey remains in droppings and new experimental approaches to assess the actual magnitude of this ecosystem service have opened new perspectives in research. In this review, we discuss such aspects with an emphasis on temperate regions, and identify new research frontiers. These comprise: (1) detecting new bat species that consume pests, and further pest insects that bats might eat; (2) exploring sublethal effects of bat echolocation calls on tympanate moth pests; (3) getting a better understanding of bat predation over blood-sucking arthropods that parasitize livestock; (4) unveiling indirect effects of bat predation on plant pathogens; (5) implementing models to map the occurrence of bat insectivory and the potential to promote it; and (6) analyse bat droppings for active surveillance of arthropod pests and the diseases they carry. We also highlight that so-called "common" bat species, often neglected in conservation actions, are likely to provide the bulk of pest suppression in agroecosystems. All such aspects merit investigation and may lead to novel management practices aimed at conjugating bat conservation with economic and social sustainability of farming.

1. Background and objectives

Insectivory in farmland constitutes an ecosystem service that has paramount value to humans: even in today's pesticide era, natural enemies account for almost all pest suppression in farmed ecosystems (Debach and Rosen, 1974; Naylor and Ehrlich, 1997). Bats are a diverse group (> 1350 species) occurring in all geographic regions with the exception of the poles, and provide a range of important ecosystem services. The main biological services bats provide comprise, in the tropics, pollination and seed dispersal, and globally, transfer of organic matter into cave ecosystems and arthropod suppression (see Kunz et al., 2011 for a review).

Although bats show an outstanding diversity in diet among species, insectivory is widespread – ca. 70% of all bat species feed primarily on arthropods (Simmons, 2005). Bats may eat impressive numbers of insects per night. Captive bats are estimated to consume daily ca. a quarter of their body mass in insects (Brisbin, 1966; Neuhauser and Brisbin, 1969; O'Farrell et al., 1971; Coutts et al., 1973), but in wild conditions and demanding energetic phases such as lactation this figure raises to 70% (Kunz et al., 1995) and sometimes, astonishingly, > 100% (Kunz and Stern, 1995). Foraging strategies differ both among and within bat species (Denzinger and Schnitzler, 2013), allowing for consumption of a broad range of prey, including a number of arthropods harmful to human health or economy (Kunz et al., 2011).

Bats are frequent in farmed landscapes (Park, 2015; Heim et al., 2017), where they may prey upon a broad range of potentially harmful insects, more commonly on the wing but also gleaning them from the substrate (Fig. 1). For instance, some *Myotis* species glean blood-feeding flies from cowshed walls or ceiling (Krull et al., 1991; Kervyn et al., 2012; Siemers et al., 2012). According to the relatively few case studies so far examined, bats in farmland perform an outstanding predatory action. In the sole North America, reduction in crop damage and avoidance of pesticides are worth 22.9 billion USD/year, and even assuming this figure as an overestimate of the real impact, halving or quartering it would still represent an impressive contribution (Boyles et al., 2011). In most cases, bats attack adult insects, preventing them from laying eggs and consequently larvae – often responsible for crop damage – to develop (Maine and Boyles, 2015). Bat predation may

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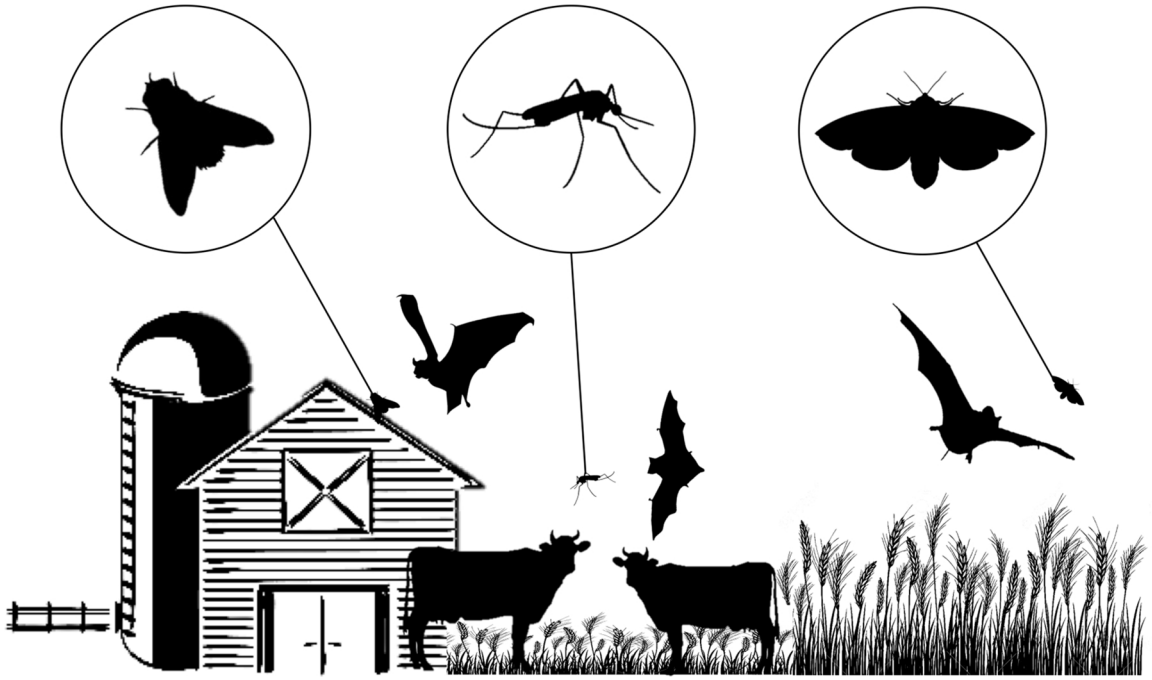

Fig. 1. Bats in farmland consume a range of insects that are potentially harmful to agri-pastoral activities, such as many moth species whose larvae attack crops, as well as blood sucking mosquitoes or flies that parasitize livestock. Most prey is caught on the wing, but diurnal flies may also be gleaned from cowshed walls or ceiling.

therefore exert cascade effects on agricultural pests (Cleveland et al., 2006).

Land use change, often caused by expansion of intensive farmland, poses one of the most serious threats to the survival of bats and weakens their effects on insect prey (Treitler et al., 2016). Agricultural intensification exposes bats to significant risks via loss or fragmentation of foraging habitat (Park, 2015) and biomagnification of pesticides (e.g. O'Shea et al., 2016). Given the vast extension of agricultural land worldwide (Bruinsma, 2003) and the precarious status of many bat populations, developing bat-friendly farmland management strategies is vital to sustain bat populations, but would also favor crop production, considering the ever-growing evidence that bat insectivory in farmland brings about crucial benefits.

Previous reviews have addressed the topic of insectivory in farmland (Kunz et al., 2011; Riccucci and Lanza, 2014; Williams-Guillén et al., 2016). The picture is fluid, however, and research is still providing exciting insights into bat foraging ecology, showing important implications for management. In this review, we summarize the latest picture on provision of this ecosystem service in farmland, placing special emphasis on temperate regions. We consider the behavioral aspect of predator-prey interaction under a new dimension, that of "soundscapes of fear", remark the functional importance of common species, often neglected in conservation plans, highlight new methodological approaches and conceptual aspects that should be pursued by future research, and discuss the potential to conjugate bat conservation with crop protection, benefiting both sides.

2. High taxonomic resolution in bat diet studies: more pest-consuming bat species than we might think

Strong limitations given by the coarse morphological identification of prey remains in bat droppings have long hampered diet studies, in many cases making prey identification to species level an impossible task (e.g. Rydell and Arlettaz, 1994). Retrieving insect fragments in droppings large enough to be species-diagnostic is in fact uncommon, especially when it comes to moths (McAney et al., 1997) – a group of insects comprising many of the major agricultural pests affecting crops worldwide (e.g. Alford, 1999). Moth remains in bat droppings generally consist of wing scales and small, undigested fragments of little taxonomic value (McAney et al., 1997), which renders identification too uncertain to provide valuable information on the real consumption of pests. The advent of modern molecular techniques such as DNA metabarcoding and environmental DNA analyses (Arrizabalaga-Escudero et al., 2015; Brown et al., 2015) has allowed a gigantic step forward in this field, revealing that previously overlooked bat species frequently feed on pest arthropods. For instance, a Europe-wide investigation into the diet of Schreiber's bats *Miniopterus schreibersii* done by ascertaining identity of prey remains through e-DNA analysis has detected 22 major and 22 minor agricultural pests that affect many crop types in the continent, from rice paddies to vineyard, from corn to olive groves (Aizpurua et al., 2018). *M. schreibersii* seems to shape its trophic niche opportunistically, according to food availability as driven by locally available farmland (Aizpurua et al., 2018). This bat species forms large colonies in caves (Rainho and Palmeirim, 2013) and moves over long distances to forage (Vincent et al., 2011), thus providing important benefits to farms within a considerable range around the roost. We take this case to make the point that the number of bat species potentially preying on agricultural pests is probably still largely underestimated, and that many more pest species than previously thought may actually be eaten by bats.

Population or individual characteristics might also influence the degree of consumption of arthropod pests. For instance, *Tadarida teniotis* shows intersexual differences in diet only recently revealed thanks to state-of-art molecular techniques (Mata et al., 2016). Sexual segregation in foraging habitat or altitude may probably cause such differences: the magnitude of pest consumption might thus be population-specific and depend on population sex ratio (Mata et al., 2016). Extending high-resolution molecular assessment of diet to more bat species will likely emphasize further the importance of pest consumption by bats, and help tailor strategies to favor the delivery of this important ecosystem service.