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Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects

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ABSTRACT

Landscape conversion to agriculture is the primary cause for habitat loss worldwide. As partial mitigation, agricultural landscapes may be designated as ecological corridors due to their presumed habitability and permeability to wildlife. Behavioral changes following anthropogenic disturbance can affect species' spatio-temporal activity patterns and modify interactions, and thus influence habitat preferences. Understanding how human activity affects wildlife behavior and how such behavioral changes scale up to the community may enhance the effectiveness of conservation schemes. We used camera traps to measure the activity of five mammal species along a disturbance gradient in an agricultural-natural mosaic landscape designated as a national ecological corridor. Wildlife diurnal activity was minimal around towns, where humans were active during the day. Nevertheless, predator activity increased near towns and at other sites of high disturbance. Although attracted to highly disturbed areas, predators avoided humans temporally by restricting activity to night-time, whereas prey activity relative to less disturbed areas was negligible. We conclude that perceived threat from humans during daytime combined with elevated nocturnal predation risk exclude prey species from large areas of an agricultural region designated as ecological corridor. Human activity may have triggered a cascading effect mediated by predators' diel activity shifts, which reduced landscape permeability to prey. Our study underlines the need to consider wildlife diel activity patterns for conservation and environmental management planning.

1. Introduction

The conversion of natural landscapes into agriculture is the leading form of habitat loss globally (Green et al., 2005; Sala et al., 2000), and is the primary risk factor for about 80% of all threatened terrestrial bird and mammal species (Tilman et al., 2017). Land transformation compels wildlife to adapt to new resources, threats and pressures (Clinchy et al., 2016; Newsome et al., 2015; Oriol-Cotterill et al., 2015) through changes in population densities, space use, movement patterns and other behaviors (Gaynor et al., 2018; Kuijper et al., 2016; Smith et al., 2015; Tucker et al., 2018). Agricultural landscapes are productive, accessible to wildlife, often interspersed with natural patches, and therefore are usually considered habitable and permeable to wildlife (Zamora et al., 2007). However, human activity may render open landscapes fragmented (i.e. not permeable) by introducing physical and nonphysical barriers, that may isolate populations and exclude species from previously occupied habitats (Hobbs, 2001; Martínez-Ramos et al., 2016; Peres, 2001). Understanding the behavioral drivers of fragmentation or changes in permeability is crucial for effective mitigation and conservation efforts (Hilty et al., 2006; Michalski and Peres, 2005). Identifying the mechanisms that govern species' distributions is key for understanding the processes behind wildlife behavioral changes that affect the permeability of modified landscapes (Doherty and Driscoll, 2018; Rubenstein, 2016). The temporal and spatial scales at which these mechanistic processes are studied may determine the depth of understanding of the forces governing a species' habitat use and spatial distribution (Tucker et al., 2018), yet the temporal aspect of species distributions has received relatively little attention in ecological modelling, conservation science and decision-making (Frey et al., 2017). Here, we explore anthropogenic changes to wildlife temporal niches

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(diel activity patterns), and the emergent spatial consequences of those changes.

The temporal niche is the portion of the 24-hour diel cycle in which a species is active. It is underpinned by circadian rhythms, which allow organisms to anticipate, and to respond optimally to, the 24-hour periodic environmental fluctuations (Aronson et al., 1993; Hut et al., 2012a; Kronfeld-Schor and Dayan, 2003). In mammals, external and physiological pressures can override the internal pacemaker, shifting activity time and switching the temporal niche in response to changes in surrounding environmental conditions or biological processes (Cohen et al., 2010; Hut et al., 2012b; Kronfeld-Schor and Dayan, 2003). However, even long-term pressures that have appreciable selective effects do not necessarily alter a species' underlying circadian rhythm, and the native rhythm may be restored when the pressure is removed (Cohen et al., 2010; Gattermann et al., 2008; Levy et al., 2007). Hence, the temporal niche in mammals enhances individual fitness by adapting to external conditions while retaining responsiveness to further fluctuations (Aronson et al., 1993; Hut et al., 2012a; Kronfeld-Schor and Dayan, 2003).

Species' spatio-temporal distributions reflect a cost-benefit trade-off between resource availability and the risk associated with resource utilization (Oriol-Cotterill et al., 2015); the latter is believed to have a stronger impact on species' distribution than either resource availability or habitat structure (Laundré, 2010; Oriol-Cotterill et al., 2015; Owen-Smith and Traill, 2017). The temporal niche can be thought of as the species' distribution through the diel, and it reflects its suite of behavioral responses to perceived risk and opportunity, which typically fluctuate over the 24-hour cycle. The sources of risk and the consequent responses, however, can be expected to differ among species. For example, carnivores tend to avoid other carnivores spatially, but avoid humans temporally, giving up activity at times when humans are usually encountered (Carter et al., 2015; Ciuti et al., 2012; Clinchy et al., 2016). Since anthropogenic disturbance is usually higher during the day than during the night, mammals worldwide are becoming increasingly nocturnal (Gaynor et al., 2018). The spatial requirements of ungulates and carnivores in particular often come in conflict with human activity (Tucker et al., 2018), instigating these shifts in diel patterns. We hypothesized that disturbance from humans, inferred from the duration and type of human activity throughout the diel cycle, instigates qualitatively similar changes in species' temporal activity patterns (i.e. avoiding times of human activity), but divergent spatial responses due to interspecific interactions (Shamoon et al., 2017). Our hypothesis holds that prey species will respond in space and time to pressure from both humans and predators, and will cease activity when and where predator densities and human activity co-occur and are too high.

1.1. Aims of this study

The flexibility of the mammalian temporal niche facilitates resource utilization and is crucial for persistence in sub-optimal conditions (Gaynor et al., 2018; Kronfeld-Schor and Dayan, 2003). However, it reduces activity time predictability, and is generally overlooked in studies of movement ecology under habitat modification (Doherty and Driscoll, 2018; Tucker et al., 2018). In this study, we aim to highlight the importance of incorporating species' temporal as well as spatial activity patterns, and the factors that may alter those, into predictive ecological models and conservation planning. We examine wildlife circadian patterns along a disturbance gradient to address temporal shifts in wildlife activity and the possible cascading effects of such shifts. We show how changes in diel activity patterns can lead, through direct and indirect links, to behavioral changes that may accelerate fragmentation in seemingly open landscapes. By quantifying activity shifts in space and time we reveal their implications to landscape permeability, which is crucial for wildlife management and conservation (Díaz and Concepción, 2016; Doherty and Driscoll, 2018). We also demonstrate that species' temporal responses to perturbation vary widely depending on ecological interactions, which may make such responses difficult to predict.

Mountain gazelles, *Gazella gazella*, are considered strictly diurnal (Wakefield et al., 2006) and sensitive to human presence (Manor and Saltz, 2003). We hypothesized that gazelles' spatio-temporal activity patterns respond to changes in diel activity patterns of golden jackal, *Canis aureus*, the largest predator in this area, and to the activity of humans, which may be a threat to both gazelles and jackals. We also examine the spatio-temporal patterns of other co-occurring mammals: Indian crested porcupine (*Hystrix indica*), red fox (*Vulpes vulpes*), and wild boar (*Sus scrofa*).

2. Methods

2.1. Study area

The study was conducted in a patchy agricultural-natural landscape in the Mediterranean coastal region of northern Israel at Ramat Hanadiv Nature Park, Alona Hills nature reserve, and vineyards at Hanadiv Valley. This area has been designated as part of a national ecological corridor network (Shkedy and Sadot, 2000), intended to provide connectivity between the northern and southern sections of Israel's Mediterranean region, otherwise separated by cities and political borders. Agriculture is the main land use in ecological corridors throughout this region (Shkedy and Sadot, 2000). Ramat Hanadiv Nature Park is a 4.5 km^2 area located on the southern edge of Mt. Carmel (32°32′56″N, 34°56′42″E). It comprises evergreen Mediterranean garrigue, with sclerophyllous trees and shrubs, open patches, and conifer plantations. Alona Hills nature reserve, approximately 32 km^2, is located to the east of Ramat Hanadiv park (32°33′40″N, 34°59′24″E). This is relatively a large natural area that mostly consists of evergreen Mediterranean maquis, with sclerophyllous trees and shrubs. Embedded within the hills are agricultural plots, mostly vineyards. Hanadiv Valley is located between Ramat Hanadiv and Alona Hills (32°32′N, 34°58′E). It is an agricultural matrix with a total area of approximately 46 km^2, comprising mostly vineyards and stone fruit. Towns in the periphery of the agricultural matrix cover a combined area of approximately 20 km^2.

2.2. Camera trap design

Camera trap encounter counts were used to model seasonal and diel activity rates of mid-sized vertebrates at Alona Hills, Ramat Hanadiv, and Hanadiv Valley. The agricultural-natural landscape was sampled at 100 camera locations divided into five categories A–E, which represent a human activity gradient where A is lowest, C is intermediate and E is highest:

A) Alona Hills natural area is used for recreation but many areas are only accessible by foot or bicycle. Recreational activity is relatively low. To sample areas with low human activity, we placed cameras at remote sites with minimal human presence.
B) Ramat Hanadiv Nature Park is open to visitors year round. The hiking trails and dirt roads are easily accessible, making it a popular tourist location. The park opens right after sunrise and closes at sunset. Visitors are not allowed in the park after dark. This category comprises of relatively unaltered habitat with considerable human presence, but without the land modification and agricultural machinery typical to categories D and E (below).
C) Vineyards embedded within Alona hills natural area represent low to moderate human activity, mainly farmers. People and agricultural machinery occasionally work these areas, but wildlife are free to seek shelter in the surrounding natural habitat.
D) Vineyards in the core of Hanadiv valley agricultural area, where additional human activity (besides the farmers') takes place, and