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Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia

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Managing populations of large carnivore species that are threatened yet in competition with each other presents a conservation challenge over which species to prioritise. We investigated interspecific competition between the Endangered tiger and two sympatric carnivore species (Near-Threatened leopard and Endangered dhole) in Malaysia. We used a spatially-explicit camera trapping method to sample the three carnivore species in order to assess their: relative abundance; spatial co-occurrence; and, temporal overlap. Our focal landscape consists of two adjacent study areas that have different forest management regimes: 1) Royal Belum State Park (RBSP) which has relatively higher levels of enforcement resulting in high tiger and prey densities, and 2) Temengor Forest Reserve (TFR) which has no enforcement resulting in low tiger and prey densities. Our analyses found interspecific competition in the form of fine-scale spatial avoidance of tiger by leopard in RBSP, but not in TFR. Thus, leopard was less likely to occur in forest patches with greater tiger presence in RBSP. Dhole was not detected in RBSP, and showed no fine-scale spatial avoidance of tiger on TRF. It was unclear if absence of dhole in RBSP was due to the high tiger density, or another factor such as disease. Regardless, our results indicate dhole can persist in human-degraded forest landscapes. Neither leopards nor dholes showed any major temporal avoidance of tigers on either site. Our findings of fine-scale spatial avoidance by leopard towards tiger and possible exclusion of dhole by tiger in areas of high tiger density were similar to that found in other areas of Asia. Our study demonstrates that degraded forest can be important for threatened carnivores. It also provides a reminder that efforts to recover tiger populations, a conservation priority, may require flanking measures to secure meso-predator populations, especially those forced into edge environments where they come into greater contact with people.
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1. Introduction

Species coexistence within a carnivore guild can be achieved through differentiation of prey species (Taber et al., 1997), temporal activity (Fedriani et al., 1999) and spatial habitat use (Palomares et al., 1996). The management of apex predators within these guilds, with a primary aim to increase their population abundance, can therefore have a profound impact on other sympatric carnivore species through increasing interference competition. Under such circumstances, higher encounter rates with the dominant predator is predicted to elicit spatial and/or temporal avoidance that causes shifts in foraging patches though a regulatory process that eventually reduces the population density of the inferior sympatric predators (Seidensticker and McDougal, 1993). This presents a wildlife management challenge when the carnivore species in question are considered to be conservation flagship species that are also at-risk of extinction.

Interspecific competition plays a central role in structuring predator communities in the forest ecosystems of Asia (Odden et al., 2010; Harihar et al., 2011). Studies from India and Nepal have shown that leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) exhibit spatial avoidance of tiger (*Panthera tigris*) by hunting in refuge areas and maintaining home ranges that are peripheral to the core part of the tiger's home range. They may also switch to smaller-bodied prey to reduce competition further (Seidensticker et al., 1990; Karanth and Sunquist, 1995, 2000; Odden et al., 2010; Carter et al., 2015). In Rajaji National Park, India, an increase in tiger abundance was found to lower leopard abundance through interference competition that pushed leopards to poorer quality habitat located at the park edge which in turn increased their livestock intake and conflicts with people (Harihar et al., 2011). A similar impact to the leopard population occurred in Sariska National Park with the re-introduction of tigers there (Mondal et al., 2012).

Most tiger, leopard and dhole interaction studies are from South Asia. The dry deciduous forests and alluvial grasslands from this region

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can support naturally high densities of the apex predator that typically exceed 10 adult tigers/100 km^2 (Karanth et al., 2004). Under such circumstances interspecific competition is expected to be intense. However, the tropical humid evergreen forests of Southeast Asia are fundamentally different. A lush rainforest canopy greatly lowers on-the-ground primary productivity and therefore ungulate biomass that in turn supports lower densities of large-bodied carnivore species (Eisenberg and Seidensticker, 1976). Tiger densities in these habitats rarely exceed 3 individuals/100 km^2 (Rayan and Linkie, 2015; Linkie et al., 2008; Kawanishi and Sunquist, 2004) and competition with other sympatric carnivore species would therefore be expected to be lower.

In Southeast Asia, studies on tiger-leopard-dhole interactions are difficult to conduct because the survey methods used to investigate interspecific competition in South Asia are not directly transferrable to Southeast Asia's evergreen rainforest environment. Previous studies have tended to rely on analysing prey selection patterns from dietary analyses (Karanth and Sunquist, 1995; Andheria et al., 2007; Wang and Macdonald, 2009; Wegge et al., 2009), with the exception of Karanth and Sunquist (2000) who additionally investigated tiger-leopard spatio-temporal interactions using telemetry data and dhole pack movements using direct observations. However, in Southeast Asia, scats are notoriously difficult to encounter due to low carnivore densities and their rapid decay rates under humid conditions. Furthermore, estimating leopard density in Malaysia using a capture-mark-recapture technique is difficult because of the predominance of melanistic individuals that lack easy to distinguish markings (Kawanishi et al., 2010, but see Hedges et al., 2015).

A recent study by Steinmetz et al. (2013) was the first to use a camera trap-based sampling approach to investigate tiger-leopard-dhole interactions in Southeast Asia, in this case from Thailand. Following this approach, we aimed to investigate competition between the Endangered tiger and two sympatric carnivore species (Near-Threatened leopard and Endangered dhole) living in one of the three priority tiger conservation landscapes in Malaysia. We used a spatially-explicit camera trapping method to sample the three carnivore species in order to assess their: i) relative abundance; ii) spatial co-occurrence; and, iii) temporal overlap in two study areas under different forest management regimes that gives rises to significantly different prey base composition and relative abundance (Rayan and Linkie, 2015).

2. Materials and methods

2.1. Study area

The 1175 km^2 Royal Belum State Park (RBSP) was officially gazetted in 2007 as a strictly protected area with only non-exploitive commercial activities, such as tourism by the edge of a lake, permitted. The altitudinal range of 260 m to 1533 m a.s.l supports lowland dipterocarp (5.6%), hill dipterocarp (71.5%), upper dipterocarp (20.9%) and montane (2.0%) forest types. Being located by the southern Thai border, which has a long-running history of insurgency, there has been a Malaysian army presence in RBSP since the late 1940s. In contrast, the 1489 km^2 Temengor Forest Reserve (TFR) was officially gazetted in 1991 as a Permanent Reserved Forest and has been undergoing selective logging since the 1970s. The altitudinal range of 260 m to 2160 m a.s.l supports lowland dipterocarp (4.2%), hill dipterocarp (34.4%), upper dipterocarp (41.7%) and montane (19.7%) forest types. The TFR has no wildlife management and an estimated 5000 indigenous people reside within 24 settlements in and around the area, whereas RBSP has an estimated 740 indigenous people (Department of Orang Asli Affairs, unpublished data). The relative abundance of the principal prey species for tiger, leopard and dhole is significantly higher for sambar (77.5 times), muntjac (3.7) and wild pig (1.6) in RBSP than TFR (Rayan and Linkie, 2015).

2.2. Field methods

Camera trapping was conducted for approximately nine months in TFR (August 2009–May 2010) and then RBSP (August 2010–April 2011), with a sampling area of about 400 km^2 in each study area. Using 2 × 2 km grid cells, 35 fixed location paired camera traps were set to record both flanks of a passing tiger. To maximise study area coverage, as part of a separate study on habitat use, another 70 single placement camera traps were set in neighbouring grid cells. To increase spatial coverage within grid cells, these 70 traps were moved once within the same cell after 3–4 months of operation, corresponding to a total of 140 single placements. Including the tiger camera traps, there were 175 placements with an average inter-trap distance of 1 km. To increase target species detection rates, placements were made along forest trials, ridge trails and inactive logging roads. Camera traps were checked every 2–3 months to retrieve data and replace batteries.

2.3. Photo capture rates

To investigate the spatio-temporal interactions of tiger-leopard and tiger-dhole, camera trap data from 175 locations in each of the two study areas were used. Because leopards in the study area are melanistic and dholes lacked unique markings, individual species identification for a capture-mark-recapture analysis was precluded and a photo capture rate index (PCRI) used instead. For each camera trap location, a PCRI for tiger, leopard and dhole was calculated as the number of independent photographs (detections) per 100 trap-nights. These estimates were averaged across all camera trap locations within each study area to produce respective mean PCRI with standard errors. An independent photograph was defined as a photograph of a tiger, leopard or dhole being taken at least 30 min apart at the same camera trap location (O'Brien et al., 2003). Differences in the study area PCRIs were assessed using a Wald test (Morgan, 2008), whereby Z values larger than 1.96 (critical value at $\alpha = 0.05$) were considered significant.

2.4. Spatial co-occurrence

A likelihood-based two-species occupancy mode of inference model (MacKenzie et al., 2004), which accounts for imperfect detection for analysing species co-occurrence patterns from repeat detection/non-detection camera trap survey data, was used to test for spatial co-occurrence. This model permits the computation of occupancy (ψ) parameters for two species together, along with each species's conditional probability of occupancy when the other species is present or detected. This allows the model to directly estimate a species interaction factor ($\varphi = \psi^{AB} / \psi^{A} \times \psi^{B}$), hereafter SIF, which is then used to quantify the level of co-occurrence.

The SIF is defined as a ratio of how likely two species are to co-occur when compared against a hypothesis of independence (MacKenzie et al., 2006). Here, values of $\varphi < 1.0$ indicate that the species co-occur less often than would be expected, which suggests avoidance. Other parameters within this model include: probability that the area is occupied by species A (ψ^{A}), probability that the area is occupied by species B (ψ^{B}), probability of detecting species A, given species B is not present (p^{A}), probability of detecting species B, given species A is not present (p^{B}), probability of detecting species A, given both are present (r^{A}), probability of detecting species B, given both are present (r^{B}) and a species co-detection parameter ($\Delta = r^{AB} / (r^{A} \times r^{B})$) defined as a ratio of how likely the two species are co-detected on the same occasion when compared against a hypothesis of independence.

Each of the 175 camera trap locations were treated as a site (sampling unit), from which tiger, leopard and dhole detection histories were constructed using 10 four-week sampling occasions to enable detection probabilities (p) estimation. For each site and sampling occasion, ‘1’ indicated the detection (photograph) of the species, ‘0’ indicated the

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