Anthropogenic pressure on large carnivores and their prey in the highly threatened forests of Tanintharyi, southern Myanmar

Nay Myo Shwe, Matthew Grainger, Dusit Ngoprasert, Saw Soe Aung
Mark Grindley and Tommaso Savini

Abstract The Tanintharyi Region in southern Myanmar is rich in biodiversity yet is facing threats from varying degrees of anthropogenic pressure. In this research we examine how anthropogenic pressures are influencing large carnivores (tiger *Panthera tigris*, leopard *Panthera pardus* and dhole *Cuon alpinus*) and their major prey species (wild pig *Sus scrofa*, muntjac *Muntiacus* spp., sambar *Rusa unicolor*, gaur *Bos gaurus* and banteng *Bos javanicus*) in the Lenya Reserved Forest and adjacent areas of Sundaic forest. We used data from camera-trap surveys during May 2016–March 2018 and logistic regression to analyse the relationships between the presence of large carnivores and explanatory variables such as human disturbance, landscape variability and changes in prey distribution. Tiger presence was positively associated with the occurrence of gaur and distance to villages. The occurrence of prey did not explain the detection of leopards in the study area. We suspect this was because leopards have a broad diet, including arboreal primates, and their prey was not fully recorded in our camera-trap survey. Dholes were positively associated with wild pigs and the total number of prey but not associated with forest type and landscape variables. To restore the carnivore population and conserve the biodiversity of this area, effective protection of predators and habitat management for large ungulates are crucial.

Keywords Camera trap, dhole, human disturbance, hunting, leopard, Myanmar, palm oil, tiger

Supplementary material for this article is available at doi.org/10.1017/S0030605321001654

Nay Myo Shwe* (Corresponding author, orcid.org/0000-0003-3739-3955, nmshwe@googlemail.com), Dusit Ngoprasert and Tommaso Savini Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Bangkok, Thailand

Matthew Grainger (orcid.org/0000-0001-8426-6495) Norwegian Institute for Nature Research, Trondheim, Norway

Saw Soe Aung and Mark Grindley Myanmar Programme, Fauna & Flora International, Yangon, Myanmar

*Also at: Myanmar Programme, Fauna & Flora International, Yangon, Myanmar

Received 21 May 2021. Revision requested 29 July 2021.
Accepted 1 November 2021.

Introduction

Biodiversity is declining worldwide, particularly in South-east Asia, where the highest deforestation rate in a major tropical region has been recorded (Karger, et al., 2021; Namkhan, et al., 2021). Human activities affect wildlife mainly through habitat destruction and hunting, resulting in defaunation and ecosystem degradation (Corlett, 2007; Rao et al., 2011; Dirzo et al., 2014; Newbold et al., 2014). Within South-east Asia, Myanmar retains some of the largest forest patches in the region because of its previous slow economic development following long-term political isolation (Schmidt, 2012; WCS, 2012; Rao et al., 2013). However, since political reform in Myanmar began in 2010, increased threats to biodiversity have been observed (Donald et al., 2015; Woods, 2015; Connette et al., 2016, 2017; Shwe et al., 2020).

The Tanintharyi (formerly known as Tenasserim) Region in southern Myanmar is one of the largest continuous forest patches in mainland South-east Asia (Donald et al., 2015; Aung et al., 2017), and has been largely spared from the high rates of clearance for industrial crops that has occurred elsewhere in the region (Leimgruber et al., 2005; Connette et al., 2016). This area lies in the southern Dawna–Tenasserim Ecoregion (Olson et al., 2001) on the Isthmus of Kra and is bordered by Chumphon Province (Thailand) to the east and the Andaman Sea to the west. The Lenya and Nga Wun Reserved Forest (formerly the proposed Lenya Reserved Forest and Lenya Reserved Forest Extension; Fig. 1) has been proposed as a protected area since 2004. However, because of persistent problems in reliable land mensuration, boundary marking, management implementation and unresolved disagreements over sovereignty between the national government and ethnic Karen communities, the proposal was dropped in June 2019.

This area is important for the transboundary conservation of tigers and other large, threatened mammals of Thailand and Myanmar (Bennett, 1999). Since the late 1990s, however, a large portion of this lowland forest (< 150 m altitude, with slopes < 10°; Shwe et al., 2020) has been lost (Namkhan et al., 2021), mostly in conversion to oil palm plantations (Baskett, 2015). Although forest still covers an estimated 80% of the land area of the Tanintharyi Region, this remaining forest is under threat from development and land-use conversion (Connette et al., 2016). Lowland

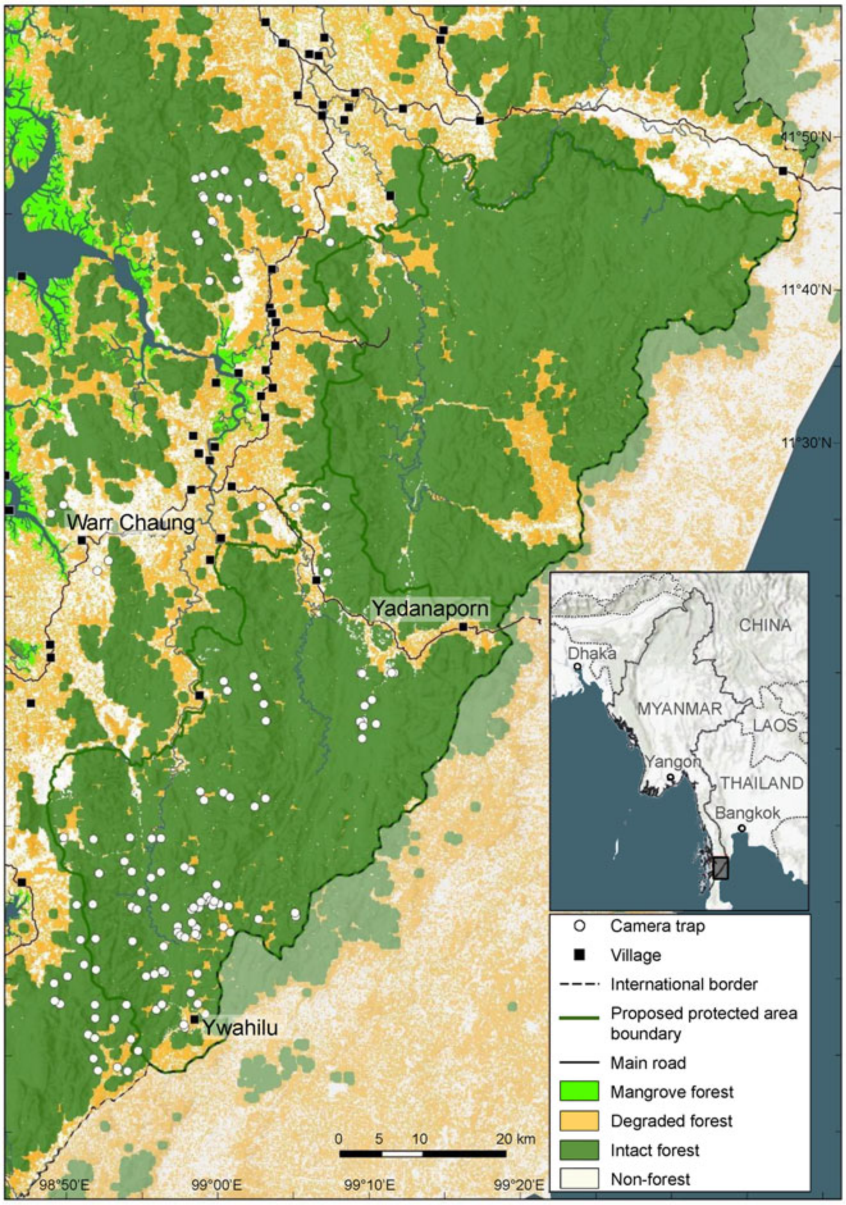

FIG. 1 The study area in southern Tanintharyi, Myanmar, showing locations of camera traps, villages, main roads and forest cover. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

forests lying close to the main roads and main access routes have been converted to oil palm, rubber cultivation or other forms of agriculture (Shwe et al., 2020). Many wildlife species are unable to adapt to oil palm and rubber plantations (Aratrakorn et al., 2006; Love et al., 2018), which support low levels of biodiversity (Danielsen et al., 2009).

The tiger *Panthera tigris*, categorized as Endangered on the IUCN Red List, is decreasing in many locations (Wikramanayake et al., 2011; Goodrich et al., 2015) because of both direct poaching (Nijman & Shepherd, 2015) and declines of its large ungulate prey (Ramakrishnan et al., 1999; Karanth et al., 2004; Moo et al., 2018). This is also the case for the Critically Endangered Indochinese leopard *Panthera pardus delacouri* and Endangered dhole *Cuon alpinus*, which are top predators in tropical Asian forests. They prey on similar sizes and species of ungulates as the tiger (Johnsingh, 1992; Karanth & Sunquist, 1995; Kamler et al., 2015; Rostro-García et al., 2016) and are considered indicators of ecosystem health (Beschta & Ripple, 2009; Prugh et al., 2009). In Myanmar, tiger populations remain in two landscapes: the Hukaung–Htamanthi complex in the upper Chindwin basin in the north-west and the Dawna–Tenasserim Ecoregion along the Thailand–Myanmar border (Lynam et al., 2006; MONREC, 2020). Leopards are widespread but are concentrated mainly in the northern Tenasserim Forest Complex on the Myanmar–Thailand border (Rostro-García et al., 2016). The distribution of dholes in Myanmar is unclear, with many reports across the country (Kamler et al., 2015; Kao et al., 2020).

Despite the importance of the Tanintharyi Region for the conservation of large carnivores, the ongoing pressures of human disturbance and land development mean that little information is currently available on the status of the Region's charismatic predator species. Our aim here is to provide quantitative information on the distribution and conservation status of large carnivores in the Reserved Forest. We hypothesized that in the Reserved Forest and adjacent areas the distributions of large carnivores and their main prey are influenced by habitat degradation following landscape conversion and human disturbance. To test this, we analysed data from extensive camera trapping undertaken by the Fauna & Flora International (FFI) Tanintharyi Conservation Programme and Wahplaw Wildlife Watch, a local partner, during 2016–2018.

Study area

The study was conducted within and outside Lenya Reserved Forest (Fig. 1), a proposed protected area, which is mostly covered by tropical evergreen forest, with smaller areas of secondary forest resulting from state-sponsored selective logging since 2007. The area is characterized by a dry season (November–March), with mean rainfall < 100 mm/month and a wet season (April–October), with mean rainfall of 750 mm/month (Baskett, 2015). Many old logging roads remain, facilitating further degradation from anthropogenic pressures such as hunting, agricultural expansion, mining and road construction (Woods, 2015; FFI, 2016; Connette et al., 2017). The area has long been inaccessible to researchers because of the insecure political situation between the Myanmar and Karen armies. This is the first camera-trap survey within and outside Lenya Reserved Forest in the southern Tanintharyi Region. The area outside Lenya Reserved Forest comprises remaining forest patches near oil palm plantations, including Yuzuna II and the Myanmar Auto Cooperation. Both plantations were licensed in the 1990s but further clearance is on hold while the regional government undertakes a review.

Methods

Camera-trap survey

Our camera-trap survey was designed to study the distribution and status of tigers and their prey in primary and degraded forests, forest near plantations and private farmland near forest. Data were collected using Bushnell 12 MP Trophy digital infrared camera traps (Bushnell, Overland Park, USA) during May 2016–March 2018. The cameras were placed at 132 locations (107 within and 25 outside the Lenya Reserve Forest, at 19–672 m altitude); two cameras were deployed in each location, facing each other, to facilitate identification of individual tigers and leopards (Miththapala et al., 1989). Camera traps were spaced at a mean distance of 2,750 m (range 1,500–4,000 m). We did not place cameras on the border with Thailand because of the presence of landmines there, or in northern and central areas of the proposed protected area, but otherwise all areas with forest were surveyed. Over the 23-month period, camera traps were placed across an area of c. 1,000 km² (Fig. 1). Camera traps were deployed in locations where we considered there was a high likelihood of detecting the target species (e.g. areas with presence of tiger or prey signs, well-used trails, or near water), and along trails and on ridges, to increase the probability of photographing wildlife (Forman & Alexander, 1998).

Cameras were secured c. 60 cm above the ground and positioned to photograph the flanks of any passing animal. One of each pair of cameras was set in hybrid mode (picture and video), and the other was set to picture mode only, to prolong battery life and reduce memory card usage. Cameras were programmed to take three photographs when triggered, with a delay of 30 s between photograph events. Following cumulative species detection curves from preliminary surveys (in 2015 in the same landscape), cameras were left in each location for an average of 45 days and then moved to another area. However, in some cases cameras were left for longer to confirm detections of individual tigers. Trap-days for some cameras were reduced because of damage by elephants *Elephas maximus*, theft or malfunction.

Because of the potential for variation in detectability using hybrid (i.e. combined video and photograph) and picture modes, we considered a detection to be the occurrence of at least one photograph or video of a target species per location per day. We used daily occasions for detection histories, from 00.00 to 23.59. The number of detections of the main prey species of large carnivores (wild pig *Sus scrofa*, barking deer *Muntiacus* spp., sambar *Rusa unicolor*, gaur *Bos gaurus* and banteng *Bos javanicus*) were used as explanatory covariates in a regression model to define the association between predators and prey. Barking deer refers to both Fea's muntjac *Muntiacus feae* and red muntjac *Muntiacus muntjak* as these two species are of similar size and differentiation in photographs is difficult. For the analysis, we summed the number of detections of each focal prey species per location. Total number of prey was defined as the sum of the number of all prey species and total number of large prey was defined as the sum of the number of gaur, banteng and sambar.

Landscape covariates

The landscape variables were: distance from the camera-trap to (1) the nearest permanent village in Myanmar, and (2) the nearest main road; (3) forest area within a 1-km radius of each camera-trap location; (4) non-forest area, i.e. bare ground and clearings, within a 1-km radius; (5) degraded forest area within a 1-km radius; (6) altitude (m); and

  doi:10.1017/S0030605321001654

(7) location within or outside (binary) the proposed Lenya Reserved Forest. The selection of these variables was based on previous studies and on the biological and ecological requirements of the study species (Hossain et al., 2018).

We measured distance to road and distance to village using *ArcGIS 10.3* (Esri, Redlands, USA). We used a forest cover map (Connette et al., 2016) to classify land as forest, non-forest and degraded forest within a 1-km radius of each camera-trap location, also using *ArcGIS*. Forest classifications follow Connette et al. (2016), with forest having a canopy cover of > 80% and degraded forest having a canopy cover of ≤ 80%.

Data analysis

We used logistic regression to analyse the relationships between the detection/non-detection of tigers, leopards and dholes and the potential explanatory covariates. We created separate models for individual prey species and all prey species. We checked continuous variables for outliers prior to running the models. We then standardized all continuous variables by subtracting the mean and dividing by twice the standard deviation (Gelman, 2008). We treated unequal camera-trap survey effort at each location by using an offset in the model formula. This is equivalent to including survey effort (trap-days) as a regression predictor but with its coefficient fixed to 1 (Gelman & Hill, 2007). We assessed spatial autocorrelation using the *spline.correlog* function in the *ncf* package (Ottar, 2018) in *R 3.2.2* (R Development Core Team, 2015). This function estimates the spatial dependence of data at discrete distance classes measured using the centred Mantel statistic (Ottar, 2018).

We did not include highly correlated ($r > 0.5$) variables in the same regression model. We compared models using the Akaike information criterion (AIC), and used Akaike model weights (wi) as evidence in favour of model i amongst the models being compared. We assessed the model classification accuracy of the logistic regression by using the area under the receiver operating characteristic curve (AUC), which varies from 0.5 (models that are no better than random) to 1.0 (high-accuracy models; Franklin, 2009). We calculated AUC thresholds using multiple cut-off points (0.2, 0.4, 0.6, 0.8), where sensitivity is equal to specificity, using the package *PresenceAbsence 1.1.9* (Freeman & Moisen, 2008) in *R*.

Results

During a total of 24,311 trap-days in the 132 locations (20,771 within and 3,540 outside Lenya Reserved Forest), we detected 49 mammal and 17 bird species. The total number of detections of prey species were: wild pig, 596 detections in 89 locations (67.4% naïve occupancy); muntjac, 628 detections in 93 locations (70.5%); sambar, 11 detections in nine locations (6.8%); gaur, 70 detections in 27 locations (20.5%); and banteng, six detections in three locations (2.3%: Table 1). The total number of detections of large carnivore species were: leopard, 89 detections in 23 locations (17.4%); tiger, 54 detections in 20 locations (15.2%); and dhole, 49 detections in 26 locations (19.7%; Table 2). Several other globally threatened mammal species were also recorded (Supplementary Table 1).

We detected tigers only within Lenya Reserved Forest. Based on the most parsimonious of the 12 models, the presence of tigers was positively associated with the presence of gaur and with increasing distance to the nearest village, with no correlation between gaur and distance to the nearest village ($r = 0.26$; Table 3). We detected tigers over altitudes of 69–662 m, and the modelling indicated that tiger presence was not correlated with either altitude or forest type. The model predicted only a 20% probability of tiger presence where camera traps were close to villages (< 20 km; Fig. 2a). Tiger presence was correlated with larger prey species (i.e. gaur, banteng and sambar) and not medium-sized prey. Detections of large prey were mostly of gaur. The probability of tiger presence increased from 0.2 to 0.5 with a doubling (from two to four detections per location) of gaur detections (Fig. 2b). The AUC value was 0.85, indicating excellent discrimination between tiger detections and non-detections (Table 4).

Detection of leopards was positively associated with forest area (canopy cover > 80%) but not with any of the other covariates (Table 3). We detected leopards in eight of the 23 locations (34.8%) outside the Lenya Reserved Forest. The probability of leopard presence was low (< 10%) at camera-trap locations with forest areas of < 2.23 km^2 within a 1-km radius of a camera trap (Fig. 2c), which comprised 21% of forest patches in the study area. Prey detection did not explain the detection of leopards in the study area. The AUC value of 0.68 could be considered acceptable for discrimination between leopard detections and non-detections (Table 4) as 0.7 lies within the range of acceptable AUC values (Hosmer & Lemeshow, 2000).

We detected dholes in only three locations outside the Reserved Forest. Of 13 candidate models, dholes were positively associated with wild pig detections (Fig. 2d), with total number of prey detections being the second most plausible model (Table 3). Dhole distribution was not associated with forest type or any of the other landscape covariates. The AUC value of 0.70 was considered acceptable for discrimination between dhole detections and non-detections (Table 4).

Discussion

Our findings confirm the importance of the study area for biodiversity, with several globally threatened mammal

  doi:10.1017/S0030605321001654

TABLE 1 The mean (and range) of six landscape variables at camera-trap locations where four prey species (wild pig *Sus scrofa*, barking deer *Muntiacus* spp., sambar *Rusa unicolor*, gaur *Bos gaurus*) of carnivores were detected or not detected, and details of the detections during the camera-trap survey from May 2016 to March 2018. These include the number of detections/non-detections inside and outside the Reserved Forest, the mean ± SD number of detections and the sum of detections for all camera traps combined. Banteng *Bos javanicus* is not included because it was only detected at two locations.

	Wild pig		Barking deer		Sambar		Gaur	
	Detected	Not detected	Detected	Not detected	Detected	Not detected	Detected	Not detected
Landscape variables								
Distance to nearest village (km)	16.1 (1.6–32.6)	12.8 (3.4–23.7)	15.1 (3.4–32.3)	14.7 (1.7–32.7)	14.6 (3.4–21.1)	14.9 (1.8–32.7)	18.9 (7.9–92.7)	13.9 (1.8–32.3)
Distance to nearest main road (km)	14.8 (0.2–31.5)	11.6 (1.6–23.4)	14.2 (1.3–31.4)	12.8 (0.2–31.5)	12.9 (3.1–19.4)	13.9 (0.2–31.4)	16.5 (7.3–31.4)	13.1 (0.2–31.4)
Forest (km^2)	2.5 (0.6–3.1)	2.4 (0.3–3.1)	2.6 (0.3–3.1)	2.3 (0.9–3.1)	2.3 (1.7–2.8)	2.5 (0.3–3.1)	2.3 (0.3–3.1)	2.5 (0.4–3.1)
Non-forest (km^2)	0.1 (0–0.9)	0.1 (0–0.9)	0.1 (0–0.5)	0.2 (0–0.9)	0.1 (0–0.4)	0.1 (0–0.9)	0.1 (0–0.4)	0.1 (0–0.9)
Degraded forest (km^2)	0.5 (0–2.3)	0.6 (0–2.7)	0.5 (0–0.3)	0.7 (0–2.3)	0.7 (0.1–1.6)	0.5 (0–2.7)	0.1 (1.1–1.5)	0.5 (0–2.4)
Altitude (m)	247 (61–647)	169 (34–662)	257 (49–662)	136 (34–630)	154 (112–157)	226 (34–662)	209 (70–662)	224 (34–647)
Detections								
Number inside Lenya Reserved Forest	77	30	81	26	7	100	25	82
Number outside Lenya Reserved Forest	12	13	12	13	2	23	2	23
Mean ± SD per camera trap	4.5 ± 5.9 (0–28)		4.8 ± 6.2 (0–39)		0.1 ± 0.3 (0–2)		0.5 ± 1.4 (0–8)	
Sum for all camera traps	596		628		11		70	

TABLE 2 The mean (and range) of six landscape variables at camera-trap locations where three predator species (tiger *Panthera tigris*, leopard *Panthera pardus*, dhole *Cuon alpinus*) were detected or not detected, and details of the detections during the camera-trap survey from May 2016 to March 2018. These include the number of detections/non-detections inside and outside the Reserved Forest, the mean ± SD number of detections and the sum of detections for all camera traps combined.

	Tiger		Leopard		Dhole	
	Detected	Non-detected	Detected	Non-detected	Detected	Non-detected
Landscape variables						
Distance to village (km)	20.1 (7.9–32.7)	14.0 (1.8–32.3)	13.9 (7.1–22.6)	15.2 (1.8–32.7)	16.4 (4.5–25.2)	14.6 (1.8–32.7)
Distance to nearest main road (km)	18.9 (7.3–31.5)	12.9 (0.2–31.4)	13.8 (2.8–25.9)	13.8 (0.2–31.5)	16.0 (1.3–26.0)	13.2 (0.2–31.5)
Forest (km^2)	2.3 (0.5–3.1)	2.5 (0.3–3.1)	2.8 (1.3–3.1)	2.4 (0.3–3.1)	2.6 (0.8–3.1)	2.5 (0.3–3.1)
Non-forest (km^2)	0.1 (0.0–0.4)	0.1 (0.0–1.0)	0.0 (0.0–0.1)	0.1 (0.0–1.0)	0.0 (0.0–0.3)	0.1 (0.0–1.0)
Degraded forest (km^2)	0.8 (0.0–2.4)	0.5 (0.0–2.8)	0.3 (0.0–1.8)	0.6 (0.0–2.8)	0.5 (0.0–2.3)	0.6 (0.0–2.8)
Elevation (m)	123 (69–662)	235 (37–662)	473 (51–640)	189 (51–661)	332 (51–647)	199 (39–662)
Detections						
Number inside Lenya Reserved Forest	20	87	15	92	23	84
Number outside Lenya Reserved Forest	0	25	8	17	3	22
Mean ± SD per camera traps	0.4 ± 1.2 (0–7)		0.7 ± 2.2 (0–15)		0.4 ± 1.0 (0–8)	
Sum for all camera traps	54		89		49	

Oryx, Page 5 of 10 © The Author(s), 2022. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605321001654

TABLE 3 Model selection for logistic regression of detections/non-detections of tigers, leopards and dholes with prey and landscape covariates, with the number of estimated parameters in the model (*K*), the Akaike information criterion (AIC), difference in the AIC (ΔAIC; models with a value of 0 have the most support) and the Akaike model weights (*wi*).

Model (by species)	*K*	AIC	ΔAIC	*wi*
Tiger				
Village + gaur	3	83.75	0.00	0.95
Gaur	2	90.63	6.87	0.03
Large prey	2	91.33	7.57	0.01
Village	2	92.49	8.75	0.01
Degraded forest	2	104.63	20.88	0.00
Forest	2	105.29	21.54	0.00
Total prey	2	105.34	21.59	0.00
Elevation	2	106.32	22.57	0.00
Pig	2	106.61	22.86	0.00
Sambar	2	106.62	22.87	0.00
Barking deer	2	107.25	23.50	0.00
Null	1	114.28	30.53	0.00
Leopard				
Forest	2	116.54	0.00	0.44
Forest + village	3	118.11	1.56	0.20
Degraded forest	2	118.31	1.77	0.18
Village + degraded forest	3	119.88	3.34	0.08
Elevation	2	122.66	6.12	0.02
Null model	1	124.11	7.57	0.01
Village	2	124.63	8.08	0.00
Barking deer	2	125.20	8.66	0.00
Total prey	2	125.32	8.78	0.00
Sambar	2	125.72	9.18	0.00
Wild pig	2	126.06	9.51	0.00
Large prey	2	126.06	9.52	0.00
Dhole				
Wild pig	2	124.12	0.00	0.15
Total prey	2	124.20	0.08	0.14
Village	2	124.99	0.87	0.10
Sambar	2	125.04	0.92	0.09
Barking deer	2	125.34	1.21	0.08
Forest	2	125.54	1.41	0.07
Elevation	2	125.70	1.57	0.07
Degraded forest	2	125.77	1.64	0.06
Gaur	2	125.77	1.64	0.06
Large prey	2	125.82	1.69	0.06
Village + wild pig	3	125.95	1.82	0.06
Village + wild pig + sambar	4	127.17	3.04	0.03
Forest + barking deer + wild pig	4	127.69	3.57	0.03
Null	1	132.99	8.86	0.00

species recorded, including the tiger, dhole, leopard, elephant, gaur, banteng, Malay tapir *Tapirus indicus* and Sunda pangolin *Manis javanica*. The long-term survival of large carnivores in the area is intrinsically linked to the presence of large and medium-sized prey species, and the protection and monitoring of the largest contiguous lowland forests of mainland South-east Asia are urgently needed.

Unsurprisingly, tiger presence was positively associated with the presence of large prey species, in particular the gaur, perhaps because it is the largest of these species, with an average weight of > 170 kg (Karanth & Sunquist, 1995; Karanth et al., 2004). Gaur is a major component of tiger diet (42–61%; Andheria et al., 2007; Steinmetz et al., 2013). Thus, to increase tiger populations in the area, conservation management for large ungulates, especially gaur, is crucial (Ramakrishnan et al., 1999). Although also reported as a key tiger prey species (Karanth et al., 2004), we detected banteng in only three locations, within the 32 km² northern part of the study area in Lenya Reserved Forest (in two grid cells, with six detections in total), probably because of a lack of grazing in the evergreen forest areas. These low numbers compared to other sites (Pedrono et al., 2009; Simcharoen et al., 2018) need to be further investigated.

Although we did not collect our data in a way that was designed to assess the effects of distance from human habitation, we covered a large area and camera traps were 2–33 km (mean 15 km) from human settlements. We therefore consider the effect of distance to be a valid indication of an effect of human settlements, with the caveat that these trends need to be further explored in future studies in the area. Tigers were detected infrequently by camera traps near villages (Table 2) and have a low probability of being found in areas close to villages (Fig. 2a). Poaching is a threat to tigers, with recent poaching incidents documented: two tigers were poached in forest and close to the border with Thailand in July 2018, most likely for trade (N.M. Shwe, unpubl. data, 2018). We detected hunters with guns, dogs or vehicles in 4.4% of the total detections. Most of those detected appeared to be local hunters but some, recorded in the southern part of study area, may have been from Thailand. We recorded extensive snaring, primarily in the southern part of the study area, mostly in the forest interior near the village of Ywahilu, which is close to the border with Thailand, where most inhabitants are employed as daily workers. Snares were mostly made of cable, targeting large mammals. In 2018, two tigers were caught in such snares (Aung Phe, pers. comm., 2018). Smaller mammals and birds are also hunted in the area, using funnel traps (Savini et al., 2022).

Our models suggest that leopard presence was positively correlated with forest area rather than with prey. This could be related to higher mammal community diversity in primary forests, which would provide leopards with a flexible diet. Leopards feed on small to large prey (Athreya et al., 2016; Lovari & Mori, 2017; Simcharoen et al., 2018) but tend to consume smaller prey where they coexist with tigers (Simcharoen et al., 2018). The high spatial overlap between the three large predators we recorded could have driven leopards to consume smaller prey species, as has been reported for other competitively subordinate felid species (Moreno et al., 2006). Alternatively, leopards could have shifted their diet towards primates, as has been reported in other locations (Karanth & Sunquist, 1995; Steinmetz

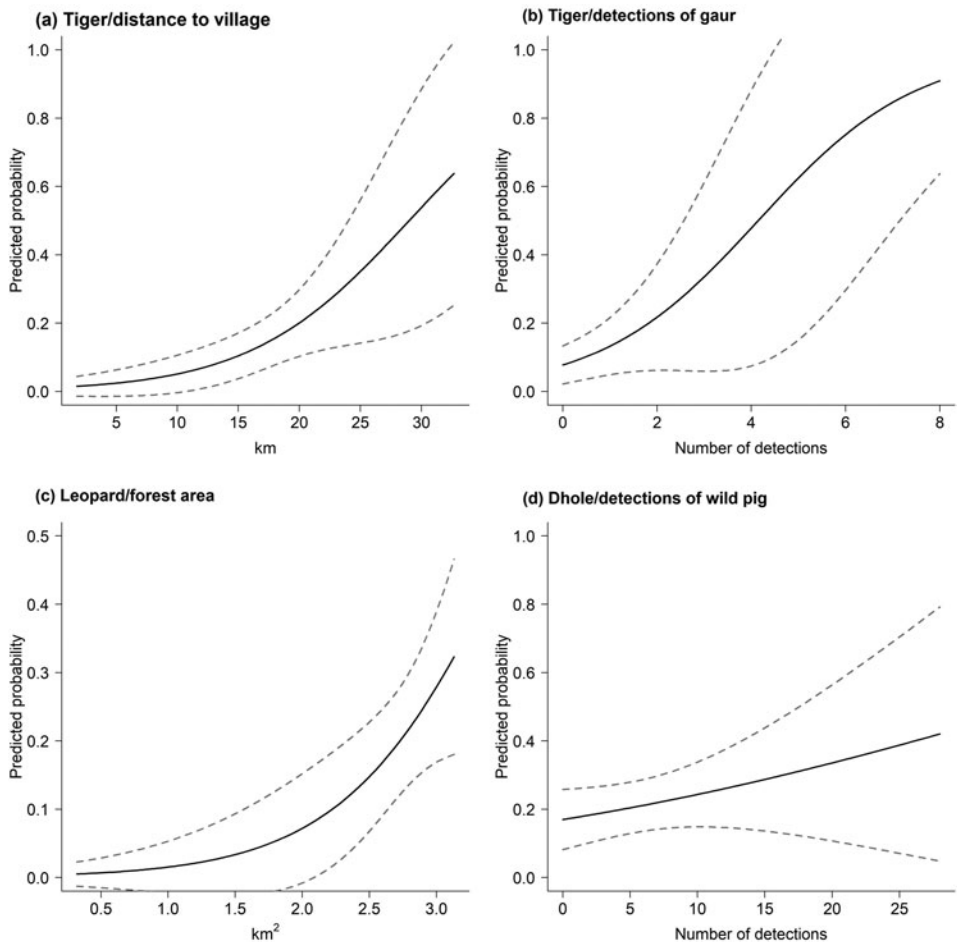

FIG. 2 The predicted probabilities of the occurrence of three large carnivore species based on the best fitting (most parsimonious) logistic regression models, with 95% CIs, showing the influence of: (a) distance to nearest village on the tiger *Panthera tigris*, (b) number of gaur *Bos gaurus* on the tiger, (c) forest area on the leopard *Panthera pardus*, and (d) number of wild pigs *Sus scrofa* on the dhole *Cuon alpinus*.

TABLE 4 Estimates of the coefficients derived from the best fitting logistic regression of detection/non-detection for each predator, with standard errors and 95% CIs, and model evaluation using the area under the receiver operating characteristic curve (AUC).

Species/variables	Estimate ± SE	95% CI	AUC
Tiger			0.85
Intercept	−7.37 ± 0.37	−8.19–−6.73	
Distance to village	1.91 ± 0.70	0.62–3.44	
Gaur	1.65 ± 0.62	0.59–2.97	
Leopard			0.68
Intercept	−6.99 ± 0.33	−7.76–−6.42	
Forest area	2.34 ± 1.01	0.71–4.73	
Dhole			0.70
Intercept	−6.60 ± 0.24	−7.09–−6.15	
Wild pig	0.53 ± 0.41	−0.27–1.35	

et al., 2013). Primates are predominately arboreal and were therefore not recorded by our camera traps. Banded langur *Presbytis femoralis*, dusky langur *Trachypithecus obscurus*, northern pig-tailed macaque *Macaca leonina* and stump-tailed macaque *Macaca arctoides* have been frequently recorded in the survey area (Grindley, 2019).

There is considerable uncertainty regarding the covariates that correlate with dhole presence. Dholes are more widespread than the other two large carnivores in our survey area and are highly correlated with the presence of wild pigs, which were recorded in every habitat type, including dense forest, degraded forest, forest near plantations and private farmland near forest. The other large prey species could also be important for dholes as the total number of prey (which includes barking deer and wild pig, the most common species) was one of the covariates in the second best model for this species. Dholes tend to select large prey, but in our study area they appear to select prey such as wild pigs and barking deer, perhaps indicating the scarcity of large ungulates (i.e. sambar; Karanth & Sunquist, 1995). When sambar are common, they are found in high proportions in dhole diets (Kamler et al., 2012; Charaspet et al., 2019), but they were uncommon in our study area (detected only in nine locations), perhaps because of hunting. This suggests that wild pigs are a particularly important and widespread prey species for dholes in the study area. Unsurprisingly, gaur did not appear to be an important prey for dholes, perhaps because of the presence of tigers. Gaur were distributed over a small range (detected in 27 locations), which could promote high levels of competition between tigers and dholes.

In general, our findings suggest the three large carnivore species may potentially face a problem of low prey abundance, as there were few detections of suitable prey species in the area. To support these carnivore species, the long-term recovery of large ungulates, such as sambar, gaur and banteng, would be an important conservation goal.

Since the opening of Myanmar following political changes in 2011, there has been an increase in human pressures and development activities, such as road expansion for village development and security purposes, in the southern region. This has resulted in extensive forest degradation (Savini et al., 2022). Recreational hunting by people crossing the border from Thailand has been recorded using camera traps and reported by villagers. The effect of this hunting needs to be quantified.

Large, interconnected areas are important for the movement of tigers and other large mammals and thus gene flow (Bennett, 1999). The survey area lies on the Isthmus of Kra, adjacent to the narrowest part of the Thai Peninsula, and almost all of the remaining habitat corridors are in Myanmar (Connette et al., 2016; Aung et al., 2017). However, no formal conservation management programme is in place to address the threats of forest clearance and uncontrolled hunting to the forested landscape and its globally threatened species. Plans to establish protected areas in the region were dropped in June 2019 and ongoing political turmoil in the country is affecting conservation activities. However, a small number of community patrol teams have been organized by FFI, who have made some progress in removing snares and deterring poachers (FFI, unpubl. data, 2018). A total of 630 activities linked with hunting (drift nets, snares, hunters encountered in the forest, hunting dogs and hunting platforms) up to 10 km within the forest boundaries were identified over 49 patrol days during March 2017–January 2020 (FFI, unpubl. data, 2020). The killing of two adult tigers in 2018 (N.M. Shwe, unpubl. data, 2018) suggests that this effort remains insufficient as village teams can only cover a limited area and have no law enforcement authority or training.

Acknowledgements We thank the Myanmar Government Forest Department for granting permission to conduct the surveys, and three anonymous reviewers for valuable comments on the manuscript. The fieldwork and analysis were undertaken by NMS as part of his PhD, sponsored by a KMUTT Petchra Pra Jom Klao Scholarship (Diamond scholar 18/2558). We thank field biologists from the FFI biodiversity team, Wahplaw Wildlife Watch Society team, and village conservation groups. The research presented here was sponsored and supported by the EU, Helmsley Charitable Trust and the Integrated Tiger Habitat Conservation Project (ITHCP1338) through the FFI Tanintharyi Conservation Programme.

Author contributions Survey design, data collection: NMS, SSA, MG; data analysis, writing: all authors.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

References

Andheria, A.P., Karanth, K.U. & Kumar, N.S. (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology*, 273, 169–175.

Aratrakorn, S., Thunhikorn, S. & Donald, P.F. (2006) Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. *Bird Conservation International*, 16, 71–82.

Athreya, V., Odden, M., Linnell, J.D.C, Krishnaswamy, J. & Karanth, K.U. (2016) A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx*, 50, 156–162.

Aung, S.S., Shwe, N.M., Frechette, J., Grindley, M. & Connette, G. (2017) Surveys in southern Myanmar indicate global importance for tigers and biodiversity. *Oryx*, 51, 13.

Baskett, J.P.C. (2015) *Myanmar Oil Palm Plantations: A Productivity and Sustainability Review*. Fauna & Flora International, Yangon, Myanmar.

Bennett, A.F. (1999) *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation (No. 1)*. IUCN, Gland, Switzerland and Cambridge, UK.

Beschta, R.L. & Ripple, W.J. (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142, 2401–2414.

Charaspet, K., Sukmasuang, R., Khiowsree, N., Songsasen, N., Simchareon, S. & Duengkae, P. (2019) Some ecological aspects of dhole (*Cuon alpinus*) in the Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani Province, Thailand. *Folia Oecologica*, 46, 91–100.

Connette, G., Oswald, P., Songer, M. & Leimgruber, P. (2016) Mapping distinct forest types improves overall forest identification based on multi-spectral Landsat imagery for Myanmar's Tanintharyi Region. *Remote Sensing*, 8, 882.

Connette, G.M., Oswald, P., Thura, M.K., Connette, K.J.L., Grindley, M.E., Songer, M. & Mulcahy, D.G. (2017) Rapid forest clearing in a Myanmar proposed national park threatens two newly discovered species of geckos (Gekkonidae: Cyrtodactylus). *PLOS ONE*, 12, e0174432.

Corlett, R.T. (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica*, 39, 292–303.

Danielsen, F., Beukema, H., Burgess, N.D., Parish, F., Brühl, C.A., Donald, P.F. et al. (2009) Biofuel plantations on forested lands: double jeopardy for biodiversity and climate. *Conservation Biology*, 23, 348–358.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345, 401–406.

Donald, P.F., Round, P.D., Dai We Aung, T., Grindley, M., Steinmetz, R., Shwe, N.M. & Buchanan, G.M. (2015) Social reform and a growing crisis for southern Myanmar's unique forests. *Conservation Biology*, 29, 1485–1488.

FFI (2016) *Tanintharyi Mining Assessment*. Tanintharyi Conservation Programme, Fauna & Flora International, Yangon, Myanmar.

Forman, R.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207–231.

Franklin, J. (2009) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press, Cambridge, UK.

FREEMAN, E.A. & MOISEN, G. (2008) *PresenceAbsence*: an *R* package for presence absence analysis. *Journal of Statistical Software*, 23, 1–31.
GELMAN, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, 27, 2865–2873.
GELMAN, A. & HILL, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge, UK.
GOODRICH, J., LYNAM, A., MIQUELLE, D., WIBISONO, H., KAWANISHI, K., PATTANAVIBOOL, A. et al. (2015) *Panthera tigris*. In *The IUCN Red List of Threatened Species* 2015. dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15955A50659951.en.
GRINDLEY, M. (ed.) (2019) *Terrestrial Biodiversity of Southern Tanintharyi: 2013–2018 Survey Results and Conservation Recommendations*. Fauna & Flora International, Cambridge, UK.
HOSMER, D.W. & LEMESHOW, S. (2000) *Applied Logistic Regression*. 2nd edition. John Wiley, New York, USA.
HOSSAIN, A.N.M., LYNAM, A.J., NGOPRASERT, D., BARLOW, A., BARLOW, C.G. & SAVINI, T. (2018) Identifying landscape factors affecting tiger decline in the Bangladesh Sundarbans. *Global Ecology and Conservation*, 13, e00382.
JOHNSINGH, A.J.T. (1992) Prey selection in three large sympatric carnivores in Bandipur. *Mammalia*, 56, 517–526.
KAMLER, J.F., JOHNSON, A., VONGKHAMHENG, C. & BOUSA, A. (2012) The diet, prey selection, and activity of dholes (*Cuon alpinus*) in northern Laos. *Journal of Mammalogy*, 93, 627–633.
KAMLER, J.F., SONGSASEN, N., JENKS, K., SRIVATHSA, A., SHENG, L. & KUNKEL, K. (2015) *Cuon alpinus*. In *The IUCN Red List of Threatened Species* 2015. dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T5953A72477893.en.
KAO, J., SONGSASEN, N., FERRAZ, F. & TRAYLOR-HOLZER, K. (eds) (2020) *Range-Wide Population and Habitat Viability Assessment for the Dhole,* Cuon alpinus. IUCN SSC Conservation Planning Specialist Group, Apple Valley, USA.
KARANTH, K.U. & SUNQUIST, M.E. (1995) Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, 64, 439–450.
KARANTH, K.U., NICHOLS, J.D., KUMAR, N.S., LINK, W.A. & HINES, J.E. (2004) Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854–4858.
KARGER, D. N., KESSLER, M., LEHNERT, M., & JETZ, W. (2021) Limited protection and ongoing loss of tropical cloud forest biodiversity and ecosystems worldwide. *Nature Ecology & Evolution*, 5, 854–862.
LEIMGRUBER, P., KELLY, D.S., STEININGER, M.K., BRUNNER, J., MÜLLER, T. & SONGER, M. (2005) Forest cover change patterns in Myanmar (Burma) 1990–2000. *Environmental Conservation*, 32, 356–364.
LOVARI, S. & MORI, E. (2017) Seasonal food habits of the endangered Indochinese leopard (*Panthera pardus delacouri*) in a protected area of north west Thailand. *Folia Zoologica*, 66, 242–247.
LOVE, K., KURZ, D.J., VAUGHAN, I.P., KE, A., EVANS, L.J. & GOOSSENS, B. (2018) Bearded pig (*Sus barbatus*) utilisation of a fragmented forest–oil palm landscape in Sabah, Malaysian Borneo. *Wildlife Research*, 44, 603–612.
LYNAM, A.J., TUN KHAING, S. & ZAW, K.M. (2006) Developing a national tiger action plan for the Union of Myanmar. *Environmental Management*, 37, 30–39.
MITHTHAPALA, S., SEIDENSTICKER, J., PHILLIPS, L.G., FERNANDO, S.B.U. & SMALLWOOD, J.A. (1989) Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. *Journal of Zoology*, 218, 527–536.
MOO, S.S.B., FROESE, G.Z. & GRAY, T.N. (2018) First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. *Oryx*, 52, 537–543.
MORENO, R.S., KAYS, R.W. & SAMUDIO, R. (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy*, 87, 808–816.
MONREC (MINISTRY OF NATURAL RESOURCES AND ENVIRONMENTAL CONSERVATION) (2020) *The Republic of the Union of Myanmar: National Tiger Action Plan (2020–2025)*. Publisher, Yangon, Myanmar
NAMKHAN, M., GALE, G.A., SAVINI, T. & TANTIPISANUH, N. (2021) Loss and vulnerability of lowland forests in mainland Southeast Asia. *Conservation Biology*, 35, 206–215.
NEWBOLD, T., HUDSON, L.N., PHILLIPS, H.R., HILL, S.L., CONTU, S., LYSENKO, I. et al. (2014) A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20141371.
NIJMAN, V. & SHEPHERD, C.R. (2015) Trade in tigers and other wild cats in Mong La and Tachilek, Myanmar – a tale of two border towns. *Biological Conservation*, 182, 1–7.
OLSON, D.M., DINERSTEIN, E., WIKRAMANAYAKE, E.D., BURGESS, N.D., POWELL, G.V., UNDERWOOD, E.C. et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, 51, 933–938.
OTTAR, N.B. (2018) *ncf: Spatial Covariance Functions*. *R* package version 1.2–9. CRAN.R-project.org/package=ncf [accessed 24 February 2021].
PEDRONO, M., TUAN, H.M., CHOUTEAU, P. & VALLEJO, F. (2009) Status and distribution of the endangered banteng *Bos javanicus birmanicus* in Vietnam: a conservation tragedy. *Oryx*, 43, 618–625.
PRUGH, L.R., STONER, C.J., EPPS, C.W., BEAN, W.T., RIPPLE, W.J., LALIBERTE, A.S. & BRASHARES, J.S. (2009) The rise of the mesopredator. *BioScience*, 59, 779–791.
RAMAKRISHNAN, U., COSS, R.G. & PELKEY, N.W. (1999) Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation*, 89, 113–120.
RAO, M., HTUN, S., PLATT, S.G., TIZARD, R., POOLE, C., MYINT, T. & WATSON, J.E. (2013) Biodiversity conservation in a changing climate: a review of threats and implications for conservation planning in Myanmar. *Ambio*, 42, 789–804.
RAO, M., ZAW, T., HTUN, S. & MYINT, T. (2011) Hunting for a living: wildlife trade, rural livelihoods and declining wildlife in the Hkakaborazi National Park, north Myanmar. *Environmental Management*, 48, 158–167.
R DEVELOPMENT CORE TEAM (2015) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
ROSTRO-GARCÍA, S., KAMLER, J.F., ASH, E., CLEMENTS, G.R., GIBSON, L., LYNAM, A.J. et al. (2016) Endangered leopards: range collapse of the Indochinese leopard (*Panthera pardus delacouri*) in Southeast Asia. *Biological Conservation*, 201, 293–300.
SAVINI, T., SHWE, N.M. & SUKUMAL, N. (2022) Ongoing decline of suitable habitat for the Critically Endangered Gurney's pitta *Hydrornis gurneyi*. *Oryx*, 56, 202–208.
SCHMIDT, C. (2012) As isolation ends, Myanmar faces new ecological risks. *Science*, 337, 796–797.
SHWE, N.M., SUKUMAL, N., GRINDLEY, M. & SAVINI, T. (2020) Is Gurney's pitta on the brink of extinction? *Oryx*, 54, 16–22.
SIMCHAROEN, A., SIMCHAROEN, S., DUANGCHANTRASIRI, S., BUMP, J. & SMITH, J.L.D. (2018) Tiger and leopard diets in western Thailand: evidence for overlap and potential consequences. *Food Webs*, 15, e00085.

  doi:10.1017/S0030605321001654

Steinmetz, R., Seuaturien, N. & Chutipong, W. (2013) Tigers, leopards, and dholes in a half-empty forest: assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, 163, 68–78.

Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M. et al. (2011) A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters*, 4, 219–227.

Wildlife Conservation Society (2012) *Myanmar Biodiversity Conservation Investment Vision*. Wildlife Conservation Society, Yangon, Myanmar and New York, USA.

Woods, K. (2015) *Commercial Agriculture Expansion in Myanmar: Links to Deforestation, Conversion Timber, and Land Conflicts*. Forest Trends Report Series. Forest Trends Association, Washington, DC, USA.