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Title: The price of persistence: Assessing the drivers and health implications of metal levels in indicator carnivores inhabiting an agriculturally fragmented landscape

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Abstract

Patterns and practices of agricultural expansion threaten the persistence of global biodiversity. Wildlife species surviving large-scale land use changes can be exposed to a suite of contaminants that may deleteriously impact their health. There is a paucity of data concerning the ecotoxicological impacts associated with the global palm oil (*Elaeis guineensis*) industry. We sampled wild Malay civets (*Viverra zibetha*) across a patchwork landscape degraded by oil palm agriculture in Sabah, Malaysian Borneo. Using a non-lethal methodology, we quantified the levels of 13 essential and non-essential metals within the hair of this adaptable small carnivore. We robustly assessed the biological and environmental drivers of intrapopulation variation in measured levels. Metal concentrations were associated with civet age, weight, proximity to a tributary, and access to oxbow lakes. In a targeted case study, the hair metal profiles of 16 GPS-collared male civets with differing space use patterns were contrasted. Civets that entered oil palm plantations expressed elevated aluminium, cadmium, and lead, and lower mercury hair concentrations compared to civets that remained exclusively within the forest. Finally, we paired hair metal concentrations with 34 blood-based health markers to evaluate the possible sub-lethal physiological effects associated with varied hair metal levels. Our multi-faceted approach establishes these adaptable carnivores as indicator species within an extensively altered ecosystem, and provides critical and timely evidence for future studies.

Keywords: pollution; oil palm plantation; biochemistry; hematology; hair; Malay civet

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1. Introduction

Habitat fragmentation poses a direct threat to global biodiversity (Crooks et al., 2017). In addition to the suite of ecological stressors associated with the loss and degradation of natural habitats (Newbold et al., 2015), species face elevated exposure to pollutants such as pesticides, heavy metals, endocrine-disrupters, and plastics (Smith et al., 2007; Zhou et al., 2010). Anthropogenic contaminants from agriculture (Badry et al., 2021), roads (Marcheselli et al., 2010), hunting (Arrondo et al., 2020), urbanization (Bauerová et al., 2017), and mining (Pereira et al., 2006) negatively impact wildlife worldwide. Beyond acute poisonings (Finkelstein et al., 2012), sub-lethal physiological effects of pollution exposure can undermine the long-term population viability of persisting species (Desforges et al., 2018; Köhler and Triebkorn, 2013). Thus, the identification, inventory, and dynamic assessment of pollutants within human-modified systems are critical to developing and, if necessary, deploying mitigation-oriented conservation actions (Peterson et al., 2017).

Inorganic pollutants, specifically heavy metals and metalloids, pose well-documented threats to both human and wildlife health (Dietz et al., 2013; Mohmand et al., 2015). At the cellular level, exposure can damage genetic material and processes (Harley et al., 2016), disrupt central biochemical pathways (Basu et al., 2009), elevate oxidative stress (Espín et al., 2014), and interfere with gamete functionality (Ieradi et al., 1996). Precipitated systems-level impacts include patterns of immune disruption (Bocharova et al., 2013), organ damage (Pereira et al., 2006), and maladaptive behavioural modifications (Janssens et al., 2003). Ultimately, metal pollution can affect processes such as individual growth and development (Sánchez-Virosta et al., 2018),

reproductive success (Dauwe et al., 2004), and population growth rates (Rodríguez-Estival and Mateo, 2019), which can all impact ecosystem-level functions.

Given these considerations, it is crucial to quantify the presence and biological repercussions of metals in regions directly impacted by large-scale land use changes. The palm oil (*Elaeis guineensis*) industry is a primary driver of tropical forest loss and fragmentation in some of the most biodiverse regions of the world, and likely poses a significant pollution threat to wildlife surviving the extensive landscape alterations precipitated by plantation establishment (Fitzherbert et al., 2008; Meijaard et al., 2020; Zarcinas et al., 2004). Mechanistically, crop-based practices such as the application of agrochemicals and mineral fertilizers (Fairhurst and Härdter, 2003), open vegetative burning (Comte et al., 2012), and the construction of irrigation ditch networks can inflate local metal concentrations and bioavailability (Sakai et al., 2017). Following processing, palm oil mill effluent (POME) contains high levels of inorganic pollutants (Donald, 2004), and despite regulations requiring the cleaning of these materials prior to release into natural watercourses, there are reports suggesting adherence to and enforcement of these benchmarks are lacking (McCarthy and Zen, 2010). To date, there remains a clear paucity of data assessing the ecotoxicological threat oil palm agriculture poses to tropical wildlife (Meijaard et al., 2018). Given both the current and projected global scale of the industry (Phalan et al., 2013), quantitative research is needed to inform effective and mitigation-oriented land management strategies.

To assess the *in situ* risks of environmental pollution, biomonitoring studies frequently select a focal organism as an indicator (e.g. Lazarus et al., 2020; Stankovic

et al., 2014). In Southeast Asia, the Malay civet (*Viverra zibetha*) represents a highly suitable indicator species for evaluating the contamination threats faced by wildlife within agriculturally degraded landscapes. The species is a broad dietary generalist and holds a high trophic position within the tropical system (Colón and Sugau, 2012), characteristics that can elevate the probability of exposure to and accumulation of metallic pollutants (Rodríguez-Jorquera et al., 2017). Further, Malay civets demonstrate spatiotemporal utilisation of both heavily degraded forests and oil palm plantations; indeed, GPS-collared animals concentrate foraging along these agricultural edges (Evans et al., 2021). Despite these flexible spatial behaviours, intrapopulation variations in blood-based health markers suggest close associations with plantations may come at a physiological cost to persisting individuals (Evans et al., 2020). There have been no studies evaluating the heavy metal burdens in tropical wildlife living alongside oil palm plantations. Given the spectrum of toxic effects associated with exposure to heavy metals, it is crucial conservationists assess these cryptic risks faced by seemingly adaptable species within threatened landscapes.

Biotic exposure to metallic pollutants is investigated traditionally using either direct organ biopsies or specific biomarkers, such as serum enzymes (Alleva et al., 2006). More recently, hair has been used as analytical tissue in an increasing number of studies, as sampling is non-lethal, markedly less invasive, and hence much easier to conduct (Table S1; Chaousis et al., 2018; Pozebon et al., 2017). The structure of hair creates a unique and non-specific matrix within which metals are excreted and accumulated; metal levels in hair positively correlate with more traditional organ concentrations across a range of species (e.g. wood mice *Apodemus sylvaticus* Beernaert et al., 2007; hedgehogs *Erinaceus europaeus* D'Havé et al., 2006; European

rabbits *Oryctolagus cuniculus* Gil-Jiménez et al., 2020). In addition to the clear conservation value of non-lethal sampling, the tissue has several logistical advantages; it is minimally invasive to collect, does not necessitate specific health and safety training to handle, and does not require cold storage conditions, an aspect particularly relevant for field research in remote areas. Furthermore, due to the low metabolic activity of hair tissue, it serves as a stable analytical matrix and long-term record of metallic excretion (Foo et al., 1993; Mina et al., 2019), in contrast to the relatively brief temporal exposure ‘snapshot’ provided by blood or urine samples (Gil et al., 2011).

Therefore, we aimed to characterise the first essential and non-essential metal levels in the hair of Malay civets captured across a highly degraded agricultural landscape in Malaysian Borneo. Through our non-lethal sampling protocol, we sought to establish civets as indicator species persisting within and alongside oil palm plantations. We robustly quantified the biological and environmental drivers of intrapopulation variation in hair metal concentrations. To explicitly evaluate the hypothesis of oil palm plantations representing sources of target elements, we deployed GPS collars to determine the associations between observed metal levels and agricultural space use by tracked civets. Finally, we explored potential sub-lethal physiological implications of elevated metal levels by investigating the relationships between hair concentrations and haematology and serum biochemistry profiles. Through this multi-faceted approach, we aimed to provide ecotoxicological insights into the vulnerability of wildlife persisting within landscapes degraded by palm oil production.

2. Materials and methods

2.1 Study site

Our study was based in the Lower Kinabatangan Floodplain in Sabah, Malaysian Borneo. The climate of the region is considered humid tropical; temperatures ranged from 22°–24°C and mean annual rainfall was 2,680 mm throughout the study period. With a total catchment area of 1.68 million ha, the Kinabatangan River is the largest river in Sabah (Harun et al., 2015). At least 29 palm oil mills are situated within the watershed, and have historically failed to meet water quality discharge standards (DOE, 2009). High levels of sedimentation, dissolved organic material, and eutrophication have been recorded within the system, and have largely been attributed to the extensive agricultural conversion of the lower floodplains (Harun et al., 2015; Jawan and Sumin, 2012). The Kinabatangan oil palm estates account for nearly 28% of the total oil palm cultivation in the state; the majority of the floodplain has been converted to this agriculture (Abram et al., 2014). The remaining patches of natural habitats consist of lowland tropical, semi-inundated, and swamp forests interspersed with small grasslands. This array of riparian patches forms a discontinuous 45,000 ha protected area network presided over by the Sabah Wildlife Department and the Sabah Forestry Department. The Lower Kinabatangan Floodplain is a key mosaic landscape to assess the impacts of large-scale oil palm agriculture on biodiversity persisting within degraded forest fragments.

2.2 Trapping and sample collection

Trapping periods for wild Malay civets spanned March 2013–December 2017. Detailed capture, anaesthesia, and sampling protocols can be found in Evans et al. (2016). Briefly, animals were live-trapped, anaesthetised, and sampled by an experienced team following protocols approved by the Sabah Wildlife Department,

the Sabah Biodiversity Centre (license ref.no: JKM/MBS.10000-2/2 JLD.6[8]), and within the guidelines of the American Society of Mammalogists (Sikes et al., 2016). A small patch of hair (approximately 2 x 2 cm) was shaved from the dorsal scapular junction of each anaesthetised animal using a commercial razor. The withers are the body region least likely to be contaminated by exogenous metal deposition (Hubbart et al., 2012), and this standardised collection method also facilitated the sterile insertion of a subdermal identifying RFID microchip. Clippers were thoroughly washed with ethanol between procedures. If a civet was not anaesthetised, hair samples were collected through the trap prior to the release of the animal. Hair was stored in clean polypropylene tubes containing metal-free desiccating silica beads (Sigma-Aldrich), and sealed at room temperature until analysis. Adult male civets were fitted with GPS collars to record hourly nocturnal movements (Evans et al., 2016); the spatial behaviours of these animals, including use of oil palm plantations at the home range scale, were characterised in Evans et al. (2021). We recorded sex, weight, and estimated age for each individual, and collected blood samples for serum biochemistry and haematology assessment by venepuncture methods described in Evans et al. (2020). A certified laboratory (Gribbles Pathology Laboratory Sdn Bhd) determined 34 analytical parameters from these blood samples (Fig. S1).

2.3 Sample preparation

All hair samples were washed to remove exogenous lipids and surface metallic contamination. Hair was rinsed with 5 mL reagent-grade acetone (99.9 % HPLC grade Chromasolv, Merck, Germany), followed by two 5 mL rinses of Milli-Q ultrapure water (Type 1 [18.2 M Ω], Merck, Germany), and a final 5 mL rinse of acetone, following methods outlined by the International Atomic Energy Agency

(Ryabukin, 1978). Washed hair was left to dry at room temperature for at least 24 h before further handling.

Metal content of hair was analysed by inductively coupled plasma mass spectrometry (ICP-MS) following complete acid digestion of samples (Puchyr et al., 1998).

Washed and dried hair samples (100 ± 1 mg) were accurately weighed into acid-washed Teflon digestion vessels (Milestone Srl, Italy). Vessels were transferred to a fume hood and 10 mL concentrated HNO_3 (67–70% w/w TraceMetal Grade, Fisher Scientific, USA) were added. Glassware was thoroughly washed with ultrapure water (PURELAB Flex 3, ELGA LabWater, UK), soaked in $\geq 5\%$ HNO_3 , and rinsed with ultrapure water prior to use. For each digestion batch ($n = 15$ vessels), an acid-only blank was included to identify methodological contamination. Vessels were placed in a microwave digestion system (ETHOS UP, Milestone Srl, Italy) and underwent a two-phase digestion program (1800 W ramp to 70 °C over 5 min; hold at 70 °C for 15 min; ramp to 115 °C over 5 min; hold at 115 °C for 15 min; cool for 60 min). Cooled samples were quantitatively transferred to acid-washed volumetric flasks and made up to 50 mL with ultrapure water. Samples were stored in pre-washed 60 mL HDPE plastic bottles (VWR, UK) until ICP-MS analysis. Following each digestion batch, vessels underwent an acid washing cycle whereby 5 mL ultrapure water and 5 mL HNO_3 were added and run through a microwave cleaning cycle (200 °C for 20 min). All reagents were analytical grade and trace metal certified, including washing reagents.

2.4 Instrumentation and operating parameters

The metal content of digested hair samples was analysed by an inductively coupled plasma mass spectrometer in He analysis mode (ICP-MS Agilent 7900, Agilent Technologies, USA; Tables S2–S3). In addition to standard washes and blanks, a 0.5 ppm Au-containing solution (Multi-element Calibration Standard #4, PerkinElmer, USA) was run to clear persisting Hg in the system prior to sample introduction. Batch blanks (every 15 samples) were run to identify any potential metal carryover from the digestion vessels. Metal content was processed using MassHunter software (Agilent Technologies), where each reading was comprised of five ICP-MS measurements per target element. Digested civet samples were run twice, thus individual values are reported as an arithmetic mean as mg kg^{-1} dry weight of civet hair.

2.5 Calibration and quantitative analysis

A multi-element internal standard (5188-6525, Agilent Technologies) diluted to 100 ppb was used to control for instrumental drift; rhodium, terbium, and lutetium were selected as optimal internal standards for target analytes (Table S4). Hair metal concentrations were externally quantified against multi-element standards (Multi-Element Calibration Standard #3, PerkinElmer; Multi-Element Calibration Standard #2A-HG, Agilent Technologies) using a five-point calibration (0 – 1 $\mu\text{g/mL}$ for most target metals; 0 – 0.2 $\mu\text{g/mL}$ for Hg). Calibrations were performed every 45 measurements and accepted if $R \geq 0.992$; batch limits of detection were determined from series blanks (Table S4). Civet samples that exceeded the calibration range (Fe and Al) were diluted with acidified (2% HNO_3) ultrapure water and re-analysed. Recovery of metals from hair samples was evaluated using domestic dog hair. Domestic dog hair samples were digested and spiked with 0.1 $\mu\text{g/mL}$ of each target

element and analysed as above. Recovery rates fell between the accepted ranges of 90–110% (Table S4; Creed et al., 1994).

2.6 Statistical analyses

Analyses were performed using R 3.5.0 (R Core Team, 2018). Metal concentrations falling below the limit of detection were set at half the batch limit of detection (Gil et al., 2011). Extreme outliers were identified as values exceeding the population mean by three standard deviations (Drobyshev et al., 2017). However, outliers were not automatically removed from the dataset, as the discarding of laboratory-derived values based solely on parametric mathematical identification fails to acknowledge the possibility of natural metal variations in the wild system (Pollett and van der Meij, 2017). All reported metal concentrations and blood profiles were from the first capture of each individual civet.

2.6.1 Drivers of intrapopulation variation

We assessed the effects of both biological and environmental features on recorded hair metal concentrations using general linear modelling (GLM). We included civet sex, weight, and age category as fixed biological effects. To evaluate the potential role of landscape characteristics in hair metal concentrations, each sampling site was assigned a suite of descriptive values in ArcGIS (version 10.1, ESRI, USA).

Shapefiles delineating oil palm plantations, oxbow lakes, and semi-permanent tributaries (those containing water even when river levels were low) were created from the digitization of Google Earth Pro satellite imagery. We measured the proximity of each sampling site to the nearest accessible plantation and tributary as a Euclidean distance. A feature was defined as accessible if located on the same

riverbank as the capture site and within 4 km, a threshold corresponding to the average maximum distance travelled in a night by male civets fitted with GPS collars (Evans, 2019). Proximity to oxbow lake was recoded as a binomial factor denoting if an animal did or did not have access to a lake. Continuous terms were checked for collinearity prior to analysis; none were identified. Due to the skewed distribution of hair metal concentrations, values were either log or square root transformed prior to modelling (Table 1). Models were fitted with Gaussian error distributions and identity link functions; each model fit was checked by evaluation of the standardised residuals of the global model, diagnostic plots, and minimisation of the Akaike's Information Criteria (AIC; Burnham and Anderson, 2002). We performed multimodal inference using model averaging; all possible covariate structures were compared using the dredge function in the *MuMIn* package (Bartón, 2018). We standardised independent parameters prior to model averaging (Grueber et al., 2011). Top models were identified as those within a $\Delta\text{AICc} < 2$, and final parameter estimates were calculated using the natural average method (Burnham and Anderson, 2002).

2.6.2 Case study: metal profiles of male civets fitted with GPS collars

Using the GPS collar datasets, we compared the hair metal concentrations of male civets that exclusively used remnant forests and those that used both forests and oil palm plantations. As appropriate based on data normality, values were compared with either t-tests or Mann-Whitney U tests. Hair concentrations were tested for normality with the Shapiro-Wilks test, and Fisher exact tests determined the equality of variances between datasets.

2.6.3 Potential physiological effects of varied hair metal levels

To best evaluate the interplay between hair metal concentrations and detectable Malay civet health effects, we used a two-phase approach to robustly contrast metal values against blood-based health metrics. First, we used Spearman linear correlations to assess the 1:1 relationship between each metal and blood parameter with the packages *Hmisc* (Harrell Jr. et al., 2018) and *ggpubr* (Kassambara, 2017). Hair metal values were either squared, log, or square root transformed to better meet the assumptions of normality for correlation analyses while minimising the effects of outliers.

For those significant univariate correlations, we further assessed the relationship using generalised linear models (GLMs) to account best for the potentially confounding effects of civet sex and age on blood metrics (Evans et al., 2020). In addition, this approach allowed for selection of the appropriate model family for measured blood parameters. Continuous health metrics were fitted with Gamma model families, and selection of each link function was based on optimisation of model fit plots and minimisation of the AIC. Proportional metrics were assessed with binomial models and a logit link function. We first fitted count-based data with Poisson models; however, all models were over-dispersed ($\theta > 20$; Thomas et al., 2017), and were instead fitted with a negative binomial structure using the *MASS* package (Venables and Ripley, 2002). We validated model fit by assessing residual and outlier plots. No further model refinement or selection procedures (e.g. stepwise deletion) were conducted, as we aimed to control for confounding biological effects on blood parameters whilst identifying associations between hair metal concentrations and physiological traits. For those models which identified statistically significant relationships between a blood metric and a metal, we visualized these effects using the `predict` function in R.

Although this univariate approach could increase the detection rate of false negatives (McMeans et al., 2007); given the exploratory nature of this investigation, paired with the lack of explicit source tracking, multivariate analyses would be difficult to robustly interpret in biological terms, and were thus not conducted.

3. Results

We collected hair from 71 individual Malay civets within the Lower Kinabatangan floodplain and surrounding oil palm plantations (Fig. 1; Table S5). The majority of samples contained metal concentrations above instrumentation detection limits; four samples were below the limit of detection for Cr measurements; two for Ni; and 10 for As. Two samples possessed metal concentrations classified as extreme outliers for over half the target analytes; as such, these individuals were omitted from the dataset. In terms of relative concentration within hair samples, the highest metal concentrations were Fe, Zn, and Al, in decreasing order, and the lowest measured concentrations were Co, As, and Cd.

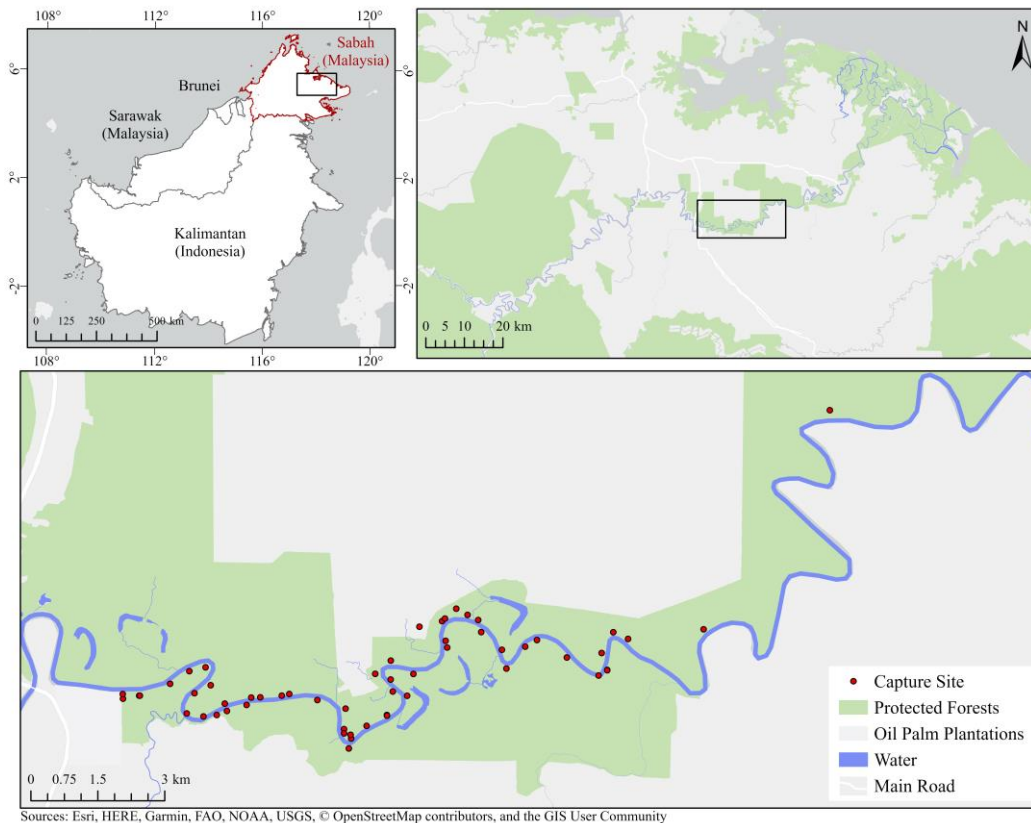


Fig. 1. Capture and sampling sites of Malay civets within the Lower Kinabatangan Floodplain in Sabah, Malaysian Borneo, 2013-2017.

3.1 Drivers of intrapopulation variation

Concentrations of seven target hair metals were significantly associated with biological or spatial terms (Table 1; Table S6); the remaining six metals were not statistically related to assessed covariates. Hair As and Hg concentrations were elevated in mature compared to immature civets, while hair As and Ni decreased with civet weight. In terms of landscape effects, hair As and Hg concentrations statistically decreased with proximity to a tributary. In contrast, Ba, Cd, and Fe measurements increased with proximity to a tributary. Lastly, hair Cr similarly increased with proximity to a tributary and with the presence of an accessible oxbow lake near the capture site (Table 1). Neither distance to plantation edge nor civet sex were

statistically significant terms in any of the top averaged models describing variation in hair metals.

Table 1 Standardised parameter estimates for statistically significant averaged models describing variation in metal concentrations of Malay civet hair. Trans denotes mathematical transformation of hair metal concentration values. Bold terms emphasise significant variables. Intercept= standardised reference interval for factorised predictor variables (e.g. no accessible oxbow lake; immature; female). SexM= male; AgeM= mature; Plant= proximity to nearest accessible oil palm plantation; Trib= proximity to nearest accessible semi-permanent tributary; Lake1= access to oxbow lake.

Element	Trans	Variable	Mean	Std. Error	z value	p value
As	Log	Intercept	-2.955	0.153	18.92	<0.001
		AgeM	1.401	0.599	2.295	<0.05
		Lake1	-0.236	0.349	0.654	0.51
		Trib	0.670	0.315	2.090	<0.05
		Weight	-1.339	0.479	2.746	<0.01
		Plant	-0.067	0.193	0.342	0.73
Ba	Log	Intercept	2.043	0.140	14.35	<0.001
		Trib	-0.879	0.288	3.055	<0.005
		AgeM	-0.097	0.247	0.394	0.69
		Lake1	0.054	0.183	0.293	0.77
Cd	Log	Intercept	-4.362	0.082	52.17	<0.001
		Trib	-0.369	0.166	2.180	<0.05
		Plant	-0.030	0.097	0.315	0.75
		Lake1	-0.029	0.100	0.287	0.77
		Weight	0.026	0.089	0.285	0.78
		SexM	-0.013	0.069	0.186	0.85
Cr ^a	Log	Intercept	0.338	0.136	2.482	<0.02
		Lake1	0.918	0.310	2.957	<0.005
		Trib	-1.050	0.276	-3.804	<0.001
Fe	Log	Intercept	5.917	0.087	66.603	<0.001
		Lake1	0.422	0.237	1.754	0.08
		SexM	0.232	0.210	1.098	0.27
		Trib	-0.412	0.178	2.272	<0.05
		AgeM	-0.234	0.330	0.703	0.48
		Plant	-0.079	0.158	0.493	0.62
		Weight	0.086	0.206	0.415	0.68

Hg	N/A	Intercept	2.328	0.119	19.119	<0.001
		AgeM	1.457	0.342	4.191	<0.001
		Trib	0.878	0.242	3.560	<0.001
		Lake1	0.095	0.209	0.449	0.65
		SexM	-0.077	0.177	0.432	0.67
		Plant	0.032	0.121	0.263	0.79
		Weight	0.038	0.166	0.229	0.82
Ni	Log	Intercept	0.008	0.101	0.073	0.94
		Weight	-0.666	0.276	2.379	<0.02
		Lake1	-0.109	0.204	0.533	0.59
		AgeM	0.141	0.305	0.458	0.65
		SexM	-0.020	0.088	0.223	0.82
		Plant	-0.016	0.081	0.194	0.84
		Trib	0.009	0.067	0.134	0.89

^adenotes a non-averaged final model (i.e. there were 0 additional models whereby $AICc < 2$; covariate t values reported instead of z values).

3.2 Case study: metal profiles of male civets fitted with GPS collars

Hair As, Ba, Co, Cr, Cu, Fe, Mn, Ni and Zn concentrations of 16 male civets fitted with GPS collars did not statistically differ between animals that utilised oil palm plantations and those that did not (Table S7). Males accessing oil palm agriculture expressed, however, significantly elevated hair concentrations of Cd, Pb, and Al compared to males exclusively using forests ($W = 5, p < 0.01$; $W = 11, p < 0.05$; $W = 12, p < 0.05$, respectively; Fig. 2). In contrast, hair from forest-only civets contained a mean Hg concentration 1.72 mg kg^{-1} greater than those that used both habitat types ($t = 3.782, df = 14, p < 0.005$).

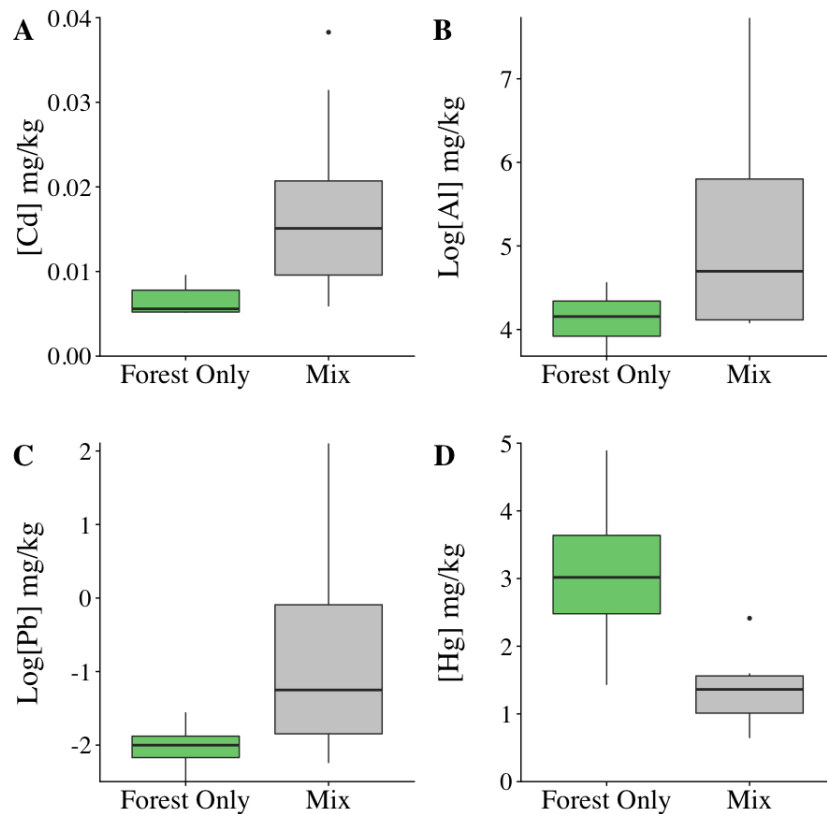


Fig. 2. Statistically significant differences between A) Cd; B) Al; C) Pb; and D) Hg (mg kg^{-1}) concentrations in the hair of GPS-collared male civets, analysed with t-tests or Mann-Whitney U (MWU) tests. Animals are grouped based on patterns of space use documented throughout tracking periods; box-whisker plots display the metal profiles for civets using solely forest ('Forest Only' $n = 8$) compared to those that entered oil palm plantations ('Mix', $n = 8$). Dots represent statistical outliers (> 3 S.D. from each group median). Log transformations of metals were only conducted for data visualisation purposes; due to the non-normal distribution of these datasets, MWU tests determined the significance levels between these two groups using untransformed data.

3.3 Potential physiological effects of varied hair metal levels

We successfully established both hair metal and blood parameter profiles from 48 Malay civets; based on the preliminary 442-univariate correlations (Fig. S1), further evaluation of 22 relationships was warranted. After controlling for civet age and sex, 13 statistically significant relationships between blood parameters and hair metal concentrations were found (Table 2). Four haematology and five biochemistry metrics were associated with variations in hair metal concentrations (Al, Ba, Cd, Cr, Fe, Hg, Ni, and Pb; select visualizations in Fig. 3; Fig. S2). Blood parameters did not predictably relate to variations in hair As, Co, Cu, Mn, or Zn concentrations.

Table 2 Generalised linear models containing statistically significant effects of hair metal concentrations on Malay civet haematology and serum biochemistry metrics. Estimates for the factor terms sex and age are relative to intercept reference categories of female and immature animals. Significant effects are denoted in bold. Haem= haemoglobin; MCHC= mean corpuscular haemoglobin concentration; MCV= mean corpuscular volume; Plat= platelets; Alb= albumin; AST= aspartate aminotransferase; Cl= chloride; Co_Ca= corrected calcium; LDL= low-density lipoprotein.

Health Metric	Parameter	Mean	Std.	t value	p value	
			Error			
Haematology	Haem	Intercept	48.624	22.868	2.126	<0.05
		Log(Fe)	8.763	3.792	2.311	0.03
		Sex	12.481	5.366	2.326	0.03
		Age	4.035	6.452	0.625	0.54
	MCHC	Intercept	259.290	6.150	42.190	<0.001
		Log(Cr)	-4.284	1.930	-2.220	0.03
		Sex	4.836	4.990	0.970	0.34
		Age	2.541	6.280	0.400	0.69
	MCV	Intercept	50.308	1.679	29.960	<0.001
		Log(Cr)	1.584	0.550	2.880	0.007
		Sex	1.135	1.408	0.806	0.43
		Age	1.146	1.750	0.655	0.52
	Plat ^a	Intercept	376.840	57.470	6.557	<0.001
		Log(Pb)	64.470	25.400	2.539	0.01
		Sex	53.670	31.630	1.697	0.09
		Age	-48.250	44.740	-1.078	0.28

Serum Biochemistry	Alb	Intercept	3.265	0.079	41.156	<0.001
		Log(Cr)	0.058	0.026	2.233	0.03
		Sex	0.053	0.067	0.781	0.44
		Age	0.002	0.084	0.023	0.98
	AST	Intercept	3.462	0.758	4.569	<0.001
		Log(Al)	0.330	0.151	2.189	0.03
		Sex	0.135	0.177	0.761	0.45
		Age	0.055	0.226	0.245	0.81
	AST	Intercept	4.428	0.240	18.455	<0.001
		Log(Ba)	0.253	0.069	3.659	<0.001
		Sex	-0.067	0.153	-0.435	0.67
		Age	0.106	0.190	0.560	0.58
	AST	Intercept	177.506	29.464	6.025	<0.001
		Log(Ni)	-44.151	14.212	-3.107	0.003
		Sex	9.908	23.595	0.420	0.68
		Age	-17.093	30.175	-0.566	0.57
	Cl	Intercept	117.691	2.167	54.312	<0.001
		Log(Cr)	-1.571	0.673	-2.335	0.02
		Sex	-0.818	1.830	-0.447	0.66
		Age	0.077	2.300	0.034	0.97
Cl	Intercept	116.143	2.155	53.893	<0.001	
	Log(Ni)	2.368	1.018	2.325	0.03	
	Sex	-1.051	1.816	-0.579	0.57	
	Age	1.377	2.305	0.597	0.55	
Co_Ca	Intercept	2.511	0.066	37.971	<0.001	
	Hg	-0.076	0.027	-2.795	0.009	
	Sex	0.041	0.050	0.816	0.42	
	Age	-0.014	0.080	-0.180	0.85	
Co_Ca	Intercept	0.987	0.048	20.487	<0.001	
	Sqrt(Fe)	-0.005	0.002	-2.382	0.03	
	Sex	0.037	0.021	1.783	0.09	
	Age	-0.054	0.028	-1.918	0.07	
LDL	Intercept	1.668	0.249	6.708	<0.001	
	Log(Cd)	0.171	0.052	3.270	0.002	
	Sex	0.107	0.061	1.747	0.09	
	Age	0.007	0.078	0.084	0.93	

^aModel is a negative binomial family; z value presented instead of t value

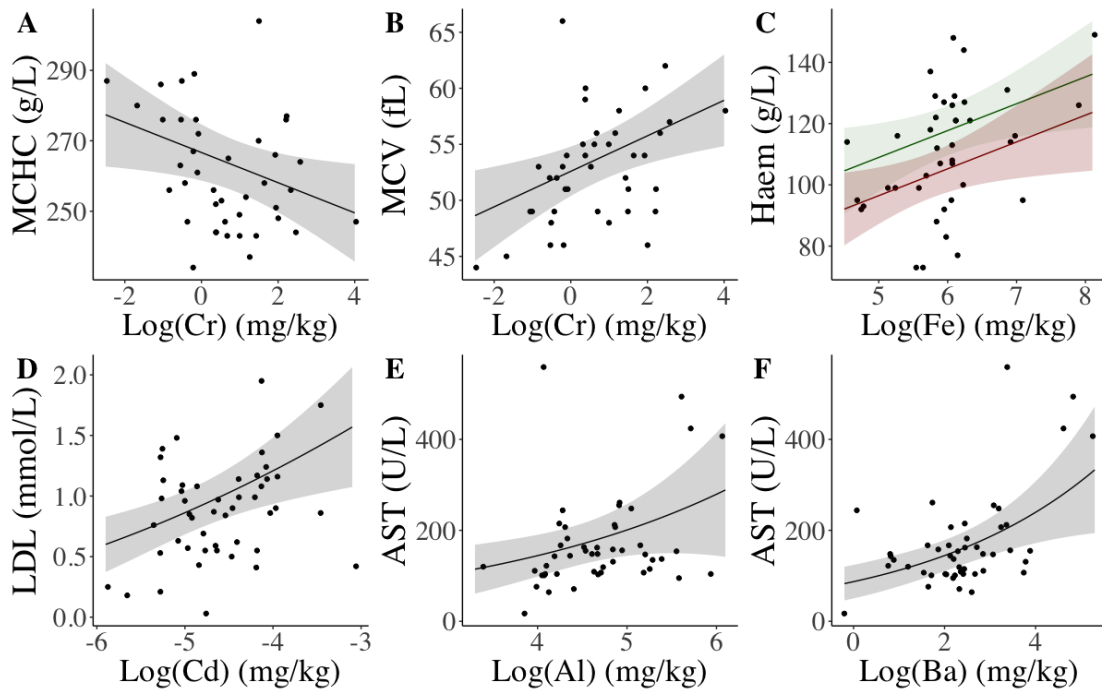


Fig. 3. Selected statistically significant relationships between transformed hair metal concentrations and blood parameters collected from wild Malay civets; shaded regions denote model confidence intervals (CI). Plots display the data and the predicted relationship accounting for the effects of civet sex and age; the fitted model and 95% CIs display the modelled trend for adult males. *Plot C) demonstrates the co-significant influence of civet sex on haemoglobin, whereby green denotes the trend in adult males and red in adult females. MCHC= mean corpuscular haemoglobin concentration; MCV= mean corpuscular volume; Haem= haemoglobin; LDL= low-density lipoprotein; AST= aspartate aminotransferase.

4. Discussion

Although agriculture is a known pollution source, there have been few critical assessments of the impacts of contamination from the oil palm plantation industry on native faunal communities. Our study presents novel ecotoxicological insights into inorganic pollution within a mosaic system of remnant forests and large-scale oil

palm agriculture. We non-lethally quantified levels of essential and non-essential metals in a wild indicator species, and, for the first time, detail possible sub-lethal effects of metal pollution on this species. By robustly assessing the biological and spatial drivers of intrapopulation variation of hair metal concentrations, we established evidence of possible water-facilitated exposure to select metals. Our targeted assessment of metals in GPS-collared animals suggests utilisation of oil palm agriculture elevates civet exposure to Al, Cd, and Pb, and implicate plantations as a likely source of contamination. The integration of hair and blood sampling provides insights into the sub-lethal physiological costs of persistence paid by adaptable mesocarnivores within plantation landscapes, and a brief exploration of potential causes.

The hair metal profiles of this generalist species are the first reported, and serve as basal reference values for civets within agriculturally fragmented lowland ecosystems. Overall, population-level hair metal concentrations were largely comparable to values reported in other carnivore species (Table S1), with the caveat that studies assessing metals such as Al, As, Ba, and Co are limited. Individual variations of essential metals within the sampled civet population likely reflect natural differences in dietary intake and species-specific toxicokinetic regulatory baselines (Kempson and Lombi, 2011; McMeans et al., 2007). Our detection of elevated non-essential metals in some civets indicates modulated exposure is occurring within the population, with variation at the scale of the individual animal. The majority of measured hair As concentrations were below the threshold reportedly leading to adverse health effects in humans (1 mg kg^{-1} ; Hindmarsh, 2002); however, one individual exceeded this concentration, while hair from another approached this limit.

Similarly, the average Hg concentration in civet hair was below the concentration reported to alter neurochemistry in polar bears (*Ursus maritimus*, 5.4 mg kg⁻¹; Basu et al., 2009) yet samples from three individuals exceeded this limit. Indeed, 85.6% (n=59) of civet samples exceeded the recommended hair concentration of 1mg kg⁻¹ for healthy humans (US EPA; FAO/WHO, 2003). Given the broad range of elemental hair concentrations reported not only between but within species (Table S1), it is crucial to establish regional baselines and address causes for variation within populations.

4.1 Drivers of intrapopulation variation

Of the 13 metals recorded, only hair concentrations of Hg, As, and Ni significantly related with the traits of the sampled individual. Higher Hg concentrations in mature compared to immature civets is consistent with trends documented across an array of species (e.g. Eurasian otters *Lutra lutra* Brand et al., 2020; pine snakes *Pituophis melanoleucus* Burger et al., 2017; brown bears *Ursus arctos* Lazarus et al., 2018). In contrast, our finding of elevated As in mature civets relative to immature animals is unexpected, as the inverse relationship has been documented in humans (Ballesteros et al., 2017) and ground squirrels (*Otospermaophilus beecheyi*; Hubbart, 2012). Ecologically, these age-mediated patterns could be explained by two processes: 1) specific exposure pathways to these metals vary with civet age (e.g. differences in dietary selection with animal age); or 2) cumulative lifetime exposure to these elements (e.g. Bauerová et al., 2020). Furthermore, civet weight, which was used in models as a continuous proxy term accounting for variable body conditions within civet age categories, showed a clearly negative relationship with hair As and Ni concentrations. Our finding is in agreement with laboratory experiments reporting

significant reductions in the body mass of test subjects following exposure to As and Ni (ASTDR, 2005; ASTDR, 2007). Interestingly, none of the assessed hair metal concentrations significantly varied between males and females, in contrast to other carnivore species (reviewed by Burger, 2007; Iberian wolves *Canis lupus* Hernández-Moreno et al., 2013). This likely reflects a lack of sexually dimorphic behaviours such as forage selection, or a consistent use of metal sources by both sexes.

In addition to these biological influences, concentrations of hair As, Ba, Cd, Cr, Fe, and Hg varied with civet capture location. Animals captured closer to tributaries contained significant and predictably higher hair Ba, Cd, Cr, and Fe concentrations, suggesting tributaries as sources of these metals. Hair Cr levels were further elevated by the presence of an oxbow lake close to civet capture locations. Civet exposure could be from direct use of tributaries as drinking water, or through the ingestion of food items associated with riparian habitats. The tributaries in the floodplain may be polluted with untreated POME, which can contain excessive concentrations of these metals (Ohimain et al., 2012). Research by Jamal et al. (2007) determined raw Malaysian POME contained Cr and Cd levels 120 and 170 times greater, respectively, than the maximum contaminant levels for drinking water set by the US EPA (EPA, 2019). Alternatively, or perhaps concurrently, these metals may be applied to oil palm plantations and distally transported into tributaries via surface runoff; Cd, Cr, and Fe are common contaminants in mineral fertilisers (Atafar et al., 2010), while barium carbonate is the active agent in some rodenticides (Kravchenko et al., 2014). The interpretation of the positive relationships between hair As and Hg concentrations and distance between civet capture location and accessible tributary is not readily apparent, but suggests exposure to these metals via contaminated water is unlikely.

Intriguingly, none of the assessed metal concentrations varied significantly with civet proximity to the edge of an oil palm plantation. The location of a capture site relative to the nearest plantation may not directly equate to the probability of a sampled civet utilising the agriculture. Indeed, all civets were sampled within three km from a plantation edge; this is within the average distance male civets travel within a night (Evans, 2019). Key to refining this relationship was our targeted exploration of metal levels in individuals with fully characterised movement patterns.

4.2 Case study: metal profiles of male civets fitted with GPS collars

Hair of GPS-collared civets that utilised oil palm plantations contained higher levels of Cd, Al, and Pb than hair of civets that exclusively remained within the forest, suggesting use of plantations facilitates civet exposure to these metals. Cd, Al, and Pb have previously been identified as environmental pollutants from excessive fertiliser application in agricultural regions, including oil palm plantations (Atafar et al., 2010; Mattsson et al., 2000; Sakai et al., 2017). Additionally, these metals are frequently found in high concentrations in common agrochemicals, such as the herbicide glyphosate, which is applied in oil palm plantations (Defarge et al., 2018). Civets may thus be exposed through direct contact with fertiliser pellets, ingestion of contaminated soils or water from irrigation ditches, or consumption of polluted oil palm fruit, invertebrates, or small mammals.

In contrast, hair Hg concentrations were greater in the forest animals than in those accessing both oil palm and forest. As suggested by Evans et al. (2020), civets living in close association with oil palm may have lower protein diets than those animals

remaining within the forests. Methyl-Hg is bioaccumulated and biomagnified across trophic levels, and thus a more carnivorous diet could result in a higher intake and accumulation of Hg. Such dietary differences determining Hg concentrations have been recorded in birds (American species Cristol et al., 2008; Bicknell's thrush *Catharus bicknelli* Rimmer et al., 2010), grizzly bears (Noël et al., 2014), and Arctic foxes (*Vulpes lagopus* Bocharova et al., 2013). Alternatively, little is known regarding regional mercury biocycling processes within Southeast Asian rainforests (Wang et al., 2016). Research in the Neotropical (Fostier et al., 2000) and boreal forests (St. Louis et al., 2001) report high atmospheric deposition of mercury within these biomes. It is possible these results provide indications of similar processes occurring within even degraded Old World forests.

4.3 Potential physiological effects of varied hair metal levels

Our study provides rigorous evidence of 13 associations between hair metal concentrations and physiological parameters of wild civets sampled across a degraded landscape, and contribute to a growing body of literature cataloguing the implications of metal pollution on biodiversity (Bauerová et al., 2017; Demir and Yavuz, 2020; Ortiz-Santaliestra et al., 2013; Villa et al., 2017). While all 13 associations provide a critical basis for future research aiming to identify the causal relations, we will focus our discussion on six examples.

In terms of haematology parameters, the positive relationship between civet haemoglobin and hair Fe was expected. Iron is essential to the formation of haemoglobin through its incorporation into heme (Harvey, 2008), which is elevated in male compared to female Malay civets (Evans et al., 2020). Positive correlations

between hair and serum Fe values have been previously established in other species, and direct haemoglobin measurements similarly correlated with both values (Shah et al., 2011). Thus, we interpret the detection of this relationship as reinforcement of the analytical rigor of our exploratory approach.

The associations between elevated hair Cr and red blood cell indices (reduced MCHC and elevated MCV) suggest exposure may drive regenerative anaemia within the civet population. Mechanistically, this type of anaemia occurs when erythrocytes are either lost or destroyed at an elevated rate, which in turn triggers the compensatory release of immature red blood cells (reticulocytes) from the bone marrow (Johnstone et al., 2011). There is molecular evidence that exposure to hexavalent Cr can trigger eryptosis (premature red blood cell death, Ray, 2016; Zhang et al., 2014), which may explain this comparatively regenerative pattern within civets with elevated hair Cr levels. Indeed, similar haematological profiles have been reported in fish and bird species exposed to Cr (Bauerová et al., 2017; Vutukuru, 2005).

In terms of serum biochemistry, we observed a positive relationship between Cd and LDL cholesterol levels. Assessments of the lipid profiles of laboratory animals and human case studies demonstrate Cd exposure interferes with lipid metabolism pathways, with possibly dangerous cardiovascular consequences (Zhou et al., 2016). Alternatively, Cd exposure may be related to civet dietary habits. There is evidence that Malay civets modulate dietary selection relative to the proximity of oil palm plantations (Evans et al., 2020). Therefore, possible sources of Cd may be linked to ingestion of high LDL levels (e.g. influences of a species' dietary breadth on Hg exposure, as described in Bocharova et al., 2013; McGrew et al., 2014).

The positive correlations between hair Al and Ba concentrations and AST activity suggest exposure to these metals may result in liver damage (Kerr, 2002). Elevation of serum AST activity has been reported following exposure to many heavy metals (e.g. Adham et al., 2011; Jayawardena et al., 2017); experimental Al exposure increased AST activity in laboratory rats (Geyikoglu et al., 2012). There is less available research on effects of Ba on liver functionality (Kravchenko et al., 2014; however, see elevated AST in rats following administration of two forms of barium salts by Mohammed and Ishmail, 2017). Given the relatively few comparative Al and Ba values within published hair research (Table S1), our results indicate further research into the status of these metals within the Kinabatangan system is warranted.

4.4 Limitations and future research

Our hair-based assessment methodologies intrinsically underestimate rates of acutely lethal metal exposures within the population, and future research will be necessary to scale up the individual-level implications of exposure to core population-level processes such as reproductive success. In addition, our multi-faceted research has identified future targets and physiological relationships that warrant closer investigation, specifically as data on toxicokinetics and toxicodynamics are difficult to obtain when studying wildlife species. Furthermore, environmental source tracking is recommended to provide a more complete and mechanistic narrative cataloguing the threats faced by adaptive wildlife (e.g. Nacci et al., 2005), particularly when the possible additive effects of concurrent stressors such as disease or additional pollutants like anticoagulant rodenticides are likely across this landscape.

5. Conclusion

Our integrative approach sets an important precedent in the evaluation of cryptic threats faced by species persisting within the degraded habitats associated with oil palm agriculture. We demonstrate that our use of Malay civets as an indicator species provides evidence-based justification for more extensive studies quantifying inorganic pollution within landscapes fragmented by oil palm plantations even though exact metal sources cannot be directly determined from hair metal profiles. Our study complements reports of suspected fatal poisonings of the endangered Bornean elephant (*Elephas maximus borneensis*) across Sabah (e.g. Milwil, 2020; Vanar, 2019), and provides both a tractable approach and substantive data that will be critical in informing efficient pollution mitigation and enforcement strategies for the region. To effectively investigate sources and distribution of metals, we strongly recommend local authorities establish real-time monitoring programs co-evaluating water quality and agricultural practices across the floodplain to address rigorously the ecotoxicological consequences of the oil palm industry. In the meantime, the adoption of precautionary alternative actions such as the application of organic fertilizers (Tohiruddin and Foster, 2013), integrated pest management schemes (Wood, 2002), and establishing more stringent POME regulations into policy would benefit not just wildlife, but also human communities living within and alongside this industry.

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