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Amorós, M., Gil-Sánchez, J., López-Pastor, B. N. and Moleón, M. 2020. Hyaenas and lions: how the largest African carnivores interact at carcasses. – Oikos doi: 10.1111/oik.06846

Supplementary material

Appendix 1.

This material includes:

Appendix A1. Overview of methods for estimating carrion biomass consumption from camera-trap data.

There are different methods to estimate carrion biomass consumed by each scavenger species from camera-trap data. Next, we enumerate and describe three of them.

1. Moleón, M. et al. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. - Oikos 124: 1391-1403

"we estimated […] 'carcass consumption rate' (carrion biomass consumed by scavengers divided by carcass consumption time), and 'percentage of carrion consumed' (percentage of the carcass, excluding the stomach content, consumed by the scavengers). The stomach content was estimated as 5% and 10% of the total carcass weight for chickens and ungulates (Selva 2004), respectively. Non-consumed parts were estimated visually from the camera pictures and inspections of the carcass sites at the moment of the camera inactivation as a proportion. We calculated the biomass consumed by each scavenger group using the carcass weight without the stomach content and nonconsumed parts, the information provided by the pictures, the maximum food intake of each scavenger species (Estes 1992, Donázar 1993) and the minimum number of different individuals of each species at the carcass. Initial carcass weight was 2 kg for chickens. For ungulates the body mass was obtained from the literature taking into account sex and age."

2. Inger, R. et al. 2016. Ecological role of vertebrate scavengers in urban ecosystems in the UK. - Ecol. Evol. 6: 7015-7023

"For each carcass, the total biomass lost during the course of the experiment was first adjusted to take into account loss due to causes other than vertebrate scavenger activity, based on mass loss data from the controls and carcasses where no scavenger behavior was recorded. The remaining mass loss was then attributed to each scavenging species assuming that (1) biomass removed was proportional to time spent feeding; and (2) biomass removed was proportional to body mass of the scavenger. Avian mean body masses were obtained from the British Trust for Ornithology (2015a,b), and mammalian body masses from Sillero-Zubiri, Hoffman, and MacDonald (2004)."

3. Mateo-Tomás, P. et al. 2017. Both rare and common species support ecosystem services in scavenger communities. - Global Ecol. Biogeogr. 26: 1459-1470

"we estimated the carrion consumed by each vertebrate species scavenging at a carcass as:

$$Carrion\ consumed_i = \sum_{j-1}^{days} n_{ij} * DFI_i$$

where n_{ij} is the abundance of species i recorded scavenging at a carcass on day j. This value was multiplied by the daily food intake of the species i (i.e., DFI_i) as resulting from the following equation (Crocker, Hart, Gurney, & McCoy, 2002):

$$Daily\ Food\ Intake\ (DFI) = \frac{Daily\ energy\ expenditure\ (kJ)}{Food\ energy\ \left(\frac{kJ}{g}\right) * (1 - moisture) * Assimilation\ efficiency}$$

[…] We assumed that each individual scavenger arriving at a carcass consumed the daily food intake for that species."

All methods have their own assumptions and are subject to different potential sources of error. However, all of them can provide reasonable estimates depending on the particular context of the study. For example, the method used by Mateo-Tomás et al. (2017) is especially appropriate when scavenger individual identification is prevented. In our study, where lions and hyaenas were frequently identified at the individual level according to comparisons of age, sex, coat patterns and other individual marks, we adopted the approach by Moleón et al. (2015). More precise estimates would require weighing carcasses once each scavenger species has visited and left the carcass. However, this is not possible when several scavenger species are simultaneously feeding at carcasses. Moreover, continuous presence of humans at carcass sites could modify the behavior of scavengers. In addition, this practice is dangerous when the scavenger community includes large predators such as lions and hyaenas.

Table A1. List of GLM analyses conducted to explain the scavenging patterns of lions and spotted hyaenas at medium and large carcasses in HiP. Rows: response variables; columns: explanatory variables. Explanatory variables included in the models are marked in grey.

					lion			hyaena			vulture			other		
		Size	Season	Section	Presence	Prior presence	Posterior presence	Presence	Prior presence	Posterior presence	Presence	Prior presence	Posterior presence	Presence	Prior presence	Posterior presence
Co-occurrence	Co-occurrence	■	■	■								■			■	
Lion	Presence of lion	■	■	■				■			■			■		
	Abundance of lion	■	■	■				■			■			■		
	Carcass detection time	■	■	■					■			■			■	
	Carrion consumed	■	■	■					■	■		■	■		■	■
	% of carrion consumed	■	■	■					■	■		■	■		■	■
	Total time around carcass	■	■	■					■	■		■	■		■	■
	Time at carcass	■	■	■					■	■		■	■		■	■
	Carcass feeding time	■	■	■					■	■		■	■		■	■
	Carcass consumption rate	■	■	■					■	■		■	■		■	■
Hyaena	Presence of hyaena	■	■	■	■						■			■		
	Abundance of hyaena	■	■	■	■						■			■		
	Carcass detection time	■	■	■		■						■			■	
	Carrion consumed	■	■	■		■	■					■	■		■	■
	% of carrion consumed	■	■	■		■	■					■	■		■	■
	Total time around carcass	■	■	■		■	■					■	■		■	■
	Time at carcass	■	■	■		■	■					■	■		■	■
	Carcass feeding time	■	■	■		■	■					■	■		■	■
	Carcass consumption rate	■	■	■		■	■					■	■		■	■

Table A2. Factors explaining the scavenging patterns of lions and spotted hyaenas at medium and large carcasses in HiP. AICc-based model selection to assess the effect of carcass "size" (medium and large), "season" (wet and dry), "section" of the study area (Hluhluwe and iMfolozi), presence of lion ("lion"), hyaena ("hyaena"), vulture ("vulture") and other scavenger ("other") at the carcass (yes, no), prior presence of lion ("prior_lion"), hyaena ("prior_hyaena"), vulture ("prior_vulture") and other scavenger ("prior_other") at the carcass (yes, no), and posterior presence of lion ("posterior_lion"), hyaena ("posterior_hyaena"), vulture ("posterior_vulture") and other scavenger ("posterior_other") at the carcass (yes, no) on the scavenging patterns of lions and hyaenas (co-occurrence of both species, presence, abundance, carcass detection time, carrion biomass consumed, % of carrion biomass consumed, total time around carcass, time at carcass, carcass feeding time, and carcass consumption rate of lions/hyaenas) in HiP. AICc values, AICc differences (ΔAICc) with the highest ranked model (i.e., the one with the lowest AICc), and the percentage of the variability of the response variables explained by the models (deviance, D_2) are shown. Only selected models, i.e., models with ΔAICc<2, are shown.

Species	Response variable	Model	AICc	ΔAICc	D_2
Both	Co-occurrence	size	25.386	0	10.88
		prior_vulture	26.220	0.834	7.26
		season	27.096	1.710	3.46
Lion	Presence	hyaena	26.981	0	10.31
		size	28.334	1.353	4.84
		vulture	28.334	1.353	4.84
		other	28.334	1.353	4.84
	Abundance	hyaena	76.663	0	13.24
	Carcass detection time	prior_vulture	80.567	0	37.34
	Carrion consumed	prior_vulture	134.790	0	34.21
		size	135.206	0.416	31.10
		posterior_vulture	136.469	1.679	20.73
		prior_other	136.710	1.920	18.58
		season	136.738	1.948	18.32
	% of carrion consumed	prior_hyaena	90.677	0	58.21
		prior_other	92.072	1.395	51.20
	Total time around carcass	size	102.072	0	42.49
	Time at carcass	prior_vulture	141.281	0	30.41
		size	141.642	0.361	25.84
		season	141.853	0.572	27.56
		posterior_vulture	142.500	1.219	20.32
		prior_other	142.590	1.309	19.51
		posterior_other	143.113	1.832	14.70
	Carcass feeding time	season	123.381	0	39.62
		posterior_vulture	123.508	0.127	38.76
	Carcass consumption rate	prior_other	12.951	0	31.81
		size	13.487	0.536	38.87
		posterior_other	14.479	1.528	10.49
		section	14.928	1.977	8.00
Hyaena	Presence	lion	14.392	0	22.58
		size	15.288	0.896	15.30
	Abundance	size	57.914	0	36.62
		other	58.081	0.167	35.84
	Carcass detection time	prior_lion	129.665	0	21.76
	Carrion consumed	size	213.735	0	40.39
	% of carrion consumed	posterior_lion	150.731	0	28.49
	Total time around carcass	size	152.469	0	50.54

Time at carcass	size	227.996	0	26.33
	posterior_other	228.819	0.823	22.17
Carcass feeding time	size	212.327	0	26.48
	posterior_other	213.113	0.786	22.53
Carcass consumption rate	posterior_vulture	23.332	0	21.50
	prior_other	24.234	0.902	13.23
	posterior_other	24.513	1.181	4.55
	prior_vulture	24.942	1.610	16.34

Table A3. Selected Generalized Linear Models (GLMs) explaining the presence of lions, hyaenas and both species (co-occurrence) at carcasses, as well as abundance and scavenging patterns of lions and spotted hyaenas at medium and large carcasses in HiP. The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degrees of freedom of the models (df) are shown. Only the models with highest D^2 are shown. See Table A2 for explanatory variables abbreviations.

Species	Response variable	Model	Parameter	Estimate	SE	df
Both	Co-occurrence	size	Intercept	0.69	0.87	16
			size(medium)	-1.67	1.10	
		prior_vulture	Intercept	0.22	0.67	16
			prior_vulture(yes)	-1.32	1.06	
		season	Intercept	-0.92	0.84	16
			season(wet)	0.92	1.05	
Lion	Presence	hyaena	Intercept	17.57	2797.44	17
			hyaena(yes)	-17.57	2797.44	
		size	Intercept	0.92	0.84	17
			size(medium)	-1.10	1.03	
		vulture	Intercept	0.92	0.84	17
			vulture(yes)	-1.10	1.03	
		other	Intercept	0.92	0.84	17
			other(yes)	-1.10	1.03	
	Abundance	hyaena	Intercept	1.50	0.33	17
			hyaena(yes)	-1.10	0.39	
	Carcass detection time	prior_vulture	Intercept	26.57	5.00	8
			prior_vulture(yes)	21.67	10.61	
	Carrion consumed	prior_vulture	Intercept	113.80	101.70	8
			prior_vulture(yes)	411.70	215.80	
		size	Intercept	387.80	137.70	8
			size(medium)	-328.40	184.70	
		posterior_vulture	Intercept	56.38	147.70	8
			posterior_vulture(yes)	268.08	198.16	
		prior_other	Intercept	116.10	122.20	8
			prior_other(yes)	267.50	211.70	
		season	Intercept	382.40	173.10	8
			season(wet)	-265.70	212.00	
	% of carrion consumed	prior_hyaena	Intercept	95.25	13.40	8
			prior_hyaena(yes)	-51.23	16.41	
		prior_other	Intercept	77.11	10.24	8
			prior_other(yes)	-48.04	17.73	
	Total time around carcass	size	Intercept	88.89	21.85	8
			size(medium)	-66.67	29.32	
	Time at carcass	prior_vulture	Intercept	188.90	145.90	8
			prior_vulture(yes)	541.10	309.40	
		size	Intercept	541.00	199.20	8
			size(medium)	-417.40	267.20	
		season	Intercept	612.00	227.30	8
			season(wet)	-454.30	278.40	
		posterior_vulture	Intercept	103.50	206.50	8
			posterior_vulture(yes)	370.10	277.00	
		prior_other	Intercept	181.70	169.40	8
			prior_other(yes)	382.30	293.50	

		posterior_other	Intercept	169.20	191.10	8
			posterior_other(yes)	314.80	286.60	
	Carcass feeding time	season	Intercept	300.00	82.43	8
			season(wet)	-216.33	100.95	
		posterior_vulture	Intercept	43.00	71.89	8
			posterior_vulture(yes)	203.00	96.45	
	Carcass consumption rate	prior_other	Intercept	1.29	0.99	8
			prior_other(yes)	-1.44	1.52	
		size	Intercept	-0.03	1.00	8
			size(medium)	1.57	1.54	
		posterior_other	Intercept	1.12	1.04	8
			posterior_other(yes)	-0.79	1.45	
		section	Intercept	1.15	1.17	8
			section(iMfolozi)	-0.70	1.49	
Hyaena	Presence	lion	Intercept	19.57	3802.12	16
			lion(yes)	-18.31	3802.12	
		size	Intercept	19.57	4390.31	16
			size(medium)	-18.06	4390.31	
	Abundance	size	Intercept	1.25	0.22	16
			size(medium)	-0.94	0.34	
		other	Intercept	<0.01	0.38	16
			other(yes)	1.07	0.42	
	Carcass detection time	lion	Intercept	22.70	3.99	14
			lion(yes)	29.35	15.43	
	Carrion consumed	size	Intercept	414.20	100.30	14
			size(medium)	-384.40	129.50	
	% of carrion consumed	posterior_lion	Intercept	68.89	10.64	14
			posterior_lion(yes)	-35.44	15.57	
	Total time around carcass	size	Intercept	115.11	13.02	14
			size(medium)	-61.26	16.81	
	Time at carcass	size	Intercept	513.30	161.40	14
			size(medium)	-449.10	208.40	
		posterior_other	Intercept	55.00	143.70	14
			posterior_other(yes)	404.70	210.30	
	Carcass feeding time	size	Intercept	299.00	95.73	14
			size(medium)	-267.44	123.59	
		posterior_other	Intercept	25.50	85.11	14
			posterior_other(yes)	242.21	124.59	
	Carcass consumption rate	posterior_vulture	Intercept	-0.93	0.78	14
			posterior_vulture(yes)	1.08	1.09	
		prior_other	Intercept	-0.11	0.63	14
			prior_other(yes)	-0.92	1.20	
		posterior_other	Intercept	-0.63	0.74	14
			posterior_other(yes)	0.49	1.06	
		prior_vulture	Intercept	-0.13	0.60	14
			prior_vulture(yes)	-1.12	1.34	

Figure A1. Lions and spotted hyaenas feeding on elephant carcasses in Hluhluwe-iMfolozi Park (HiP), South Africa. Provided that carcasses are large enough, lions and hyaenas can co-occur at the same carcass, either at different times (panels A and B, respectively) or, less often, simultaneously (panel C). Pictures were obtained by means of camera-traps during this study.

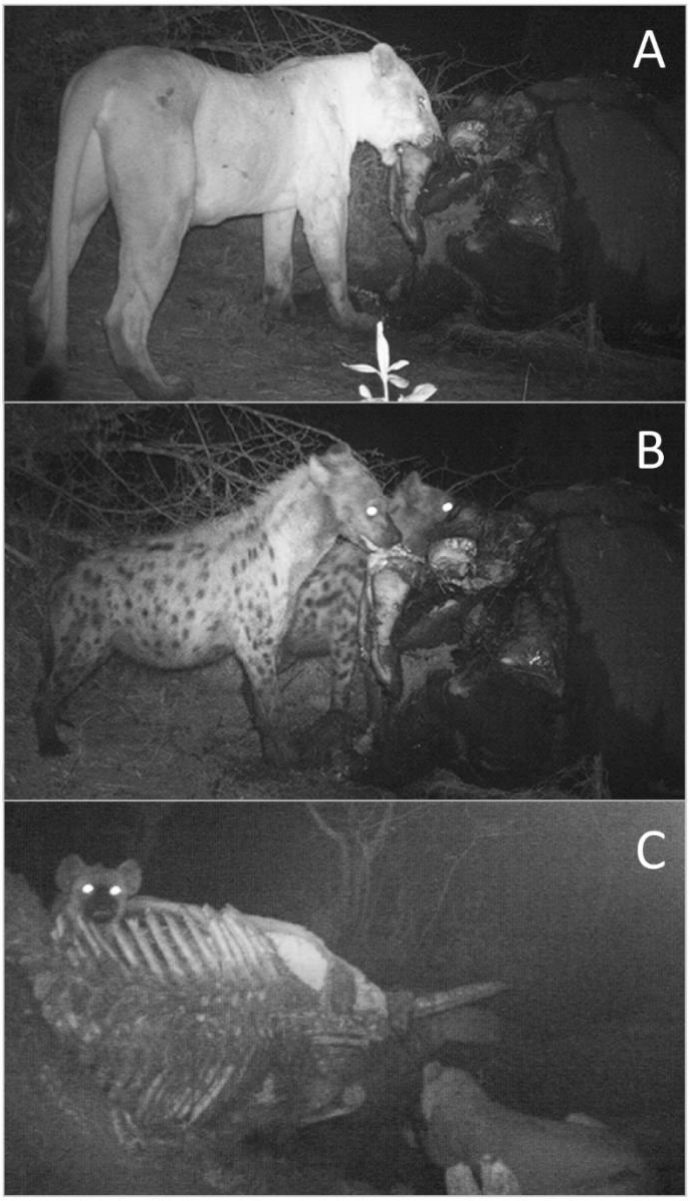

Figure A2. Spatial distribution of (A) small and (B) medium/large carcasses in HiP. Circle size is proportional to carcass size. Blue: presence of lion at the carcass; orange: presence of spotted hyaena at the carcass; white: absence of both species at the carcass.

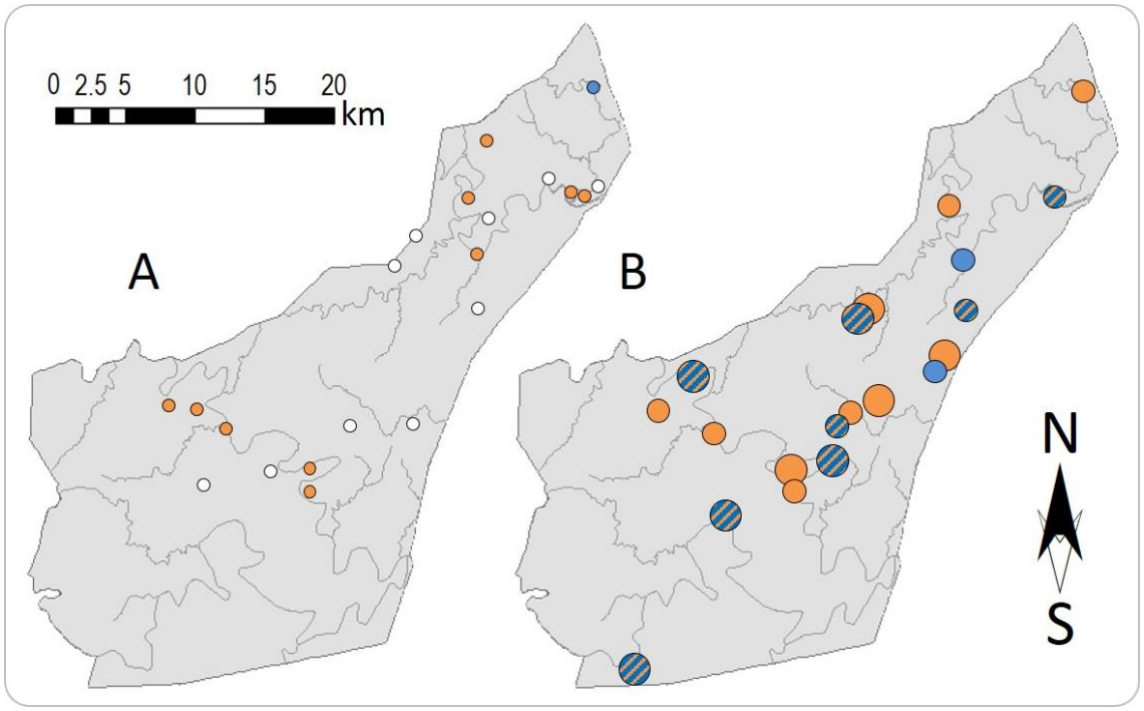

Figure A3. Examples of inter-specific relationships observed from the detailed analysis of the images captured by camera traps. (A) Sequence of consecutive photos showing pseudo-kleptoparasitism by lion (ref. C-038 in Table 3). (B) Sequence of consecutive of photos showing a possible aggressive behavior of hyaenas towards lionesses (ref. C-011 in Table 3). Hyaenas approach lionesses, and then suddenly charge. Pictures were obtained by means of camera-traps during this study.

A

B

Figure A4. Temporal segregation between lions and spotted hyaenas at the within carcass scale. Each cell represents one picture, and all cells are consecutively ordered according to pictures sequence. Blue cell: lion presence in the picture; orange cell: hyaena presence in the picture; black cell: lion and hyaena presence in the picture; white cell: absence of lion and hyaena in the picture. Carcass size is shown on the left side, and time of complete carcass consumption is indicated at the end of each picture series (in parenthesis when it is approximate).

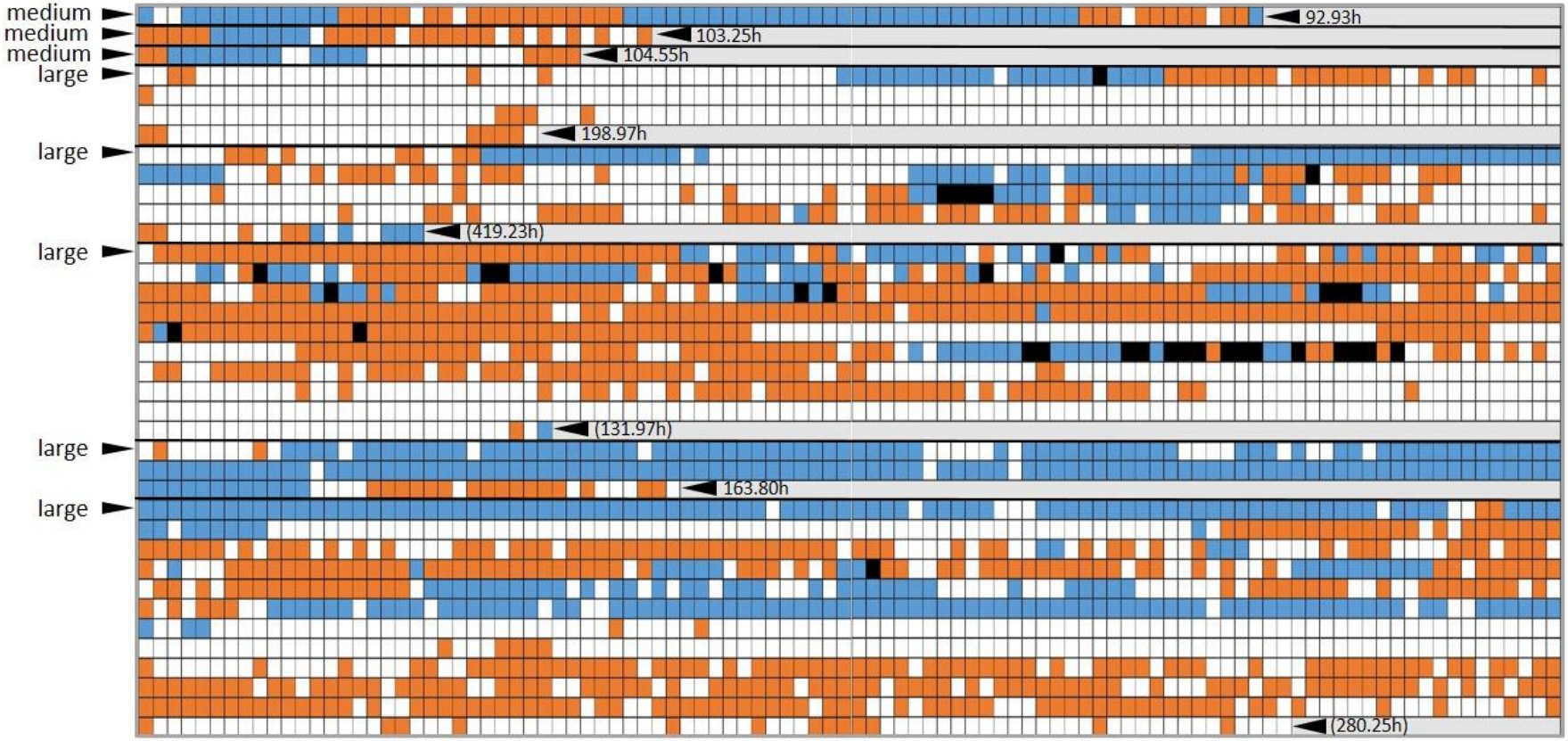

Figure A5. Correlation between carrion consumed by and carcass feeding time of lions and hyaenas at medium and large carcasses.