Quantifying the behavioural consequences of shark ecotourism

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Abstract

Shark populations globally are facing catastrophic declines. Ecotourism has been posited as a potential solution to many of the issues facing shark conservation, yet increasingly studies suggest that such activity may negatively influence aspects of shark ecology and so further pressure declining populations. Here we combine UAV videography with deep learning algorithms, multivariate statistics and hidden Markov models (HMM) to quantitatively investigate the behavioural consequences of ecotourism in the whale shark (*Rhincodon typus*). We find that ecotourism increases the probability of sharks being in a disturbed behavioural state, likely increasing energetic expenditure and potentially leading to downstream ecological effects. These results are only recovered when fitting models that account for individual variation in behavioural responses and past behavioural history. Our results demonstrate that behavioural responses to ecotourism are context dependent, as the initial behavioural state is important in determining responses to human activity. We also suggest that the responsiveness of *R. typus* to human activity hints at a previously neglected resilience to environmental change. Finally, we argue that complex models incorporating individuality and context-dependence should, wherever possible, be incorporated into future studies investigating the ecological impacts of shark ecotourism, which are only likely to increase in importance given the expansion of the industry and the dire conservation status of many shark species.

Introduction

Sharks belong to the clade *Chondrichthyes*, the earliest diverging (~ 450Ma) radiation of crown group gnathostomes to persist in modern ecosystems[1]. Whilst sharks are of intrinsic interest due to their persistence through evolutionary time, they are also critically important components of marine ecosystems and are thought to be among the most functionally diverse vertebrate clades[2]. Amongst the ecological functions performed by sharks is the distribution of predation pressure through space and time[3] and (in the case of migratory species) facilitation of energy transfer between ecosystems[2, 4]. There is mounting evidence that declines in shark populations can result in phenomena such as mesopredator release and trophic cascades[5]. Despite their ecological importance, sharks are amongst the most threatened of all vertebrates, with recent IUCN (International Union for the Conservation of Nature) estimates suggesting that more than one third of all shark and ray taxa are facing extinction[6]. Overfishing is undoubtedly the major driver of this crisis, to which sharks are particularly vulnerable due to life history traits including relatively slow maturation and low fecundity[7]. This is not the only driver of decline, with anthropogenic climate change and habitat destruction also thought to be relevant in some populations[8, 9]. Uncertainty regarding the ecological importance of sharks, the scale of the threats posed by overfishing and a general lack of public awareness have, until recently, provided major barriers to the implementation of conservation action[6, 10, 11]. Gradually these barriers are being lifted, with public perception increasingly favouring the protection of sharks[11].

Shark ecotourism, in which members of the public pay to experience interactions with wild sharks, is credited with portraying sharks in a more positive light amongst members of the public [12, 13]. Shark ecotourism is also of ever-increasing economic importance in a number of countries, thought to be valued at over 300,000,000 USD annually and responsible for the creation of thousands of jobs[14, 15]. These socioeconomic factors undoubtedly increase potential for the protection and recovery of declining shark populations; however, ecotourism also has potential ecological impacts[16], the true nature of which remain poorly understood. There is some evidence that ecotourism activities involving provisioning can influence both relative abundance and species composition[17], and even directly trigger mesopredator release – increasing the abundance of other species at lower trophic levels[18]. Whilst trophic cascades are typically considered from the perspective of depredation, this is not strictly a requirement[19], and thus it is possible that the feeding of sharks at ecotourism sites could result in functionally similar shifts in community ecology. Not all studies have recovered evidence for ecological impacts of ecotourism[20, 21], and potential effects are likely to be highly context dependent[16]. Even where provisioning is absent, disturbance and boat-related injuries remain substantial threats[16, 22]. For these reasons, further studies are urgently warranted to establish the extent to which this expanding industry may have unforeseen ecological consequences on the populations it is aiming to conserve.

Whilst there are multiple potential routes by which shark ecotourism could influence their ecology, potentially the most important is through behavioural responses. Behaviour is the suite of traits by which inter-specific interactions are directly mediated[23] and is thus a highly significant factor influencing downstream ecological consequences of anthropogenic interference. Even if such effects were limited to the focal taxon of ecotourism activities alone, disturbance and alterations to the landscape of fear have many potential consequences for bioenergetics, which in turn can have disastrous consequences for migration, reproduction, and other life-history traits[24, 25]. Emerging studies are increasingly suggesting that behavioural plasticity may play a key role in dictating population-level resilience in the face of environmental change[26, 27]. Several studies have attempted to address the effects of ecotourism on shark

behaviour, reporting evidence of ecotourism influencing foraging activity, long-distance migratory behaviour and avoidance/disturbance responses[16–31]. Despite this, different studies present conflicting results, the interpretation of which is complicated by a lack of standardisation in the behavioural assays considered between studies. The temporal resolution of such studies also provides several limitations: some studies rely on telemetry data which, whilst informative regarding some aspects of the ecology[32], do not consider effects of ecotourism at fine temporal resolutions. Those that do typically consider behaviour to fall into one of a small number of qualitatively defined categories[31], the biological significance of which are debatable. As such categories do not have rigorous quantitative definitions, they are unlikely to be an accurate representation of the full repertoire of behavioural observed in most taxa. For these reasons, studies utilising a more biologically reasoned and quantitative approach, and considering behaviour at finer temporal resolutions are essential if we are to fully understand how ecotourism activities may influence the behaviour (and subsequently the ecology and evolution) of sharks.

In this study we combine Unoccupied Aerial Vehicle (UAV) videography with deep learning algorithms, multivariate statistics and Hidden Markov Models (HMM) to investigate the ecological consequences of interactions between sharks and humans for shark behaviour, using whale sharks (*Rhincodon typus*) as a case study. This approach considers behavioural consequences of ecotourism for sharks at a finer temporal resolution than any previous study and uses explicit and rigorous quantitative definitions of behaviour. This increases potential for direct comparison between studies, aiding in ease of interpretation and considering the full range of movements observed during individual behavioural sequences. We comment on the implications of these results for ecotourism practices, for the ecology of the *R. typus* and the wider community.

Methodology

The goal of this study was to amass aerial footage of *R. typus* both in isolation and in the presence of humans, quantify shark movement within the footage using neural networks, and establish the extent to which human activity influences the behaviour of *R. typus*.

Ethics statement

Data collection and analysis procedures in this study complied with national animal welfare laws and ARRIVE guidelines and regulations; all data collection procedures were authorized by Mexican wildlife authorities under the permit SPARN/DGVS/04909/22 provided by the Comisión Nacional de Acuacultura y Pesca (CONAPESCA). This permit, issued by CONAPESCA is necessary and sufficient for all procedures conducted during this study (including the involvement of human and animal participants), and negates the requirement for IRB ethics approval, which is not required by Mexican law for such studies in Mexican territory.

Data collection

Aerial videos of whale sharks and their interactions with ecotourism activities were obtained using a DJI Phantom 3SE UAV (flown at a constant altitude of 15m), between the 30th of November 2022 and 6th of February 2023 in the whale shark refuge area in the Bay of La Paz, Mexico (Fig. 1a). This large, shallow bay hosts seasonal aggregations for juvenile whale sharks, which have become the focus of local ecotourism activities[33]. After filming sharks in isolation, a swimmer entered the water and mimicked typical ecotourist behaviour, swimming parallel to the shark with a minimum distance of two metres between them and the shark at all times. Aerial videos were gathered both of sharks in isolation and interacting with swimmers. In total, 39 videos were obtained, with video clips (following trimming) ranging from 167 to 1121 frames (5.6 to 37.4 seconds) in duration.

Video analyses

Aerial footage was analysed using the Python-based[35] deep learning system SLEAP[36], outputting coordinate data indicating the position of sharks and humans within the field of view of the drone. Sharks were modelled as a single point, corresponding to the anterior-most point on the midline of the dorsal body surface (Fig. 1b). Humans, where present, were labelled as a single point corresponding to the head (Fig. 1b). The use of a single point to model organisms minimised the potential impact of image distortion, which was deemed negligible following preliminary tests and extensive footage visualisation. Initially, 20 frames were labelled at random intervals within each video. SLEAP offers two neural network training modes: top-down training first identifies animals and then separately estimates the pose of each, whereas bottom-up training first identifies all of the body parts in a frame and separately assigns parts to each animal[36]. We chose a top-down mode following preliminary tests for training efficacy. The neural network was trained to predict the position of humans and/or sharks in 20 additional frames and ceased after five rounds of training, after which a

manual review of the predicted frames was conducted. Following any necessary corrections, the trained neural network was used to generate track data for all individuals across the entire video. To distinguish between humans and sharks, a centroid cost function was used, assigning identity on the basis of the distance travelled between frames. A Hungarian matching algorithm, which matches individual identity between frames by maximising total similarity[36], was utilised to compile the final track data for each individual in each video.

Parameter estimation:

To obtain behavioural parameters for statistical analysis, SLEAP output was converted into trajectory data. Each frame transition in each video is modelled by a step length (indicating the distance between an individual's location in two consecutive frames) and a turning angle (indicating change in directionality between two consecutive frames) using the *trajr* package in the *R* statistical environment[37, 38]. As larger sharks are likely to swim faster than smaller sharks, a body size correction was applied to each trajectory in accordance with the literature[39, 40]. Trajectories were visualised and smoothed accordingly (using a Savitzky-Golay filter of length 21 and polynomial order 3) in *trajr* prior to parameter estimation to remove noise associated with head yaw (lateral movements of the head), which could influence the distribution of parameters related to directionality. Smoothing parameters were chosen in line with previous studies and following visualisation of the data[38]. The following parameters were calculated for each video: minimum, maximum, mean and standard deviation values for speed, acceleration and turning angle; mean directional autocorrelation[41], 'eMaxA'[42], 'eMaxB'[42] and 'Sinuosity2'[43].Where humans were present, the distance between shark and human – referred to hereafter as inter-organismal distance (IOD) was also calculated for each frame of every video. For the calculation of all trajectory-based parameters, a correlated random walk model of animal movement was applied under the assumptions of Brownian motion and that direction of movement in consecutive frames is correlated[44].

Statistical analyses:

To test for statistical differences in the overall behavioural repertoire of individuals in the presence and absence of humans, an 'ethospace' visualisation was generated through Principal Component Analysis (PCA). This approach is typically used to visualise ecological and morphological disparity[45], but also provides a valuable tool by which multiple components of 'behaviour' can be compressed into a single ordination[46]. PCA analysis incorporating all parameters (*z*-transformed to account for scale differences between parameters) was performed using the packages *factoextra*[47, 48] and *ggplot2*[48] in the *R* statistical environment[37]. Linear models were fitted for each of the parameters incorporated in the PCA in the *R* statistical environment[37] and visualised using the package *ggplot2*[48], first using the presence or absence of humans as a binary predictor variable, and subsequently using IOD as a continuous predictor variable.

Hidden Markov models

Whilst parameters such as mean speed, turning angle and acceleration are potentially biologically informative, they do not take into account the full range of behavioural plasticity exhibited by individuals. To increase the proportion of behavioural plasticity captured by the analyses whilst maintaining a biologically-reasoned approach that takes into account the ecology of the species in question, we applied discrete-time Hidden Markov models (HMM) to the non-smoothed trajectory data using the package *moveHMM*[37, 49] in the *R* statistical environment[37]. HMMs consist of a set of observations (in this case a series of step lengths and turning angles for each frame interval of each video), the distribution of which depends on the distribution of the hidden state (a proxy for individual behaviour, which takes one of a predefined set of discrete values at any given frame interval) which 'evolves' over time as a Markov process, described by a matrix of transition probabilities between each of the possible state values[50]. We applied two sets of separate HMMs to the data –first incorporating the presence/absence of humans as a binary covariate, and subsequently incorporating IOD as a continuous covariate. Each of these models was tested against a null model without covariates. Step length and turning angle were modelled by Gamma and Von Mises distributions respectively[49], defined by the parameters mean step length (μ), step length standard deviation (σ), mean turning angle (θ) and angle concentration factor (κ). Plausible parameter ranges were identified by visualising the actual step length and turning angle distributions, with these ranges being incorporated into a numerical likelihood optimization routine[51] to identify parameter values corresponding to the AIC (Akaike Information Criterion) global optimum. AIC balances model fit with model complexity[52] and thus this global optimum should represent the model that explains the greatest proportion of variance in the data whilst maximising the simplicity and interpretability of the model. As some behavioural sequences featured frames in which no movement occurred, zero mass parameters (ζ) were incorporated into each model, the value of which corresponded to the proportion of steps of length zero in the dataset. 75 sets of parameter values were considered for each HMM (including one-state, two-state and three-state models), with final models selected on the basis of AIC and log likelihood scores[52].

Multinomial logistic regression was then performed on both HMMs to quantify the effects of shark-human interactions on behavioural transition probabilities. All HMM analyses assumed a correlated random walk model of animal movement in accordance with the literature[44, 49].

Results

Ethospace occupation of R. typus

PCA incorporating 16 behavioural variables did not recover any evidence of significant behavioural differences in the presence or absence of humans (Fig. 2). Whilst individuals in the presence of humans qualitatively appear to occupy a greater ethospace range, there is no statistically significant difference (as evidenced by overlapping confidence ellipses, $p \geq 0.05$) between the mean behaviour of the groups (Fig. 2). The first three principal components cumulatively explained 83.7% of observed behavioural variance (46.6%, 30.0% and 7.1% respectively), with the parameters standard deviation of speed (Dim 1, 9.9%), mean speed (Dim 2, 16.9%) and minimum angle (Dim 3, 74.9%) explaining the greatest proportion of variance in each principal component respectively.

Linear models of behavioural variables

Linear regression of 16 behavioural variables against a binary variable representing the presence or absence of humans failed to recover evidence of statistically significant relationships between the presence of humans and the behaviour of *R. typus* individuals (Table 1). When regressing behavioural variables against IOD, the variables mean speed, minimum speed and eMaxB display a significant positive relationship with IOD (Table 2; Fig. 3a-c) whereas no significant relationship was found for remaining variables (Table 2).

Table 1
Regression output for each parameter against a binary variable representing human presence/absence, where a value of 0 represents human absence and a value of 1 represents human presence

Parameter	Coefficient	Intercept	T value	p value	standard error	residual error	R^2 (%)	Adjusted R^2 (%)	df	F value
Mean Speed	8.29E-03	1.04E-01	4.66E-01	6.44E-01	1.7799E-02	5.5560E-02	0.58	-2.1	1,37	2.17E-01
Min Speed	2.45E-03	1.99E-02	2.60E-01	7.96E-01	9.4160E-03	2.9390E-02	0.18	-2.52	1,37	6.76E-02
Max Speed	5.11E-02	2.23E-01	1.06E+00	2.95E-01	4.8150E-02	1.5030E-01	2.96	0.33	1,37	1.13E+00
Speed SD	7.51E-03	3.16E-02	9.34E-01	3.56E-01	8.0380E-03	2.5090E-02	2.3	-0.34	1,37	8.73E-01
Mean Acceleration	2.00E-03	1.30E-02	6.94E-01	4.92E-01	2.8890E-03	9.0170E-03	1.28	-1.39	1,37	4.81E-01
Min Acceleration	-2.00E-06	8.10E-05	-4.30E-02	9.66E-01	4.5000E-05	1.3900E-04	0.01	-2.7	1,37	1.88E-03
Max Acceleration	2.09E-02	7.29E-02	8.23E-01	4.16E-01	2.5330E-02	7.9080E-02	1.8	-0.86	1,37	6.78E-01
Acceleration SD	2.28E-03	1.10E-02	8.16E-01	4.20E-01	2.7910E-03	8.7110E-03	1.77	-0.89	1,37	6.65E-01
Mean Angle	5.24E-03	1.64E-01	3.01E-01	7.65E-01	1.7416E-02	5.4360E-02	0.24	-2.45	1,37	9.04E-02
Min Angle	-5.70E-05	3.84E-04	-4.11E-01	6.83E-01	1.3800E-04	4.3100E-04	0.46	-2.24	1,37	1.69E-01
Max Angle	-1.49E-01	1.86E+00	-4.64E-01	6.45E-01	3.2090E-01	1.0020E+00	0.58	-2.11	1,37	2.16E-01
Angle SD	-1.73E-02	2.16E-01	-5.00E-01	6.20E-01	3.4490E-02	1.0770E-01	0.67	-2.01	1,37	2.50E-01
Directional Autocorrelation	-1.51E-02	8.21E-01	-3.48E-01	7.30E-01	4.3210E-02	1.3490E-01	0.33	2.37	1,37	1.21E-01
eMaxA	-4.22E+00	4.90E+01	-3.68E-01	7.15E-01	1.1478E+01	3.5830E+01	0.37	-2.33	1,37	1.35E-01
eMaxB	-1.86E-01	5.61E+00	-8.60E-02	9.32E-01	2.1535E+00	6.7220E+00	0.02	-2.68	1,37	7.45E-03
Sinuosity2	-3.15E-02	8.37E-01	-2.90E-01	7.73E-01	1.0853E-01	3.3880E-01	0.23	-2.47	1,37	8.42E-02

Table 2
Regression output for each parameter against IOD. P values lower than 0.05 are represented in bold.

Parameter	Coefficient	Intercept	T value	p value	standard error	residual error	R^2 (%)	Adjusted R^2 (%)	df	F value
Mean Speed	5.19E-03	-9.90E-03	2.94E+00	**< 0.001**	1.7640E-03	5.5870E-02	32.4	28.7	1,18	8.64E+00
Min Speed	2.94E-03	-4.78E-02	3.40E+00	**< 0.001**	8.6420E-04	2.7370E-02	39.1	35.7	1,18	1.15E+01
Max Speed	3.79E-03	2.52E-01	3.75E-01	7.12E-01	1.0104E-02	3.2000E-01	0.78	-4.74	1,18	1.41E-01
Speed SD	9.17E-04	2.38E-02	7.41E-01	4.68E-01	1.2370E-03	3.9180E-02	2.96	-2.43	1,18	5.50E-01
Mean Acceleration	4.63E-04	4.24E-03	1.32E+00	2.02E-01	3.4960E-04	1.1070E-02	8.87	3.8	1,18	1.75E+00
Min Acceleration	5.22E-06	-4.57E-05	1.40E+00	1.80E-01	3.7400E-06	1.1850E-04	9.77	4.75	1,18	1.95E+00
Max Acceleration	2.32E-03	5.28E-02	6.46E-01	5.27E-01	3.5990E-03	1.1400E-01	2.26	-3.17	1,18	4.17E-01
Acceleration SD	3.81E-04	5.27E-03	1.07E+00	2.98E-01	3.5540E-04	1.1250E-02	5.99	0.77	1,18	1.15E+00
Mean Angle	-1.23E-03	2.01E-01	-7.31E-01	4.74E-01	1.6760E-03	5.3090E-02	2.88	-2.51	1,18	5.35E-01
Min Angle	6.99E-06	9.93E-05	7.04E-01	4.91E-01	9.9400E-06	3.1480E-04	2.68	-2.73	1,18	4.95E-01
Max Angle	-4.63E-02	2.89E+00	-1.51E+00	1.48E-01	3.0590E-02	9.6880E-01	11.3	6.35	1,18	2.29E+00
Angle SD	-2.58E-03	2.68E-01	-8.01E-01	4.34E-01	3.2240E-03	1.0210E-01	3.44	-1.92	1,18	6.42E-01
Directional Autocorrelation	3.99E-03	7.08E-01	8.09E-01	4.29E-01	4.9260E-03	1.5600E-01	3.51	-1.85	1,18	6.65E-01
eMaxA	1.77E+00	1.87E+00	1.86E+00	7.90E-02	9.4780E-01	3.0020E+01	16.2	11.5	1,18	3.47E+00
eMaxB	6.34E-01	-9.71E+00	3.33E+00	**4.00E-03**	1.9070E-01	6.0410E+00	38.1	34.6	1,18	1.11E+01
Sinuosity2	-1.87E-02	1.26E+00	-2.10E+00	5.00E-02	8.9180E-03	2.8250E-01	19.7	15.2	1,18	4.40E+00

HMM state allocation and model fit

In the case of models incorporating human presence/absence (ΔAIC$\geq$ 14202

, ΔLL (maximum log-likelihood)$\geq$7115) and inter-organismal distance (IOD) (ΔAIC$\geq$ 7835, ΔLL$\geq$3932) as covariates, models including three discrete behavioural states received more support than models including either one or two behavioural states. In both cases, the model of best fit incorporating covariates received significantly more support than null models not accounting for human activity (Table 3). Whilst the precise model parameter values differ between models incorporating human presence/absence and IOD, the three states allocated to each model functionally represent the same classes of behaviour and cover similar ranges of their respective step length and turning angle distributions (Table 3). State 1 covers relatively low step lengths and a high angle concentration factor (Table 3), reflecting highly directed movement at relatively low velocity[51], such as may be observed when transiting between areas of high prey density. State 2 covers relatively large step lengths and a relatively low angle concentration factor (Table 3), reflecting high velocity and highly angular movement, such as might be expected in predator escape responses and avoidance/disturbance behaviour. State 3 covers intermediate step lengths and an intermediate angle concentration factor (Table 3),

encompassing the ranges of velocity and angularity observed during both resting and surface feeding behaviours. Henceforth these states will simply be referred to as State 1, 2 and 3 to avoid controversy regarding the use of subjective terminology to describe behaviour. The biological interpretations of these states must be treated as hypotheses based on the quantitative definitions of each state, which are framed with respect to the velocity and angularity of trajectories. Transitions between states will be referred to as State $x \rightarrow y$, where x is the initial state and y is the final state.

Table 3
HMM models of best fit including presence/absence and IOD as covariates respectively. Model fit determined on the basis of the difference between the Akaike Information Criterion (AIC) and log-likelihood (LL) values of covariate models and null models (ΔAIC and ΔLL). State parameters refer to mean step length, step length standard deviation, mean turning angle, angle concentration factor and zero mass parameter as defined in the methodology.

Model Covariate	AIC	ΔAIC	LL	ΔLL	State 1	State 2	State 3
Presence/Absence	19539	140	-9741	76.2	μ: 2.21E-02	μ: 3.76E-01	μ: 2.74E-01
					σ: 1.37E-02	σ: 3.64E-01	σ: 6.93E-02
					θ: 1.53E-02	θ: -1.15E+00	θ: -2.15E-02
					κ: 1.10E+00	κ: 4.22E-02	κ: 6.09E-01
					ζ: 9.73E-04	ζ: 7.26E-03	ζ: 4.11E-11
IOD	9206	103	-4574	57.8	μ: 2.10E-02	μ: 3.79E-01	μ: 2.52E-01
					σ: 1.18E-02	σ: 3.74E-01	σ: 5.38E-02
					θ: 5.22E-03	θ: -1.44E-01	θ: -4.16E-02
					κ: 1.16E+00	κ: 1.82E-01	κ: 5.66E-01
					ζ: 9.31E-04	ζ: 7.43E-03	ζ: 1.82E-08

HMM state occupancy and multinomial logistic regression

The human presence/absence model suggests that regardless of whether humans are present, the long-term probability of an individual being in State 1 (typified by highly directional movement) is greater than that of an individual being in State 3 (typified by intermediate speed and directionality), which is in turn greater than the probability of an individual being in State 2 (typified by rapid, erratic movement consistent with escape behaviour) (Fig. 4a). However, the presence of humans results in an increase in the long-term probability of an individual being in State 2 (Fig. 4a). Whilst human presence appears to result in a decrease in the long-term probability of an individual being in either State 1 or State 3, these relationships were not found to be significant. Multinomial logistic regression applied to this model suggests that human presence has a significant influence on all transition probabilities except State $3 \rightarrow 1$ and State $1 \rightarrow 3$ (Fig. 5a).

The IOD model suggests that where IOD is low (humans and sharks are close), the long-term probability of an individual being in State 1 (typified by highly directional movement) and State 3 (typified by intermediate speed and directionality) are greater than that probability of an individual being in State 2 (typified by rapid, erratic movement consistent with escape behaviour), however when IOD is high, the long-term probability of an individual being in State 2 is greater than that of an individual being in State 1 or State 3 (Fig. 4b). The long-term probability of an individual being in State 1 is consistently lower than that of an individual being in State 3, however for higher IOD values this difference is not significant (Fig. 4b). Multinomial logistic regression applied to this model suggests that human presence has a significant influence on all State transition probabilities except State $2 \rightarrow 1$ and State $1 \rightarrow 3$.

Discussion

Our results demonstrate that the presence of humans and their proximity to *R. typus* individuals has important behavioural consequences for these sharks, and that these consequences are only detected by models that account for hidden behavioural states and individual variation in behaviour (Fig. 4; Fig. 5). Of particular significance with regards to ecology and conservation, ecotourism activity increases the probability of individuals being in a disturbed behavioural state typified by relatively angular and rapid movement (Fig. 4a). Moreover, ecotourism activity significantly influences the probability of transitioning between states (Fig. 5), specifically reducing the probability of transitioning from a disturbed to an undisturbed state (Fig. 5a: State $2 \rightarrow 1$, State $2 \rightarrow 3$). Whilst several of the IOD-based results may appear to reject this suggestion by suggesting that behaviours associated with disturbance are more prevalent where humans and sharks are far apart (Fig. 3a; Fig. 3b; Fig. 4b; Fig. 5b), we suggest that this is simply because a disturbed individual will typically swim at a faster speed than a human can maintain, thus resulting in high IOD (distance between human and shark). This is supported both by the presence/absence-based model (Fig. 4a; Fig. 5a), and qualitative observation of video footage. The primary behavioural consequence of shark ecotourism for *R. typus* individuals appears to be an increase in the proportion of time spent in a disturbed state typified by increased energetic expenditure[53], relative to states encompassing less rapid and angular movements (Fig. 3c; Fig. 4; Fig. 5).

Avoidance behaviours increase energetic expenditure as a result of the energy required to generate such behaviours[53], however expenditure also increases indirectly as a result of displacement of individuals from areas of high foraging success[54, 55]. We recovered evidence of increases in energetic expenditure as human presence significantly increased the long-term probability of individuals engaging in behaviours typically associated with avoidance/disturbance (Fig. 4a). Whilst such displacement would incur fitness costs in any species *R. typus* individuals aggregate in the Bay of La Paz specifically to forage[33, 56] and subsequently engage in vast oceanic migrations[57, 58]. For these reasons reduced foraging success in the Bay of La Paz could influence the ability of individuals to complete migrations and maintain body condition whilst doing so. In addition to the physiological consequences of reduced foraging success[59–61], these behavioural changes could reduce reproductive success through modification of reproductive phenology[54] and increase the risk of injuries associated with boat strikes[22, 62] given that even minor displacement would see individuals exit the protected area[34]. Inferring population-level consequences of these individual behavioural responses is not trivial[63], however temporally persistent avoidance behaviours at the population level can result in area abandonment[64], in turn triggering cascading ecological effects that influence entire communities[54]. Migratory sharks such as *R. typus* are known to act as a major biological nutrient flux between isolated ecosystems[2, 4, 65], and thus area abandonment could have profound long-term consequences for nutrient cycling[65]. Agent-based models have been developed to predict population-level consequences of disturbance responses similar to those reported in this study[59, 63], however most of these studies consider marine mammals, and as of yet none have been applied to elasmobranchs. For this reason, the details of such consequences in *R. typus* and other elasmobranch populations remain poorly constrained and should be a focus of future work.

Whilst the relationship between bioenergetics and disturbance responses may appear straightforward, behavioural responses to disturbance (and their ecological consequences) are often highly nuanced and context-dependent[66, 67]. An individual displaying an 'undisturbed' behavioural state does not necessarily imply that the stimulus in question is not adversely affecting this individual. Various physiological stress responses are known in a range of taxa[68–70], many of which are thought to incur fitness costs even in the absence of obvious behavioural effects (Hing et al., 2016). Stress physiology has been studied in elasmobranchs[71], but not in the context of ecotourism. Many studies have reported evidence of a relationship between individual behaviour (typically in the context of foraging behaviours or predator avoidance) and past history of energetic states and ecological interactions – often termed 'experience'[64, 72–75]. The utility of terms such as 'personality' and 'experience' to behavioural ecology is debatable[76, 77], however the initial behavioural state of individuals can often be of great importance in determining their response to a given stimulus. Our results support this concept as behavioural responses differed between *R. typus* individuals (Fig. 2) and the initial behavioural state of individuals was found to be important in determining the way in which they respond to human presence (Fig. 5). Behavioural differences in the presence and absence of humans was only detected when fitting models that account for individual variation in behaviour, and these models are supported despite their increased complexity (Table 3). Consequently, the behavioural, physiological and ecological consequences of a single disturbance event are not limited to the immediate time interval in which disturbance occurs but may persist for some as of yet undefined duration. This also raises the question of state-behaviour feedback, which has been reported in other taxa[78–80]. *R. typus* individuals aggregating at common ecotourism sites are likely to experience a number of interactions with humans in any given day, and if disturbance responses demonstrate synergism then the true ecological consequences of ecotourism in this taxon may be far greater than previously considered. Further studies will be required to elucidate

the extent of the relationship between past behavioural/energetic context and contemporary *R. typus* behaviour, however we suggest that shark behaviour should always be assessed prior to ecotourism activity to minimise potential disturbance. Even if this advice is heeded, these results suggest that some negative ramifications of ecotourism may be unavoidable unless such activity ceases entirely.

Behavioural modifications resulting from ecotourism activity may negatively influence some aspects *R. typus* ecology[31], however viewed through the lens of behavioural plasticity, our results provide cause for cautious optimism with regards to the long-term conservation goals of the species. *R. typus* can respond plastically to novel environmental stimuli (Fig. 3; Fig. 4; Fig. 5), which may well be symptomatic of broader behavioural plasticity. This plasticity consequently implies population-level resilience in the face of environmental change (as per the Baldwin effect), as it facilitates phenotypic changes on a temporal scale at which genetically entrained adaptation cannot occur[81, 82]. In the context of *R. typus* and ecotourism this is particularly relevant with regards to boat strike injuries, where a high degree of behavioural plasticity may enable individuals to persist in modern ecosystems by avoiding the majority of potentially fatal interactions with motorboats. Over greater timescales the evolutionary and ecological significance of behavioural plasticity is not limited to persistence and resilience[83]. The plasticity first hypothesis argues that plasticity facilitates adaptive evolution in the face of environmental change by providing 'pre-tested' phenotypic variation that can be genetically entrained through genetic assimilation, promoting the evolution of complex adaptive traits over relatively short timescales[26, 84]. There is debate regarding the validity of this hypothesis[84], however if such a mechanism occurs it would be particularly important for taxa such as elasmobranchs, with long generation times[7], low effective population sizes[85] and mutation rates[86] that may retard the pace at which genetic adaptations evolve[87, 88]. The relationship between behavioural plasticity, selection and persistence is nuanced and context dependent[83, 89], however we suggest that the ability of *R. typus* to respond to environmental stimuli such as ecotourism activity may hint at a previously underestimated resilience of elasmobranch taxa to contemporary environmental change.

Our results demonstrate the importance of utilising multiple statistical approaches in the analysis of behavioural data. On the basis of individual parameters such as mean acceleration or standard deviation of turning angle and representing ecotourism as a binary presence/absence variable, one might suggest that ecotourism has a negligible impact on the fine-scale behaviour of *R. typus* (Table 1). This lack of responsiveness is not recovered when instead considering the distance between humans and sharks (IOD) instead of presence/absence alone (Table 2). Whilst the sensory perception of *R. typus*, and indeed the majority of elasmobranchs is poorly understood[90, 91], the field of view of the UAV utilised in this study would allow for IOD of over 20m, a distance at which sharks may either not detect humans or not deem them to be of sufficient threat to warrant avoidance behaviours. When considering 'overall' behaviour instead of single behavioural parameters the significance of human activity for *R. typus* behaviour becomes clearer (Fig. 4a; Fig. 5a; Table 3). Previous studies have produced superficially similar results[31] but do not provide comparable temporal resolution, and do not utilise a fully quantitative approach. Moreover, both multinomial logistic regression and ethospace reconstruction reveal individuality and context dependence to *R. typus* behavioural responses (Fig. 2; Fig. 5) which has not previously been reported. Whilst an HMM approach has been applied previously to shark spatial ecology[92−95], this study is (to our knowledge) the first to use such a method in the context of high-resolution shark movement data. We suggest that this approach should form an important component of future studies, without which the nuanced and context dependent nature of behavioural responses to human activity may be neglected entirely.

The importance of behavioural studies to ecology and conservation has long been understood[96]. By quantifying behaviour and applying multiple statistical approaches to these data, we have demonstrated that the influence of human activity on *R. typus* behaviour is significant, profound and context dependent. These behavioural consequences of ecotourism have concerning implications for *R. typus* ecology, however also highlight the potential resilience of this species to environmental change. In light of these results, we suggest that the initial behavioural state of individuals must be assessed prior to in-water ecotourism activities, and that regulations regarding the minimum distance between human and shark should be revisited and reviewed in detail. In particular, we suggest that sharks engaging in rapid, angular movements should be avoided. Future studies investigating the relationship between ecotourism and elasmobranch behaviour should strive to use a biologically reasoned and rigorously quantitative approach wherever possible. Such studies will form an integral component of global efforts to conserve and protect declining elasmobranch populations, and as such ensuring reproducibility and ease of interpretation between studies should be of utmost importance.

Declarations

Code and data availability statement

All data (the digitised tracks and estimated behavioural parameters) and code used in this project can be found in the following repository: https://figshare.com/s/bc287179a0b85c1c797c (to be made public following acceptance).

Raw video footage can be provided upon reasonable request. They are over 9GB in size and thus difficult to share online, however an exemplar video at low resolution has been deposited in the repository above.

Competing interests

The authors declare no competing interests.

Author contributions

JHG conceptualised the study. JHG, RDLPV and DAW carried out data collection. JHG carried out data analyses. JHG, RDLPV, DAW and WDP produced, reviewed and approved the final version of the manuscript.

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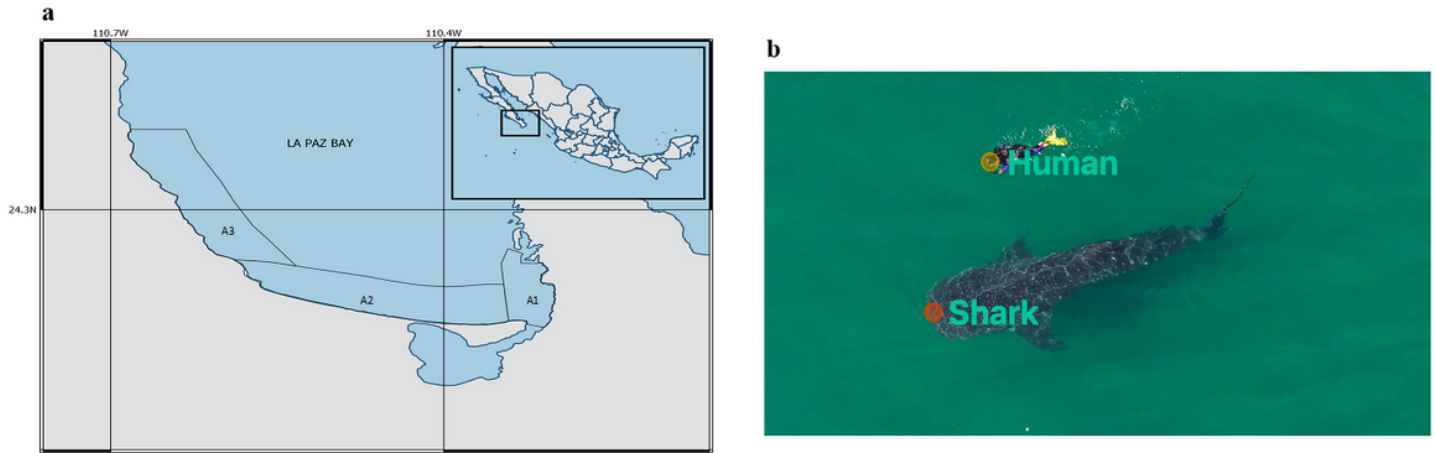
Figures

Figure 1

Images showing (a) the Bay of La Paz in Baja California Sur, Mexico where data collection took place; Polygons A1,A2 and A3 represent the whale shark refuge area in which certain restrictions regarding boat traffic apply. (b) the labelling of humans and sharks for SLEAP analyses, with human swimmer mimicking ecotourist behaviour, swimming parallel to the shark maintaining a distance of at least two metres.[34].
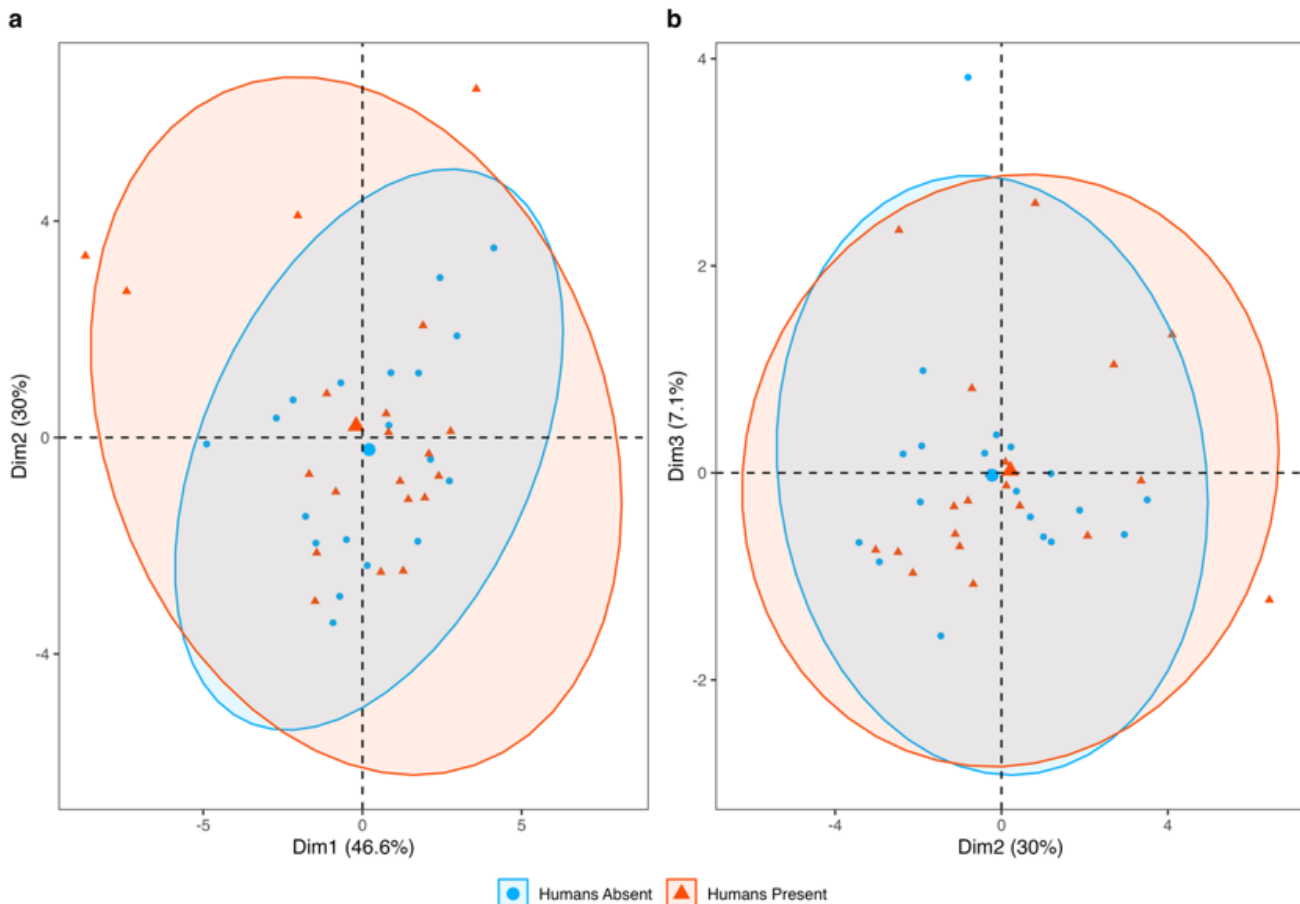
Figure 2

There is no difference in mean behaviour between individuals interacting with humans and those not interacting with humans. The total plot space represents the range of possible behaviours an individual could exhibit, with each data point representing a separate individual. Enlarged points represent mean position in ethospace of each group (blue points indicate the absence of humans whereas orange points indicate the presence of humans). As the mean value for each group overlaps with the 95% confidence ellipse of the other group, there is not statistically significant difference between the mean values.
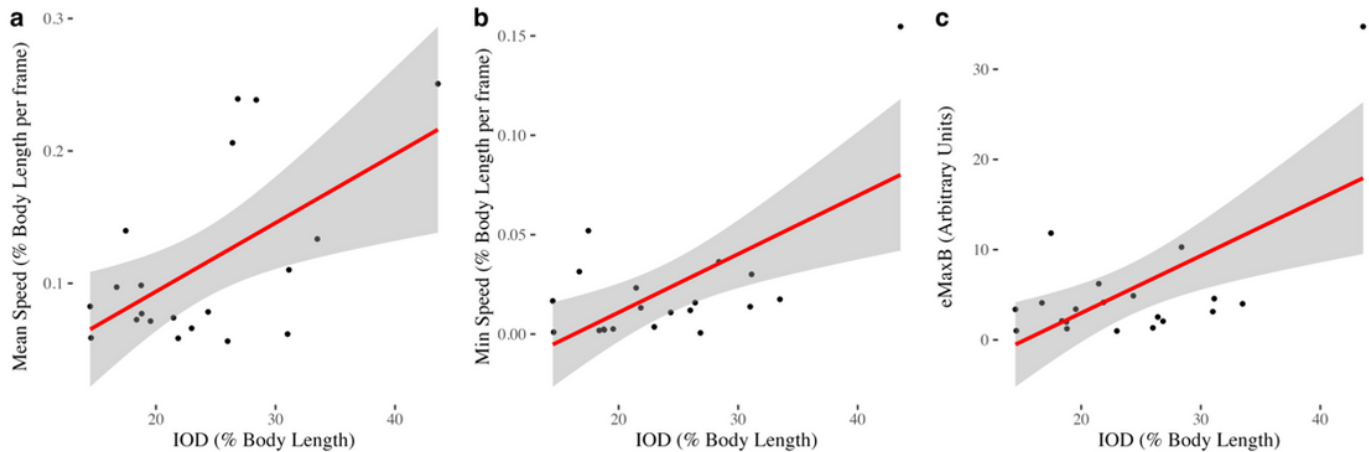
Figure 3

Linear regression plots displaying significant positive relationships between IOD and (a) mean speed, (b) minimum speed and (c) eMaxB. The grey shaded area represents the 95% confidence interval at any given IOD value, and full regression output can be found in Table 2.
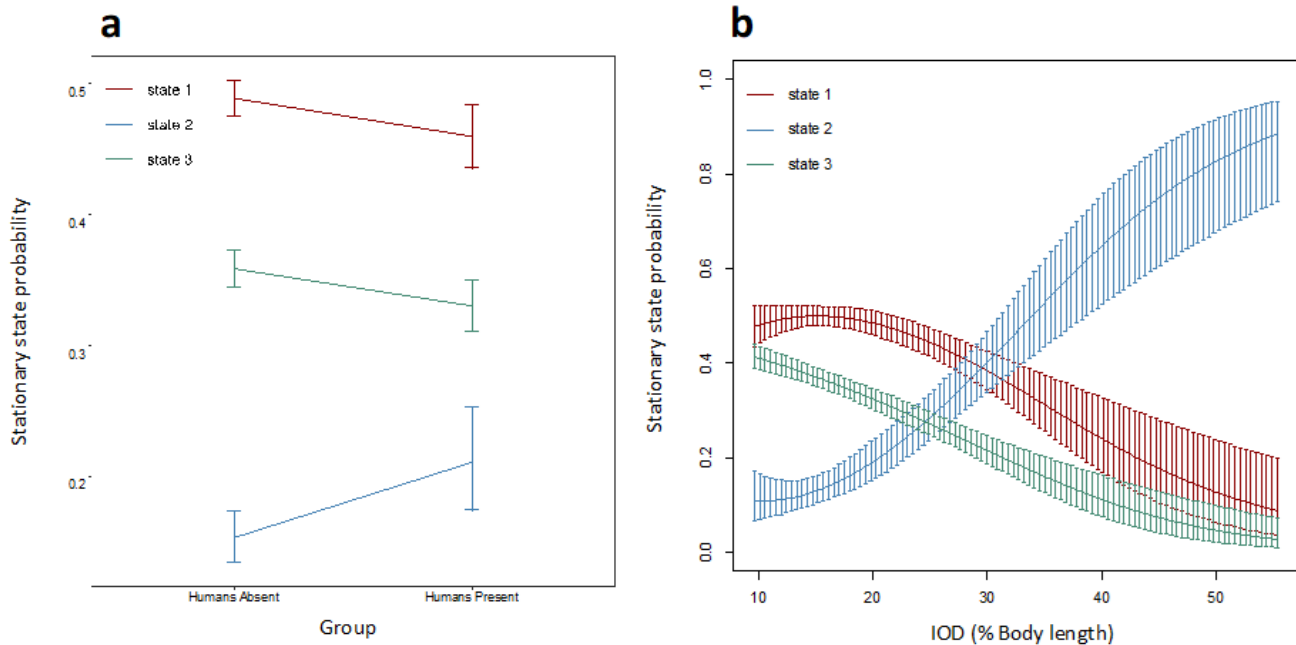

Figure 4

Human presence (a) and IOD (b) both significantly influence the long-term probability (stationary state probability) of individuals occupying a behavioural state characterised by high speed and high angularity. Red represents state 1, blue represents state 2 and
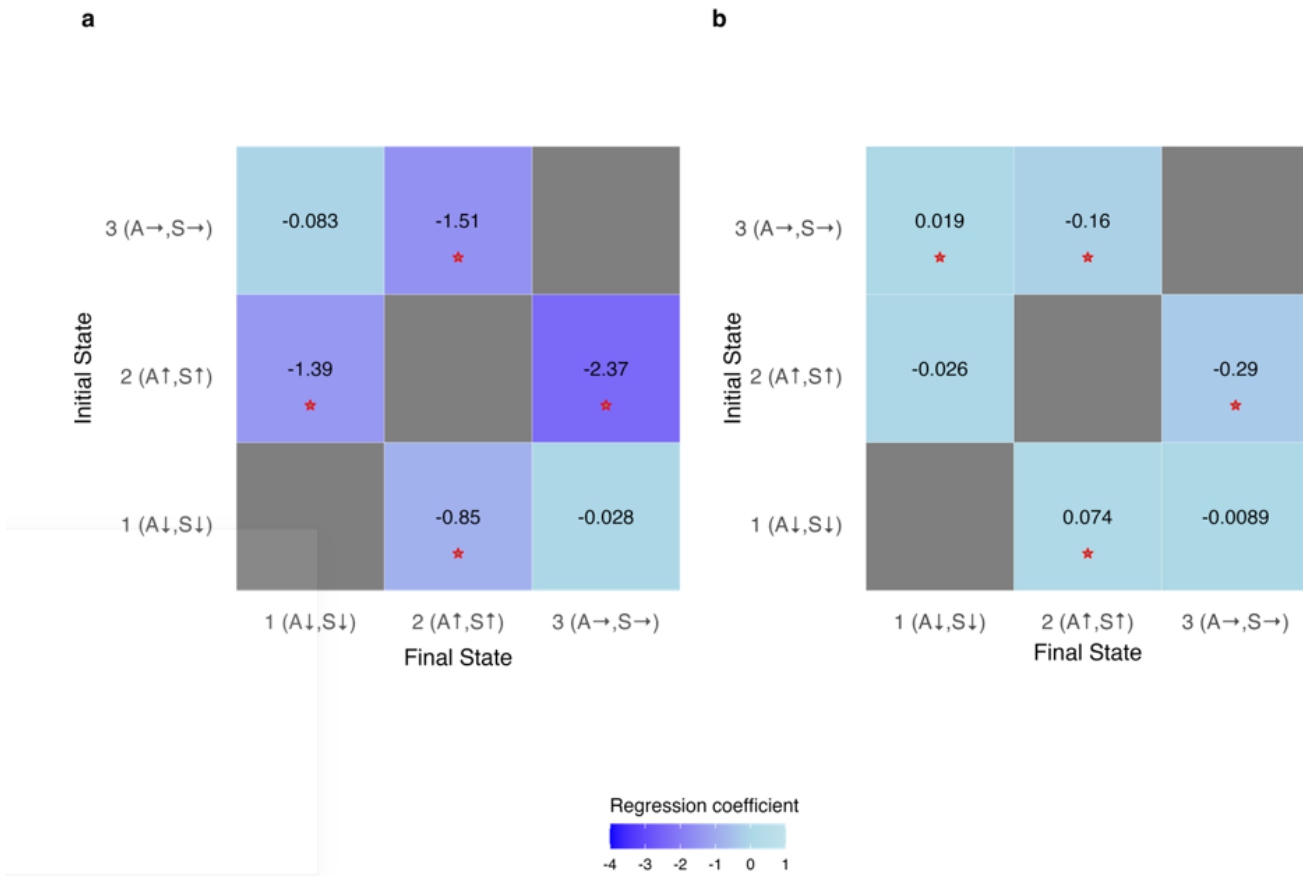
Figure 5

Multinomial logistic regression coefficients demonstrate that both (a) human presence/absence (regression treats this as a binary variable with human absence holding a value of zero and human presence a value of one) and (b) IOD significantly alter the probability of transitioning between some (but not all) behavioural states. A and S refer to the relative angularity and speed of each state, where ↑,↓ and → represent relatively high, low and intermediate values. Red stars denote relationships found to be significant ($p \leq 0.05$).