A combination of gyroscope and accelerometer for identifying alternative feeding behaviours in fish

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Running title: Method to identify feeding behaviours

SUMMARY

We examined whether we could identify the feeding behaviours of the trophic generalist fish *Epinephelus ongus* on different prey types (crabs and fish) using a data-logger that incorporated a 3-axis gyroscope and a 3-axis accelerometer. Feeding behaviours and other burst behaviours, including escape responses, intraspecific interactions, and routine movements, were recorded from six *E. ongus* individuals using data-loggers sampling at 200 Hz, and were validated by simultaneously recorded video images. For each data-logger record, we extracted 5 seconds of data when any of the 3-axis accelerations exceeded absolute 2.0 *G*, to capture all feeding behaviours and other burst behaviours. Each feeding behaviour was then identified using a combination of parameters that were derived from the extracted data. Using decision trees with the parameters, high true identification rates (87.5% for both feeding behaviours) with low false identification rates (5% for crab-eating and 6.3% for fish-eating) were achieved for both feeding behaviours.

Keywords: accelerometer, angular velocity, biologging, forage, inertial sensor, telemetry

INTRODUCTION

Cataloguing discrete behaviours (i.e. ethogram) is an essential step toward the understanding of interactions between behaviours and internal states (e.g. metabolic rate, cognitive ability and etc) of animals. Acceleration data-loggers are a useful tool to categorize behaviours in free-ranging animals (Campbell et al., 2013; Nathan et al., 2012; Sakamoto et al., 2009), but only a few studies have applied this technique to identify feeding behaviours of predators (Broell et al., 2013; Naito et al., 2013; Noda et al., 2013; Watanabe and Takahashi, 2013). A recent study suggested that it would be possible to identify feeding strikes of predatory fish if the sampling frequency was sufficiently high (>100 Hz) (Broell et al., 2013). In addition, it was found that the identification accuracy was greater if the data were obtained from a data-logger which incorporated a gyroscope and an accelerometer compared to data from only an accelerometer was used (Noda et al., 2013). However, as far as we are aware, no studies have been conducted using this method on distinguishing prey types.

Previous laboratory studies using high-speed video cameras have elucidated the modulation of feeding kinematics depending on prey types in various predators (Anderson, 1993; Deban, 1997; Ferry-Graham et al., 2001; Montuelle et al., 2012; Nemeth, 1997). In addition to jaw motion, body motions such as body posture, angular velocity and forward velocity were found to be different between prey types in these animals. Thus, a data-logger incorporating a gyroscope and an accelerometer, that can measure angular velocity and acceleration with high sampling frequency, might be usable for distinguishing feeding behaviours of these predators on different prey types.

In this study, we used a novel gyroscope/acceleration data-logger, which can monitor 3-axis angular velocities as well as 3-axis accelerations, with the aim of

identifying the feeding behaviours of a trophic generalist fish, the white-streaked grouper *Epinephelus ongus* (Bloch, 1790), on different prey types.

RESULTS AND DISCUSSION

The results of this study indicate that we can successfully identify *E. ongus* feeding behaviours on both crab (Crab-eating) and fish (Fish-eating) using the gyroscope/acceleration data-logger. Firstly, among the *E. ongus* behaviours recorded, 17 Crab-eating, 34 Fish-eating, 42 escape responses (Escape), 9 intraspecific attacks (Intra-attack), 27 intraspecific escapes (Intra-escape), and 16 routine movements (Routine) were detected by a set threshold (2.0 *G*) (supplementary material Table S1), from a total of 17 Crab-eating, 34 Fish-eating, 42 Escape, 48 Intra-attack, and 48 Intra-escape recorded by a video camera. Secondly, the featured parameters were calculated (supplementary material Table S2), after extracting the subsequent five seconds of data and then dividing into the first phase (2.1 s) and second phase (2.9 s) (See Materials and methods section and Fig. S1 for details). Finally, each of the feeding behaviours was identified by a decision tree using specific parameters (Figs 1, 2). Using this paradigm, we achieved high true identification rates (87.5% for both feeding behaviours) with low false identification rates (4.4% for Crab-eating and 5.6% for Fish-eating) for both feeding behaviours (Figs 1, 2; Tables 1, 2).

E. ongus exhibited larger pitch motions to pick up crabs (supplementary material Movie 1); the ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase ($Range_{Pitch\text{-}1}/Range_{Yaw\text{-}1}$) of the Crab-eating behaviour was larger than those of the Fish-eating, Escape, Intra-attack, and Intra-escape (ANOVA, $P<0.01$; Tukey-Kramer test, $P<0.05$; Fig. 1C). *E. ongus* did not move substantially

during the second phase of the Routine; the mean vector sum of the angular velocities in the second phase ($Mean_{MG-2}$) of the Routine was lower than those of the Crab-eating, Fish-eating, Escape, and Intra-escape (ANOVA, $P<0.01$; Tukey-Kramer test, $P<0.05$; Fig. 1D). Thus, $Range_{Pitch-1}/Range_{Yaw-1}$ was used to discriminate Crab-eating from Fish-eating, Escape, Intra-attack, and Intra-escape (Fig. 1A, C), and $Mean_{MG-2}$ was used to discriminate Crab-eating from Routine (Fig. 1A, D). The sum of sensitivity (true identification rate) and specificity (1 - false identification rate), a criterion to determine the optimal threshold (See Materials and methods section for details), revealed a peak (1.83) at the threshold of 1.19 and 11 in the $Range_{Pitch-1}/Range_{Yaw-1}$ and $Mean_{MG-2}$, respectively (Fig. 1B), at which the true identification rate was 87.5% (14/16) and the false identification rate was 5% (4/80) (Fig. 1; Table 1). In the more conservative cross-validation test, in which we derived the decision tree algorithm from five individuals at a time and tested identification success on the remaining individual, the true identification rate was 75% (12/16) and the false identification rate was 6.3% (5/80) (Table 3).

E. ongus exhibited a strong fast-start motion during Fish-eating and Escape as compared to other behaviours. The standard deviation of the lateral acceleration in the first phase (SD_{AX-1}) of Fish-eating and Escape were higher than the others (ANOVA, $P<0.01$; Tukey-Kramer test, $P<0.05$; Fig. 2C). *E. ongus* showed strong yaw motion during Escape, compared to Fish-eating (supplementary material Movies 2, 3); the ratio of the range of yaw angular velocity to the range of roll angular velocity in the first phase ($Range_{Yaw-1}/Range_{Roll-1}$) of Escape was larger than that of Fish-eating (ANOVA, $P<0.01$; Tukey-Kramer test, $P<0.05$; Fig. 2D). Therefore, SD_{AX-1} was used to discriminate Fish-eating from Crab-eating, Intra-attack, Intra-escape, and Routine (Fig.

2A, C), and $Range_{Yaw-1}/Range_{Roll-1}$ was used to discriminate Fish-eating from Escape (Fig. 2A, D). The sum of sensitivity and specificity revealed a peak (1.81) at the threshold of 0.57 and 0.69 in SD_{AX-1} and $RO_{Yaw-1}/Range_{Roll-1}$, respectively (Fig. 2B), at which the true identification rate was 87.5% (14/16) and the false identification rate was 6.3% (5/80) (Fig. 2; Table 2). In the more conservative cross-validation test, the true identification rate was 87.5% (14/16) and the false identification rate was 8.8% (7/80) (Table 4).

Although the overall identification success were high, some behaviours were more likely to be misidentified than the others. In general, Intra-attack, Intra-escape and Routine were rarely misidentified as either feeding behaviour [0% (0/16) or 6.3% (1/16) of the false identification rates even in the cross validation tests; Tables 3, 4], while Escape was more likely to be misidentified as Fish-eating [18.8% (3/16) of the false identification rate in the cross validation test; Table 4]. Previous studies that compared escape responses and feeding strikes (Fish-eating) in predatory fishes revealed that both feeding strikes and escape responses have several mechanical types, and in some types, the motions were similar between the two behaviours (Broell et al., 2013; Harper and Blake, 1991; Noda et al., 2013). Even in this study, there were overlaps in the distributions of accelerations and angular velocities between the Fish-eating and Escape (Figs 1C, 2C; supplementary material Table 2), and thus some Escape events were misidentified as Fish-eating.

In addition, Crab-eating and Fish-eating were sometimes confused with each other, even though there were significant differences in $Range_{Pitch-1}/Range_{Yaw-1}$ and SD_{AX-1} between the two behaviours (Figs 1C, 2C). This is because, in a few cases, *E. ongus* attacked and swallowed crabs without a large pitch motion but with its body

rolled, and in other cases, *E. ongus* attacked fish with large pitch motions, probably for adjusting its body posture towards the vertically evading fish.

Over the last two decades, researchers have attempted to record the feeding behaviours of predators in nature using electronic devices, such as animal-borne video cameras (Davis et al., 1999; Watanabe and Takahashi, 2013), stomach/oesophageal temperature and impedance telemetry (Austin et al., 2006; Hanuise et al., 2010; Meyer and Holland, 2012), and accelerometers/hall sensors attached to jaws or heads (Hanuise et al., 2010; Naito et al., 2013; Watanabe and Takahashi, 2013; Wilson et al., 2002). However, very few studies have attempted to distinguish prey types (Wilson et al., 2002), except for studies using cameras. This study shows that as long as the mechanical motions are distinct in each of the feeding behaviours, the gyroscope/acceleration data-logger is usable for distinguishing prey types. Body motions in various predators such as lizard, salamander, frog, and other reef fishes were reportedly different between prey types (Anderson, 1993; Deban, 1997; Ferry-Graham et al., 2001; Montuelle et al., 2012; Nemeth, 1997), and thus this method could also be applied to these predators.

MATERIALS AND METHODS

Ethics statements

Animal care and experimental procedures for the tagging surgery and live predator-prey experiments were approved by the Institutional Animal Care and Use Committee (permit number: ECSER12-02) in accordance with the Guidelines for Animal Experimentation of Nagasaki University.

Study animals

E. ongus is an abundant generalist predator in the Indo-Pacific coral reefs, where it feeds mainly on benthic crustaceans and fishes (supplementary material Table S3). Six *E. ongus* [total length (TL): 254±24 mm] were collected by hook-and-line while snorkelling around the Yaeyama Islands, Okinawa, Japan, and were transferred to the Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute, Fisheries Research Agency, Okinawa, Japan. The fish were held in two 2000-L circular FRP tanks for at least 2 days prior to experimental testing.

Two different prey types: the mangrove swimming crab *Thalamita crenata* (Portunidae) (carapace length: 26±7 mm) and the whitetail dascyllus *Dascyllus aruanus* (Pomacentridae) (TL: 33±9 mm) were utilized in this study. These species were chosen since they are abundant in the *E. ongus* habitat and because the primary prey types of *E. ongus* are benthic crustaceans and fishes such as Portunidae and Pomacentridae, respectively (supplementary material Table S3).

Data-logging device

We employed a data-logger incorporating a 3-axis accelerometer and a 3-axis gyroscope [LP-BLKU02, Biologging Solutions Inc., Kyoto, Japan; www.biologging-solutions.com (the data-logger is commercially available); 60 mm × 5 mm × 13 mm, weight in air 6.5 g, sampling frequency 200 Hz, recording duration 150 min; resolution 16 bit]. This device allowed for multiple-scheduled recordings (e.g., 30 min of recording each day).

Attachment procedure

The fish were first anaesthetized using 0.1% 2-phenoxyethanol until they reached stage-4 anaesthesia. Next, two small holes (approximately 2 mm in diameter) were drilled into their dorsal musculature above their approximate centre of mass (39% of the TL), and the logger was attached using two plastic cables that passed through the holes, and were set on the right side of the body. The surgery had no observable effects on fish swimming and feeding behaviours.

Recording of behaviours

Experiments were performed in a 1000 L circular FRP tank with seawater to a depth of 300 mm. The water temperature during the experiments was 28.13±0.31 °C. Three *E. ongus* were introduced into the experimental tank and allowed to acclimate for approximately 22 hours. The data-loggers were scheduled to record data at 17:00–18:30; this period was chosen because this species increases their foraging activity in crepuscular periods (Kawabata et al., 2011). During the experiments, one to five crabs (*T. crenata*) or fish (*D. aruanus*) were introduced into the tank, and feeding behaviours of *E. ongus* were recorded. We also recorded escape responses and intraspecific interactions to test whether the method can accurately identify each of the feeding behaviours, which can also manifest as burst movements similar to feeding behaviours. Escape responses were elicited by thrusting a PVC pipe near the fish (Broell et al., 2013; Domenici et al., 2004), and intraspecific interactions were recorded by introducing three individuals into the same tank. These behaviours were simultaneously recorded using a USB camera (HD Pro Webcam C920, Logitech International S.A., Morges, Switzerland) 2.8 m above the tank bottom.

Data analyses

We first reconstructed 3D motions of the fish through the 3-axis accelerations and 3-axis angular velocities datasets (See Luinge and Veltink, 2005; Noda et al., 2014, for detailed analysis in which the reconstructed motions were compared with the video images) to investigate mechanical differences of motions among behaviours, and created animations using the 3D editor Blender 2.68 (The Blender Foundation, 2013). Next, the reconstructed 3D animations and video images were observed to identify distinct parameters of each of the feeding behaviours.

The threshold acceleration value was set to 2.0 *G*, since all the feeding behaviours exceeded the absolute 2.0 *G* in at least one of the three axes. We included two phases for calculating parameters, since the fast-start behaviours include the initial fast motions (e.g. strike or escape) and the subsequent motions (e.g. swallowing prey, swimming or resting). The different cut-off periods (0.1~3.0 seconds) and total periods (3~13 seconds) were tested using the sum of sensitivity and specificity, and 2.1 seconds and 5 seconds were chosen as the optimal periods (supplementary material Fig. S1). Featured parameters (maximum value, mean, range and standard deviation) were calculated based on the 3-axis accelerations and 3-axis angular velocities in each phase (supplementary material Table S2). On the basis of the distinct motion of each of the behaviours, these parameters and inter-axial parameters (e.g. ratio of maximum forward acceleration to maximum lateral acceleration) were considered and selected for identification analysis. The analysis of variance (ANOVA) and Tukey-Kramer post hoc test were used to determine any significant differences of parameters between behaviours.

We chose a uniform sample size for each of the behaviours (n=16) to conduct

the identification analysis, because there were no data concerning the occurrence of each of the behaviours in the natural environment. Decision trees were constructed, since there was no single parameter that can differentiate each of the feeding behaviours from all the other behaviours. The optimal threshold of parameters was obtained from the sum of sensitivity and specificity (Akobeng, 2007; Valenzuela et al., 1997). The sensitivity and specificity represent the rates correctly identified and rejected, respectively, and were calculated as follows.

$$\text{Sensitivity} = (\text{True Positive})/(\text{True Positive} + \text{False Negative}) \quad (1)$$

$$\text{Specificity} = (\text{True Negative})/(\text{False Positive} + \text{True Negative}) \quad (2)$$

The criteria (sum of sensitivity and specificity) is based on the concept that the optimal threshold should strike a balance between the high true identification rate and low false identification rate of the target event (Akobeng, 2007). We first used the same data set for deriving the decision tree algorithm and for testing identification success. Then, a more conservative cross-validation test was employed, in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual. All the data analyses were performed using R 3.0.1 (The R foundation for Statistical Computing, Vienna, Austria) (See Appendix S1 for the custom-made program).

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AUTHOR CONTRIBUTIONS

Y.K. designed the experiment. Y.K., Y.N., A.N., T.S., T.T., T.Y., and K.S. conducted the experiment. T.N., H.M., and N.A. designed and developed the data-logger. Y.K. and T.N. analysed the data. T.N. created the 3D animation. Y.K. wrote the manuscript. All authors provided critiques on the manuscript.

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Figure legends

Fig. 1. Decision tree algorithm to identify feeding behaviour on crab (Crab-eating). (A) A decision tree that uses derived parameters. The numbers in the parenthesis in each square indicates the percentage of Crab-eating behaviour (before a slash) and percentage of others (after a slash). (B) The sum of sensitivity and specificity, used to determine the threshold values, were plotted against the derived parameters. Arrows represent the determined thresholds: 1.19 in $Range_{Pitch\text{-}1}/Range_{Yaw\text{-}1}$, 11 in $Mean_{MG\text{-}2}$. (C, D) Comparisons of selected parameters ($Range_{Pitch\text{-}1}/Range_{Yaw\text{-}1}$ and $Mean_{MG\text{-}2}$) between behaviours. The boxes indicate the medium, lower, and upper quartiles, and the ends of the whiskers indicate the minimum and maximum values. Open circles represent the values over 1.5 times the upper quartile. The lower case letters represent significant differences in the Tukey-Kramer post hoc test ($P<0.05$). Dotted blue lines represent threshold values based on the sum of sensitivity and specificity.

$Range_{Pitch\text{-}1}/Range_{Yaw\text{-}1}$, ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase; $Mean_{MG\text{-}2}$, mean vector sum of the angular velocities in the second phase;

Fig. 2. Decision tree algorithm to identify feeding behaviour on fish (Fish-eating). (A) A decision tree that uses derived parameters. The numbers in the parenthesis in each square indicates the percentage of Fish-eating behaviour (before a slash) and percentage of others (after a slash). (B) The sum of sensitivity and specificity, used to determine the threshold values, were plotted against the derived parameters. Arrows represent the determined thresholds: 0.57 in $SD_{AX\text{-}1}$, 0.69 in $Range_{Yaw\text{-}1}/Range_{Roll\text{-}1}$. (C, D)

Comparisons of selected parameters ($SD_{AX\text{-}1}$ and $Range_{Yaw\text{-}1}/Range_{Roll\text{-}1}$) between behaviours. The boxes indicate the medium, lower, and upper quartiles, and the ends of the whiskers indicate the minimum and maximum values. Open circles represent the values over 1.5 times the upper quartile. The lower case letters represent significant differences in the Tukey-Kramer post hoc test ($P<0.05$). Dotted blue lines represent threshold values based on the sum of sensitivity and specificity.

$SD_{AX\text{-}1}$, standard deviation of the lateral acceleration in the first phase; $Range_{Yaw\text{-}1}/Range_{Roll\text{-}1}$, ratio of the range of yaw angular velocity to the range of roll angular velocity in the first phase.

Table 1. The result of the decision tree for identifying the feeding behaviour on crab (Crab-eating), in which a same data set was used for deriving the decision tree algorithm and for testing identification success

	Crab-eating	Fish-eating	Escape	Intra-attack	Intra-escape	Routine
Crab-eating	**14 (87.5)**	3 (18.8)	0 (0)	0 (0)	0 (0)	1 (6.3)
Others	2 (12.5)	**13 (81.3)**	**16 (100)**	**16 (100)**	**16 (100)**	**15 (93.8)**

Numbers (%) of trials identified correctly are shown in bold letters.

Table 2. The result of the decision tree for identifying the feeding behaviour on fish (Fish-eating), in which a same data set was used for deriving the decision tree algorithm and for testing identification success

	Fish-eating	Crab-eating	Escape	Intra-attack	Intra-escape	Routine
Fish-eating	**14 (87.5)**	4 (25)	1 (6.3)	0 (0)	0 (0)	0 (0)
Others	2 (12.5)	**12 (75)**	**15 (93.8)**	**16 (100)**	**16 (100)**	**16 (100)**

Numbers (%) of trials identified correctly are shown in bold letters.

Table 3. The result of the more conservative cross-validation test for identifying feeding behaviour on crab

(Crab-eating), in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual

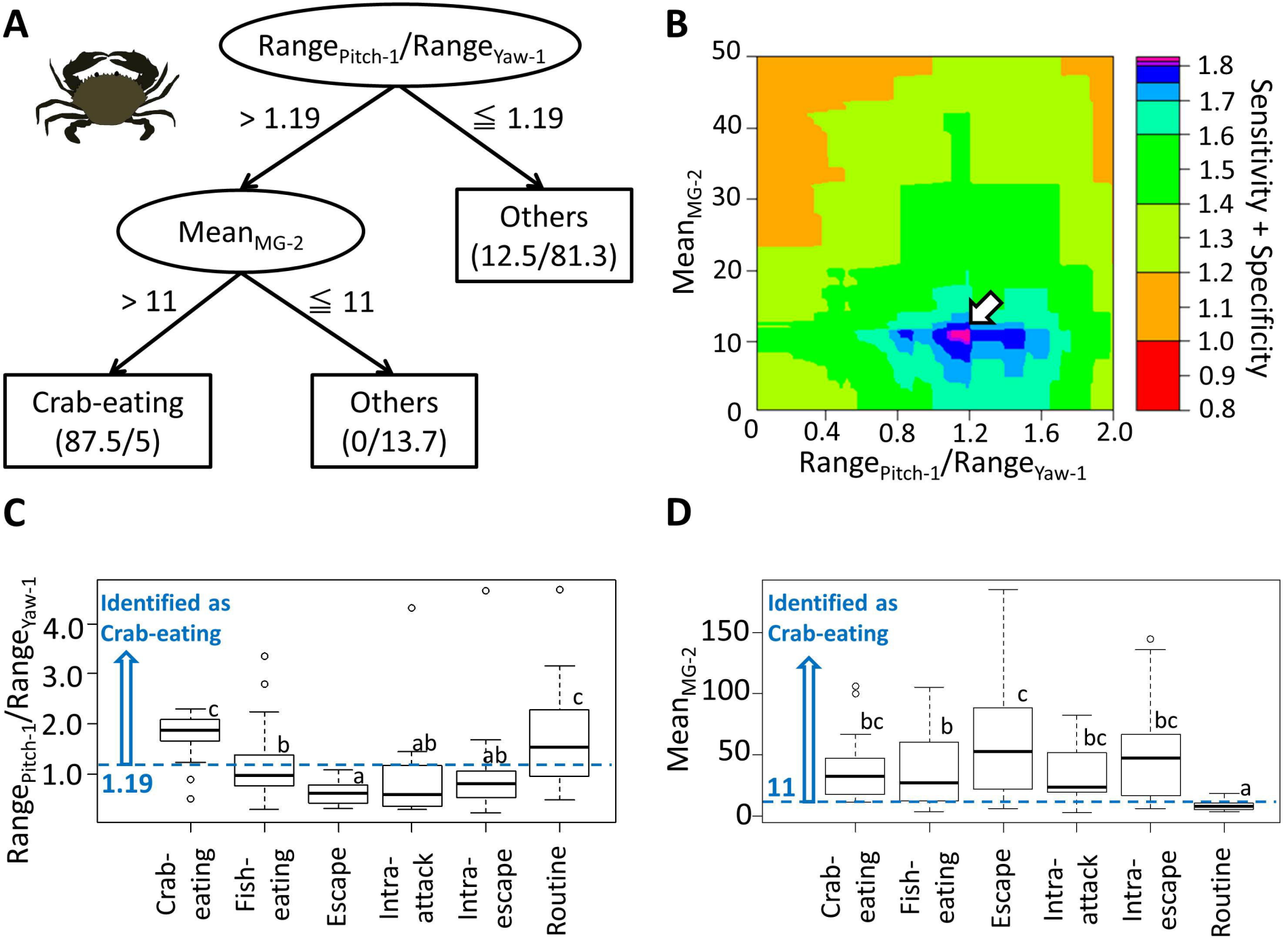
	Crab-eating	Fish-eating	Escape	Intra-attack	Intra-escape	Routine
Crab-eating	**12 (75)**	3 (18.8)	0 (0)	0 (0)	1 (6.3)	1 (6.3)
Others	4 (25)	**13 (81.3)**	**16 (100)**	**16 (100)**	**15 (93.8)**	**15 (93.8)**

Numbers (%) of trials identified correctly are shown in bold letters.

Table 4. The result of the more conservative cross-validation test for identifying feeding behaviour on fish (Fish-eating), in which we derived the decision tree algorithm from five individuals at a time and then tested identification success on the remaining individual

	Fish-eating	Crab-eating	Escape	Intra-attack	Intra-escape	Routine
Fish-eating	**14 (87.5)**	4 (25)	3 (18.8)	0 (0)	0 (0)	0 (0)
Others	2 (12.5)	**12 (75)**	**13 (81.3)**	**16 (100)**	**16 (100)**	**16 (100)**

Numbers (%) of trials identified correctly are shown in bold letters.


A
Range Pitch-1/Range Yaw-1
> 1.19
≦ 1.19
Mean MG-2
Others
(12.5/81.3)
> 11
≦ 11
Crab-eating
(87.5/5)
Others
(0/13.7)
B
Mean MG-2
Range Pitch-1/Range Yaw-1
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C
Range Pitch-1/Range Yaw-1
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Crab-eating
1.19
Crab-eating
Fish-eating
Escape
Intra-attack
Intra-escape
Routine
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Fish-eating
Escape
Intra-attack
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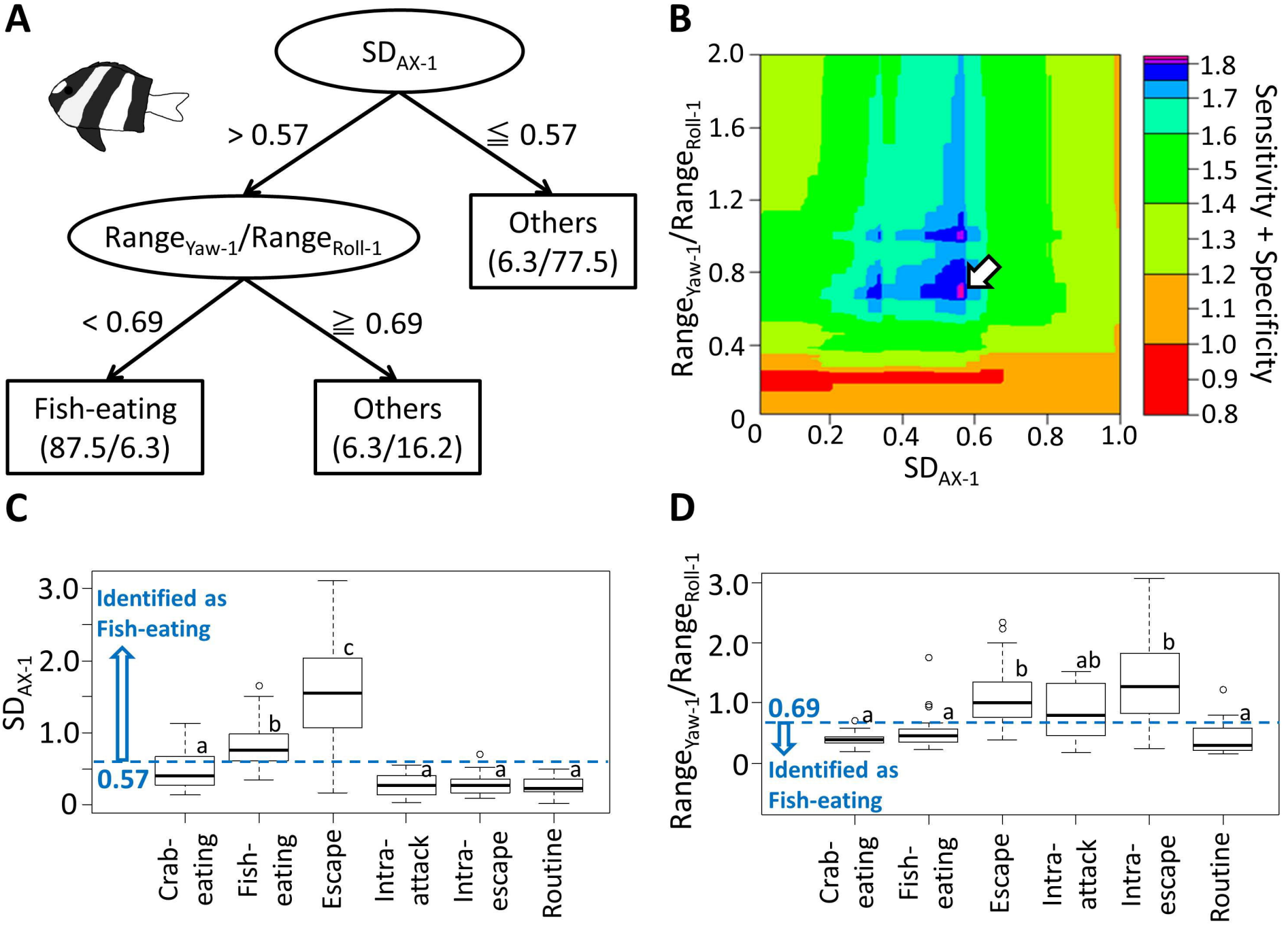
Routine


A
SD AX-1
> 0.57
≦ 0.57
Range Yaw-1/Range Roll-1
Others (6.3/77.5)
< 0.69
≧ 0.69
Fish-eating (87.5/6.3)
Others (6.3/16.2)
B
Range Yaw-1/Range Roll-1
SD AX-1
Sensitivity + Specificity
C
Identified as Fish-eating
0.57
SD AX-1
Crab-eating
Fish-eating
Escape
Intra-attack
Intra-escape
Routine
D
Range Yaw-1/Range Roll-1
0.69
Identified as Fish-eating

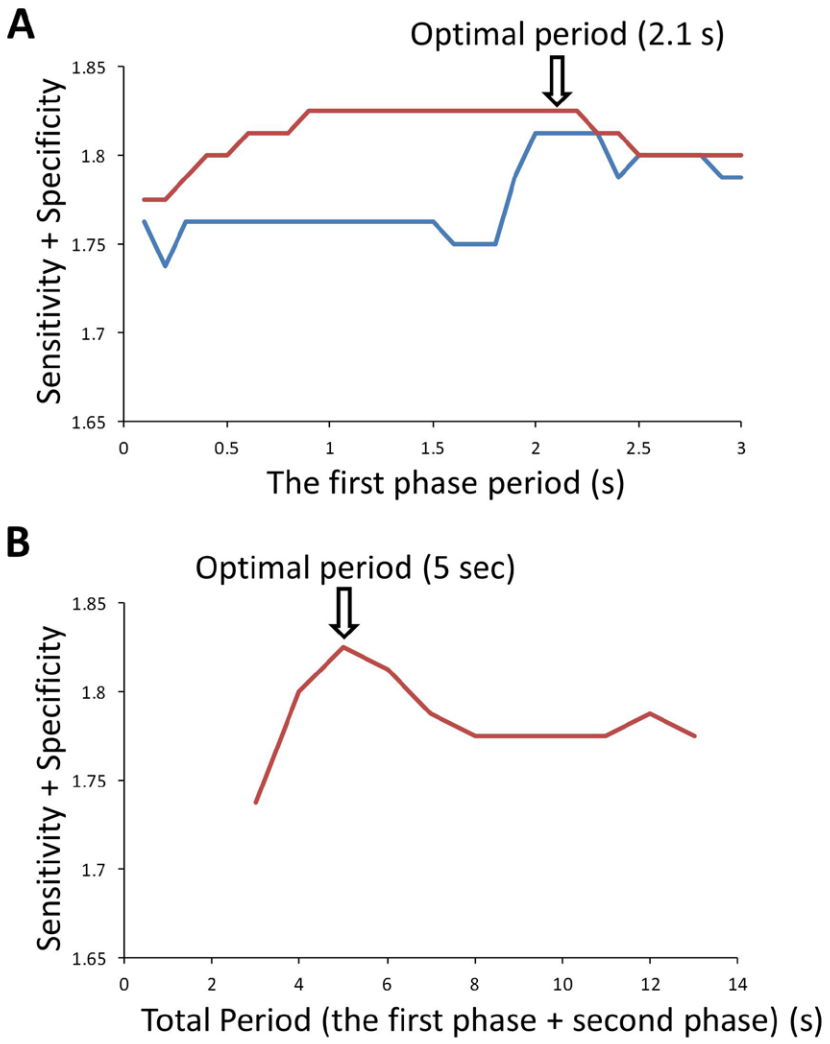


Fig. S1. Optimal periods for parameter calculations. (A) Different cut-off periods (0.1~3.0 seconds) and (B) total periods (3~13 seconds) were tested using the sum of sensitivity and specificity. Arrows indicate the optimal cut-off period (2.1 s) and total period (5 s). Red and blue lines represent the feeding behaviours on crab and fish, respectively. There was only the feeding behaviour on crab in the total period (B) because both of the two parameters used for identifying the feeding behaviour on fish were based on the first phase.

Movie 1. The body motion during the feeding behaviour on crab (crab-eating), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the distance moved is not incorporated in the animation because estimation errors are significant when the acceleration values are relatively low during crab-eating.

Movie 2. The body motion during the feeding behaviour on fish (fish-eating), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the cumulative distance is incorporated in the animation because the acceleration values are relatively high during fish-eating.

Movie 3. The body motion during the escape response (escape), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the cumulative distance is incorporated in the animation because the acceleration values are relatively high during escape.

Movie 4. The body motion during the intraspecific interaction (intra-attack), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the distance moved is not incorporated in the animation because the acceleration values are relatively low during intra-attack.

Movie 5. The body motion during the intraspecific interaction (intra-escape), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the distance moved is not incorporated in the animation because the acceleration values are relatively low during intra-escape.

Movie 6. The body motion during the routine movement (routine), reconstructed through the 3-axis accelerations and 3-axis angular velocities datasets. The data were taken at 200 Hz and the animation is played at 10 Hz. Note that the distance moved is not incorporated in the animation because the acceleration values are relatively low during routine.

Table S1. Summary of the behavioural data detected by the set threshold (2.0 *G*) for six white-streaked groupers, *Epinephelus ongus*

ID	TL (mm)	BW (g)	Crab-eating	Fish-eating	Escape	Intra-attack	Intra-escape	Routine
A	247	217	0/0	0/0	8/8	3/16	6/9	0
B	220	151	1/1	2/2	9/9	0/0	10/22	1
C	293	354	5/5	2/2	6/6	4/21	0/0	3
D	255	256	5/5	11/11	5/5	1/4	3/4	5
E	245	219	2/2	1/1	7/7	0/1	8/13	3
F	261	297	4/4	18/18	7/7	1/6	0/0	4
Total			**17/17**	**34/34**	**42/42**	**9/48**	**27/48**	**16**

The numbers indicate the number of the detected behaviour (before the slash) and the number of the observed behaviour (after the slash).

TL, total length; BW, body weight; Crab-eating, feeding behaviour on crab; Fish-eating, feeding behaviour on fish; Escape, escape response; Intra-attack, intraspecific interaction (attack); Intra-escape, intraspecific interaction (escape); Routine, routine movement.

Table S2. Summary of the means and standard errors of the parameters (maximum value, range, mean, standard deviation) derived from the 3-axis accelerations and 3-axis angular velocities in all behaviours

Phase	Parameter		Crab-eating (n=17)			Fish-eating (n=34)			Escape (n=42)			Intra-attack (n=8)			Intra-escape (n=27)			Routine (n=16)			ANOVA	
			mean	s.e.m	TK	mean	s.e.m	TK	mean	s.e.m	TK	mean	s.e.m	TK	mean	s.e.m	TK	mean	s.e.m	TK	*F*-value	*P*-value
Phase1	AX (*G*)	max	5.78	1.05	a	8.95	0.70	b	13.70	0.99	c	3.10	0.79	a	2.46	0.28	a	2.75	0.40	a	30.73	<0.01
		range	9.25	1.60	a	14.74	0.92	b	21.81	1.59	c	4.40	1.10	a	3.45	0.46	a	4.25	0.64	a	34.50	<0.01
		mean	0.03	0.06	a	0.09	0.04	a	0.30	0.06	b	0.13	0.08	a	0.48	0.05	b	0.17	0.07	a	8.09	<0.01
		s.d.	0.48	0.07	a	0.84	0.06	b	1.51	0.12	c	0.27	0.06	a	0.29	0.03	a	0.26	0.03	a	34.67	<0.01
	AY (*G*)	max	4.87	0.82	a	9.02	0.62	b	14.02	1.10	c	3.10	1.37	a	2.69	0.29	a	3.27	0.75	a	28.04	<0.01
		range	8.10	1.34	a	13.90	0.92	b	20.69	1.62	c	4.35	1.62	a	3.91	0.42	a	5.04	1.01	a	28.28	<0.01
		mean	-0.03	0.03	b	-0.15	0.03	a	0.00	0.02	ab	-0.01	0.04	bc	0.07	0.02	b	-0.04	0.05	bc	8.33	<0.01
		s.d.	0.45	0.06	a	0.82	0.06	b	1.43	0.13	c	0.26	0.07	a	0.29	0.03	a	0.26	0.05	a	26.49	<0.01
	AZ (*G*)	max	4.61	0.62	ab	6.98	0.63	b	9.72	0.83	c	2.13	0.25	a	2.33	0.23	a	3.72	0.64	ab	18.16	<0.01
		range	7.94	1.23	ab	11.98	1.08	b	16.20	1.41	c	2.54	0.49	a	3.02	0.43	a	5.83	1.16	ab	19.39	<0.01
		mean	0.87	0.03	-	0.90	0.01	-	0.84	0.02	-	0.94	0.01	-	0.88	0.02	-	0.71	0.17	-	1.70	0.14
		s.d.	0.45	0.06	ab	0.66	0.05	b	1.02	0.10	c	0.16	0.03	a	0.23	0.03	a	0.34	0.05	ab	18.30	<0.01
	MA (*G*)	max	7.29	1.24	a	12.01	0.82	b	18.41	1.32	c	5.23	1.23	a	3.87	0.34	a	5.30	0.93	a	28.73	<0.01
		range	6.88	1.24	a	11.46	0.83	b	17.91	1.33	c	4.70	1.26	a	3.21	0.35	a	4.71	0.96	a	28.79	<0.01
		mean	1.06	0.03	a	1.22	0.03	a	1.58	0.07	b	1.04	0.01	a	1.13	0.01	a	1.08	0.05	a	18.11	<0.01
		s.d.	0.61	0.10	a	1.13	0.08	b	1.99	0.18	c	0.28	0.07	a	0.26	0.03	a	0.37	0.06	a	29.00	<0.01
	GX (degree/s)	max	895	117	ab	1048	69	bc	1248	104	c	282	66	a	464	53	a	733	130	ab	12.12	<0.01
		range	1540	219	ab	1610	98	b	2119	202	c	443	111	a	729	81	a	1211	227	ab	10.91	<0.01
		mean	8	2	-	1	2	-	1	4	-	-4	3	-	5	4	-	5	3	-	0.78	0.57

		s.d.	102	14	a	104	7	a	167	18	b	36	7	a	78	8	a	69	11	a	9.30	<0.01
	GY (degree/s)	max	1380	139	ab	2089	132	cd	2078	157	d	572	97	ab	529	60	a	1382	245	bc	19.33	<0.01
		range	2411	250	ab	3678	256	d	3636	279	d	896	189	ab	830	97	a	2289	409	bc	20.01	<0.01
		mean	3	4	-	2	2	-	6	3	-	-4	5	-	0	2	-	1	2	-	1.21	0.31
		s.d.	149	13	a	226	14	b	264	18	b	69	10	a	85	8	a	130	19	a	22.45	<0.01
	GZ (degree/s)	max	544	59	a	1306	105	b	2383	182	c	463	95	a	627	62	a	465	80	a	32.60	<0.01
		range	902	94	a	1686	113	a	3634	304	b	600	121	a	872	81	a	691	115	a	31.74	<0.01
		mean	-3	7	-	-6	8	-	-23	11	-	-4	11	-	-9	7	-	-1	6	-	0.85	0.51
		s.d.	86	10	a	154	12	b	322	22	c	74	17	ab	112	11	ab	55	9	a	34.93	<0.01
	MG (degree/s)	max	1569	166	a	2559	133	b	2997	204	b	746	109	a	885	75	a	1583	279	a	23.99	<0.01
		range	1563	166	a	2553	133	b	2988	204	b	739	109	a	876	75	a	1580	279	a	24.01	<0.01
		mean	99	13	a	112	8	a	219	16	b	69	13	a	113	11	a	57	7	a	21.12	<0.01
		s.d.	178	16	a	281	16	b	406	27	b	94	14	a	126	10	a	155	20	a	29.47	<0.01
Phase2	AX (*G*)	max	2.66	1.09	-	0.98	0.29	-	1.96	0.45	-	0.90	0.46	-	1.28	0.51	-	0.35	0.06	-	1.90	0.10
		range	3.99	1.65	b	1.40	0.51	ab	2.48	0.64	ab	1.33	0.84	ab	1.26	0.78	ab	0.18	0.03	a	1.98	0.08
		mean	0.01	0.07	ab	0.02	0.04	a	0.24	0.06	bc	0.12	0.07	abc	0.40	0.08	c	0.14	0.09	abc	5.14	<0.01
		s.d.	0.21	0.05	b	0.13	0.02	ab	0.24	0.04	b	0.16	0.05	ab	0.11	0.03	ab	0.04	0.01	a	3.68	<0.01
	AY (*G*)	max	1.56	0.63	-	0.97	0.39	-	1.56	0.49	-	0.83	0.66	-	0.52	0.25	-	0.23	0.04	-	1.26	0.29
		range	2.46	0.98	-	1.49	0.65	-	2.19	0.71	-	1.04	0.79	-	0.69	0.32	-	0.13	0.03	-	1.38	0.23
		mean	-0.04	0.02	a	-0.08	0.02	a	0.11	0.01	b	0.00	0.02	ab	0.05	0.01	b	-0.10	0.05	a	15.39	<0.01
		s.d.	0.13	0.04	-	0.10	0.03	-	0.16	0.03	-	0.09	0.04	-	0.09	0.02	-	0.03	0.01	-	1.66	0.15
	AZ (*G*)	max	3.66	1.22	-	1.36	0.15	-	1.59	0.21	-	1.36	0.24	-	1.86	0.76	-	0.94	0.04	-	2.46	<0.05
		range	4.60	1.87	b	0.93	0.35	ab	1.49	0.37	ab	0.81	0.46	ab	1.74	1.31	ab	0.11	0.03	a	2.29	<0.05

		mean	0.89	0.02	ab	0.94	0.01	b	0.85	0.02	ab	0.95	0.01	ab	0.91	0.01	ab	0.75	0.12	a	2.76	<0.05
		s.d.	0.21	0.07	b	0.07	0.02	a	0.12	0.02	ab	0.06	0.02	ab	0.10	0.04	ab	0.03	0.01	a	2.42	<0.05
	MA (*G*)	max	4.08	1.39	-	1.92	0.43	-	2.82	0.57	-	1.74	0.58	-	2.07	0.79	-	10.99	0.03	-	1.57	0.17
		range	3.40	1.44	-	1.09	0.45	-	2.02	0.59	-	0.89	0.59	-	1.13	0.82	-	16.75	0.03	-	1.73	0.13
		mean	0.98	0.03	a	1.00	0.01	a	1.04	0.02	ab	1.01	0.01	ab	1.09	0.01	b	0.60	0.01	a	6.89	<0.01
		s.d.	0.23	0.09	-	0.09	0.03	-	0.16	0.04	-	0.07	0.05	-	0.08	0.05	-	2.93	0.01	-	1.66	0.15
	GX (degree/s)	max	429	157	b	142	51	ab	196	55	ab	74	32	ab	191	90	ab	1	2	a	2.26	0.05
		range	710	258	b	244	91	ab	325	83	ab	115	52	ab	251	106	a	0	3	a	2.72	0.02
		mean	2	1	-	2	1	-	-1	1	-	1	2	-	5	4	-	1	1	-	1.47	0.20
		s.d.	39	13	b	19	5	ab	32	6	b	10	3	ab	29	6	b	0	0	a	3.16	<0.01
	GY (degree/s)	max	593	203	b	207	60	ab	310	96	ab	208	137	ab	159	68	a	19	5	a	2.56	<0.05
		range	995	342	b	357	109	a	525	160	ab	378	259	ab	264	119	a	33	9	a	2.48	<0.05
		mean	-3	2	-	-3	1	-	3	1	-	-2	3	-	-1	2	-	-1	1	-	2.49	<0.05
		s.d.	61	18	b	31	7	a	51	9	b	29	13	ab	26	6	ab	6	1	a	3.49	<0.01
	GZ (degree/s)	max	228	75	ab	178	47	ab	320	73	b	222	113	ab	216	79	ab	17	2	a	1.72	0.13
		range	336	119	ab	235	62	ab	495	115	b	290	133	ab	298	103	ab	25	4	a	2.07	0.07
		mean	5	4	-	1	5	-	-1	4	-	2	6	-	3	5	-	-2	1	-	0.25	0.94
		s.d.	31	8	abc	31	5	ab	58	9	c	41	13	ab	44	9	b	5	1	a	3.96	<0.01
	MG (degree/s)	max	746	248	b	264	73	ab	472	127	ab	293	164	ab	317	136	ab	25	5	a	2.23	0.05
		range	742	248	b	260	73	ab	467	127	ab	290	164	ab	314	135	ab	24	5	a	2.23	0.06
		mean	39	7	bc	38	5	b	62	7	c	34	9	bc	50	8	bc	9	1	a	5.96	<0.01
		s.d.	75	22	b	39	9	ab	63	12	b	44	16	ab	46	10	ab	5	1	a	2.75	<0.05

Different lower case letters in TK represent significant differences detected by a Tukey-Kramer *post hoc* test (P<0·05).

Crab-eating, feeding behaviour on crab; Fish-eating, feeding behaviour on fish; Escape, escape response; Intra-attack, intraspecific interaction (attack); Intra-escape, intraspecific interaction (escape); Routine, routine movement; ANOVA, analysis of variance; s.e.m, standard error; TK, Tukey-Kramer test; s.d., standard deviation; AX, lateral acceleration; AY, forward acceleration; AZ, vertical acceleration; MA, vector sum of the accelerations; GX, pitch angular velocity; GY, roll angular velocity; GZ, yaw angular velocity; MG, vector sum of the angular velocities

Table S3. Summary of the stomach content analysis of 158 white-streaked groupers, *Epinephelus ongus* (252±26 mm total length)

Prey types		Family	N	W (g)	F
Crustaceans			**27**	**50.53**	**21**
	Crabs	Portunidae	12	39.005	10
		Xanthidae	4	2.82	4
		Majoidae	1	0.08	1
	Shrimps	Hippolytidae	8	6.555	7
		Alpheidae	1	1.02	1
		Unidentified	1	1.05	1
Fishes			**14**	**41.16**	**14**
		Pomacentridae	4	12.58	4
		Labridae	1	10.47	1
		Holocentridae	1	0.48	1
		Pempheridae	1	4.5	1
		Lutjanidae	1	7.16	1
		Unidentified	6	5.97	6
Others			**1**	**18.69**	**1**
	Octopus	Unidentified	1	18.69	1
Total			**42**	**110.38**	**33**

Thirty three individuals had some prey items in their stomachs.

N, total number; W, total weight; F, frequency of occurrence

Script 1. The custom R program to find the optimal thresholds of the parameters using the sum of sensitivity and specificity.

```
#########################################################################
## Note that rather than the conventional "<-", we use "=" as the
## assignment operator.
#########################################################################

### 1. Finding the start-point for data extraction ###

# Read the time-series data (3-axis accelerations and 3-axis
# angular velocities) from the data file. The data file is a comma
# separated file, has 7 columns of values, and each column is assigned
# to a variable. The variable names are "point" (sequential serial number),
# "ax" (lateral acceleration), "ay" (forward acceleration)
# "az" (vertical acceleration), "gx" (pitch angular velocity)
# "gy" (roll angular velocity), "gz" (yaw angular velocity)

original = read.csv("data1.csv")

# calculations of the vector sum of accelerations ("ma") and
# angular velocities ("mg")

original$ma = sqrt(original$ax^2 + original$ay^2 + original$az^2)
original$mg = sqrt(original$gx^2 + original$gy^2 + original$gz^2)

# find the maximum absolute value in the 3-axis accelerations

temp1 = data.frame(abs(original$ax),
                   abs(original$ay),
                   abs(original$az))
original$max3 = apply(temp1, 1, max)

## find the start-point and save to a csv file after looping over
## nrow(pointdata)-1.
filename1 = "startpoint.csv"
```

```
pointdata = original[original$max3 > 2,]
   # We set the max3 to > 2, because all the feeding behaviours
   # exceeded the absolute 2.0 G in at least one of the three axes.
out = paste("startpoint", sep = ",")
write(out, file = filename1, append = TRUE)
out = paste(pointdata[1, 1] + 1, sep = ",")
write(out, file = filename1, append = TRUE)

index = 0
for(i in 1:(nrow(pointdata) - 1)){
  if (index <= 1000){
    # We set the index to <= 1000, because we want to extract
    # 5 seconds of the data (200Hz * 5 sec = 1000 data points)
    index = index + pointdata[i + 1, 1] - pointdata[i, 1]
  }
  else{
    out = paste(pointdata[i + 1, 1] + 1, sep = ",")
    write(out, file = filename1, append = TRUE)
    index = 0
  }
}

### the end of 1 ###


### 2. Calculating the parameters ###
# The following packages are required.
require(e1071)
require(stringr)
require(plyr)
require(reshape2)

# Custom functions for parameter calculations
absmax = function(x){
  max(abs(x))
}
```

```
range = function(x){
  max(x) - min(x)
}

fn1 = function(x) c(
  absmax = absmax(x),
  range = range(x),
  avg = mean(x),
  sd = sd(x),
  a2 = 1
)

pointdata = read.csv(filename1)

for(i in 1:(nrow(pointdata))) {
  startpoint = pointdata[i, "startpoint"]
  if(startpoint + 999 < nrow(original)) {

    # Parameter calculations for the first phase
    timeseries = original[startpoint:(startpoint + 419),]
    # We set 419 here because we wanted to extract 0 ~ 2.1 seconds
    # of the data (200Hz * 2.1 sec = 420 data points)
    timeseries = timeseries[c("ax", "ay", "az", "gx",
                          "gy", "gz", "ma", "mg")]
    output = data.frame(aaply(t(timeseries), 1, fn1))
    output$names = row.names(output)
    output = reshape(output, idvar = "a2", timevar="names",
                  direction="wide")

    # Parameter calculations for the second phase
    timeseries2 = original[(startpoint + 420):(startpoint + 999),]
    # We set 420 and 999 here because we wanted to extract 2.1 ~ 5
    # seconds of the data
    timeseries2 = timeseries2[c("ax", "ay", "az","gx", "gy",
                            "gz", "ma", "mg")]
```

```
    output2 = data.frame(aaply(t(timeseries2), 1, fn1))
    output2$names = row.names(output2)
    output2 = reshape(output2, idvar = "a2", timevar="names",
                    direction="wide")

    out = data.frame(output[2:ncol(output)], output2[2:ncol(output2)])
    out$startpoint = startpoint
    write.table(out, file = "parameters.csv",
              row.names = FALSE, col.names = FALSE, append = TRUE,
              quote = FALSE, sep = ",")
  }
}

### the end of 2 ###


### 3. Calculating the sum of sensitivity and specificity to find
### the optimal thresholds

# Read the datasets (fish ID, behavioral data that were determined by
# the video, and calculated parameters are needed).

# Here, our datasets have "fish" ("a"~"f"), "behavior"
# (Fc, Feeding-crab; Ff, Feeding-fish; Es, Escape; Ia, Intra-attack;
# Ie, Intra-escape; Rm, Routine movements) , "gxgyrange" (the ratio of
# the range of pitch angular velocity to the range of yaw angular
# velocity in the first phase), "avgmg2" (the mean vector sum of the
# angular velocities in the second phase), "sdax" (the standard
# deviation of the lateral acceleration in the first phase), and
# "gzgyrange" (the ratio of the range of yaw angular velocity to the
# range of roll angular velocity in the first phase).

test = read.csv("data2.csv")

# Separating the modeling data and test data.
# If you want to conduct the cross validation test, then use different
```

```
# fish IDs for the "model" and "testafter"
model = test[test$fish == "a" | test$fish == "b" | test$fish == "c" |
             test$fish == "d" | test$fish == "e" | test$fish=="f", ]
testafter = test[test$fish == "a" | test$fish == "b" |
                 test$fish == "c" | test$fish == "d" |
                 test$fish == "e" | test$fish == "f", ]


## 3.1. Calculating the sum of sensitivity + specificity
## for Feeding-crab
fcname = "mapfc.csv"
out = paste("b1", "b2", "sens", "spec", "youden", sep = ",")
write(out, file = fcname, append = TRUE)


for(i in 1:100){
  b1 = 0.02 * i
  # change the "gxgyrange" cut-off value from 0.02 to 2.00 to find the
  # optimal threshold
  a = model[model$gxgyrange >= b1,]
  if(nrow(a) >= 1){
    a$node1 = 1
  }
  b = model[model$gxgyrange < b1,]
  if(nrow(b) >= 1){
    b$node1 = 0
  }
  model2 = rbind(a, b)

  for(j in 1:100){
    b2 = 0.5 * j
    # change the "avgmg2" cut-off value from 0.5 to 50 to find the
    # optimal value
    a = model2[model2$avgmg2 >= b2,]
    if (nrow(a) >= 1){
      a$node2 = 1
```

```
    }
    b = model2[model2$avgmg2 < b2,]
    if(nrow(b) >= 1){
      b$node2 = 0
    }
    model3 = rbind(a, b)

    a = model3[model3$node1 * model3$node2 == 1,]
    if(nrow(a) >= 1){
      a$estimateFc = "Fc"
    }
    b = model3[model3$node1 * model3$node2 == 0,]
    if(nrow(b) >= 1){
      b$estimateFc = "O"
    }
    model4 = rbind(a, b)
    # calculation of the sensitivity
    sens = nrow(model4[model4$behavior == "Fc" &
                       model4$estimateFc == "Fc",]) /
      nrow(model4[model4$behavior == "Fc",])
    # calculation of the specificity
     spec = nrow(model4[model4$behavior != "Fc" &
                       model4$estimateFc != "Fc",]) /
      nrow(model4[model4$behavior != "Fc",])
    youden = sens + spec
    out = paste(b1, b2, sens, spec, youden, sep = ",")
    write(out, file = fcname, append = TRUE)
  }
}

# extracting the optimal thresholds
mapfc = read.csv(fcname)
M = max(mapfc$youden)
a = which(mapfc$youden == M)
# the optimal threshold of "gxgyrange"
cutb1=mean(mapfc[a, "b1"])
```

```
# the optimal threshold of "avgmg2"
cutb2=mean(mapfc[a, "b2"])

# mapping the sum of sensitivity and specificity against the
# "gxgyrange" and "avgmg2"
mapfc = matrix(mapfc$youden, nrow = 100)
mapfc = t(mapfc)
x = 1:nrow(mapfc)
y = 1:ncol(mapfc)
filled.contour(x, y, mapfc)

## the end of 3.1 ##

## 3.2. Calculating the sum of sensitivity + specificity for
# Feeding-fish
ffname = "mapff.csv"
out = paste("b1", "b2", "sens", "spec", "youden", sep = ",")
write(out, file = ffname, append = TRUE)

for(i in 1:100){
  # change the "sdax" cut-off value from 0.02 to 2.00 to find the
  # optimal threshold
  b1 = 0.02 * i
  a = model[model$sdax >= b1,]
  if(nrow(a) >= 1){
    a$node1 = 1
  }

  b = model[model$sdax < b1,]
  if(nrow(b) >= 1){
    b$node1 = 0
  }
  model2 = rbind(a, b)

  for(j in 1:100){
    # change the "gzgyrange" cut-off value from 0.02 to 2.00 to find
```

```
    # the optimal threshold
    b2 = 0.02 * j
    a = model2[model2$gzgyrange <= b2,]
    if(nrow(a) >= 1){
      a$node2 = 1
    }
    b = model2[model2$gzgyrange > b2,]
    if(nrow(b) >= 1){
      b$node2 = 0
    }
    model3 = rbind(a, b)
    a = model3[model3$node1*model3$node2 == 1,]
    if(nrow(a) >= 1){
      a$estimateFf = "Ff"
    }
    b = model3[model3$node1*model3$node2 == 0,]
    if(nrow(b) >= 1){
      b$estimateFf = "O"
    }

    model4 = rbind(a, b)
    # calculation of the sensitivity
    sens = nrow(model4[model4$behavior == "Ff" &
                       model4$estimateFf == "Ff",]) /
      nrow(model4[model4$behavior == "Ff",])
    # calculation of the specificity
    spec = nrow(model4[model4$behavior != "Ff" &
                       model4$estimateFf != "Ff",]) /
      nrow(model4[model4$behavior != "Ff",])
    youden = sens + spec
    out = paste(b1, b2, sens, spec, youden, sep = ",")
    write(out, file = ffname, append = TRUE)
  }
}

# extracting the optimal thresholds
```

```
mapff = read.csv(ffname)
M = max(mapff$youden)
a = which(mapff$youden == M)
# the optimal threshold of "sdax"
cutb1 = mean(mapff[a, "b1"])
# the optimal threshold of "gzgyrange"
cutb2 = mean(mapff[a, "b2"])

# mapping the sum of sensitivity and specificity against the "sdax"
# and "gzgyrange"
mapff = matrix(mapff$youden, nrow = 100)
mapff = t(mapff)
x = 1:nrow(mapff)
y = 1:ncol(mapff)
filled.contour(x, y, mapff)

## the end of 3.2 ##
### the end of 3 ###
```