Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish

Yuuki Kawabata1,*, Takuji Noda2, Yuuki Nakashima1, Atsushi Nanami2, Taku Sato3, Takayuki Takebe3, Hiromichi Mitamura2, Nobuaki Arai2, Tomofumi Yamaguchi1,3 and Kiyoshi Soyano1

ABSTRACT
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 three-axis gyroscope and a three-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 s of data when any of the three-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.

KEY WORDS: 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, 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 that incorporated a gyroscope and an accelerometer compared with 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 three-axis angular velocities as well as three-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 crabs (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), nine intraspecific attacks (intra-attack), 27 intraspecific escape (intra-escape) and 16 routine movements (routine) were detected by a set threshold (2.0g) (supplementary material Table S1), from a total of 17 crab-eating, 34 fish-eating, 42 escape, 48 intra-attack and 48 intra-escape behaviours recorded by a video camera. Secondly, the featured parameters were calculated (supplementary material Table S2) after extracting the subsequent 5 s of data and then dividing into the first phase (2.1 s) and second phase (2.9 s) (see Materials and methods and supplementary material 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).

*Epinephelus ongus* exhibited larger pitch motions to pick up crabs (supplementary material Movies 1–6); the ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase (RangePitch1/RangeYaw1) of the crab-eating behaviour was larger than that of the fish-eating, escape, intra-attack and intra-escape behaviours (ANOVA, *P*<0.01; Tukey–Kramer test, *P*<0.05; Fig. 1C). *Epinephelus ongus* did not move substantially during the second phase of routine behaviour; the mean vector sum of the angular velocities in the second phase (MeanMG2) of the routine behaviour was lower than those of the crab-eating, fish-eating, escape and intra-escape behaviours (ANOVA, *P*<0.01; Tukey–Kramer test, *P*<0.05; Fig. 1D). Thus, RangePitch1/RangeYaw1 was used to discriminate crab-eating from fish-eating, escape, intra-attack and intra-escape behaviours (Fig. 1A,C), and MeanMG2 was used to discriminate crab-eating from routine behaviour (Fig. 1A,D). The sum of sensitivity (true identification rate) and specificity
The identification rate was 6.3% (5/80; Table 3). The mean MG-2 was 1.83 at thresholds of 1.19 and 11 in the RangePitch-1/RangeYaw-1 and threshold (see Materials and methods for details), revealed a peak at 87.5% (14/16) and the false identification rate was 5% (4/80; Fig. 1, Table 3). 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).

**Epinephelus ongus** exhibited a strong fast-start motion during fish-eating and escape compared with the other behaviours (supplementary material Movies 1–6). The standard deviation of the lateral acceleration in the first phase (SDAX-1) of fish-eating and escape was higher than that of the other behaviours (ANOVA, P<0.01; Tukey–Kramer test, P<0.05; Fig. 1C). **Epinephelus ongus** showed strong yaw motion during escape compared with 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 (RangePitch-1/RangeRoll-1) of escape was larger than that of fish-

**Fig. 1. Decision tree algorithm to identify feeding behaviours on crab (crab-eating).**

(A) A decision tree that uses derived parameters. The numbers in parentheses in each square indicate the percentage of crab-eating behaviour/percentage of others. (B) Sum of sensitivity and specificity, used to determine the threshold values, plotted against the derived parameters. Arrow represents the determined thresholds: 1.19 in RangePitch-1/RangeYaw-1 and 11 in MeanMG-2.

(C,D) Comparisons of selected parameters (RangePitch-1/RangeYaw-1 and MeanMG-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. Different lowercase letters represent significant differences in the Tukey–Kramer post hoc test (P<0.05). Dashed blue lines represent threshold values based on the sum of sensitivity and specificity. RangePitch-1/RangeYaw-1, ratio of the range of pitch angular velocity to the range of yaw angular velocity in the first phase; MeanMG-2, mean vector sum of the angular velocities in the second phase.

**Fig. 2. Decision tree algorithm to identify feeding behaviours on fish (fish-eating).**

(A) A decision tree that uses derived parameters. The numbers in parentheses in each square indicate the percentage of fish-eating behaviour/percentage of others. (B) Sum of sensitivity and specificity, used to determine the threshold values, plotted against the derived parameters. Arrow represents the determined thresholds: 0.57 in SDAX-1, 0.69 in RangePitch-1/RangeRoll-1.

(C,D) Comparisons of selected parameters (SDAX-1 and RangePitch-1/RangeRoll-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. Different lowercase letters represent significant differences in the Tukey–Kramer post hoc test (P<0.05). Dashed blue lines represent threshold values based on the sum of sensitivity and specificity. SDAX-1, standard deviation of the lateral acceleration in the first phase; RangePitch-1/RangeRoll-1, ratio of the range of yaw angular velocity to the range of roll angular velocity in the first phase.
Table 1. Decision tree results for identifying feeding behaviour on crab (crab-eating), in which the same data set was used for deriving the decision tree algorithm and for testing identification success

<table>
<thead>
<tr>
<th></th>
<th>Crab-eating</th>
<th>Fish-eating</th>
<th>Escape</th>
<th>Intra-attack</th>
<th>Intra-escape</th>
<th>Routine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crab-eating</td>
<td>14 (87.5)</td>
<td>3 (18.8)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (6.3)</td>
</tr>
<tr>
<td>Others</td>
<td>2 (12.5)</td>
<td>13 (81.3)</td>
<td>16 (100)</td>
<td>16 (100)</td>
<td>16 (100)</td>
<td>15 (93.8)</td>
</tr>
</tbody>
</table>

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

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

<table>
<thead>
<tr>
<th></th>
<th>Fish-eating</th>
<th>Crab-eating</th>
<th>Escape</th>
<th>Intra-attack</th>
<th>Intra-escape</th>
<th>Routine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish-eating</td>
<td>14 (87.5)</td>
<td>4 (25)</td>
<td>1 (6.3)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Others</td>
<td>2 (12.5)</td>
<td>12 (75)</td>
<td>15 (93.8)</td>
<td>16 (100)</td>
<td>16 (100)</td>
<td>16 (100)</td>
</tr>
</tbody>
</table>

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

Methods and Techniques

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. The present 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 lizards, salamanders, frogs 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 statement

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 no. ECSER12-02) in accordance with the Guidelines for Animal Experimentation of Nagasaki University.
study animals

Epinephelus 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 fibre-reinforced plastic (FRP) tanks for at least 2 days prior to experimental testing.

Two different prey types – the mangrove swimming crab, Thalamita crenata (Porudaeae) (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 because 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 three-axis accelerometer and a three-axis gyroscope (LP-BLKU02, Biologging Solutions Inc., Kyoto, Japan; 60×5×13 mm, mass 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 (~2 mm in diameter) were drilled into their dorsal musculature above their approximate centre of mass (39% of 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 or 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 ~22 h. The data loggers were scheduled to record data at 17:00–18:30 h; this period was chosen because this species increases its foraging activity during 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 intranspecific 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 intranspecific 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 three-axis acceleration and three-axis angular velocity datasets [see Luinge and Veltink (Luinge and Veltink, 2005) and Noda et al. (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, because 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, as 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 s) and total periods (3–13 s) were tested using the sum of sensitivity and specificity, and 2.1 and 5 s were chosen as the optimal periods (supplementary material Fig. S1). Featured parameters (maximum value, mean, range and standard deviation) were calculated based on the three-axis accelerations and three-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-axisal parameters (e.g. ratio of maximum forward acceleration to maximum lateral acceleration) were considered and selected for identification analysis. ANOVA and Tukey–Kramer post hoc tests were used to determine any significant differences in 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 because there was no single parameter that can differentiate each of the feeding behaviours from all 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: sensitivity= (true positive)/(true positive+ false negative) and specificity= (true negative)/(false positive+true negative).

The criterion (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 (R Foundation for Statistical Computing, Vienna, Austria) (see supplementary material Script 1 for the custom-made program).

Acknowledgements

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Competing interests

The authors declare no competing financial interests.

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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Supplementary material

Supplementary material available online at http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.108001/-/DC1

References


METHODS & TECHNIQUES


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*

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

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

<table>
<thead>
<tr>
<th>Phase</th>
<th>Parameter</th>
<th>Crab-eating (n=17)</th>
<th>Fish-eating (n=34)</th>
<th>Escape (n=42)</th>
<th>Intra-attack (n=8)</th>
<th>Intra-escape (n=27)</th>
<th>Routine (n=16)</th>
<th>ANOVA</th>
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<tr>
<td></td>
<td></td>
<td>mean s.e.m TK</td>
<td>mean s.e.m TK</td>
<td>mean s.e.m TK</td>
<td>mean s.e.m TK</td>
<td>mean s.e.m TK</td>
<td>mean s.e.m TK</td>
<td>F-value</td>
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<tr>
<td>Phase1</td>
<td>AX (G) max</td>
<td>5.78 1.05 a</td>
<td>8.95 0.70 b</td>
<td>13.70 0.99 c</td>
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<td>2.75 0.40 a</td>
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<td>14.74 0.92 b</td>
<td>21.81 1.59 c</td>
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</tr>
<tr>
<td></td>
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<td>0.09 0.04 a</td>
<td>0.30 0.06 b</td>
<td>0.13 0.08 a</td>
<td>0.48 0.05 b</td>
<td>0.17 0.07 a</td>
<td>8.09</td>
</tr>
<tr>
<td></td>
<td>s.d.</td>
<td>0.48 0.07 a</td>
<td>0.84 0.06 b</td>
<td>1.51 0.12 c</td>
<td>0.27 0.06 a</td>
<td>0.29 0.03 a</td>
<td>0.26 0.03 a</td>
<td>34.67</td>
</tr>
<tr>
<td></td>
<td>AY (G) max</td>
<td>4.87 0.82 a</td>
<td>9.02 0.62 b</td>
<td>14.02 1.10 c</td>
<td>3.10 1.37 a</td>
<td>2.69 0.29 a</td>
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<td>28.04</td>
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<td>8.10 1.34 a</td>
<td>13.90 0.92 b</td>
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<td>4.35 1.62 a</td>
<td>3.91 0.42 a</td>
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<tr>
<td></td>
<td>mean</td>
<td>-0.03 0.03 b</td>
<td>-0.15 0.03 a</td>
<td>0.00 0.02 ab</td>
<td>-0.01 0.04 bc</td>
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<td>-0.04 0.05 bc</td>
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<tr>
<td></td>
<td>s.d.</td>
<td>0.45 0.06 a</td>
<td>0.82 0.06 b</td>
<td>1.43 0.13 c</td>
<td>0.26 0.07 a</td>
<td>0.29 0.03 a</td>
<td>0.26 0.05 a</td>
<td>26.49</td>
</tr>
<tr>
<td></td>
<td>AZ (G) max</td>
<td>4.61 0.62 ab</td>
<td>6.98 0.63 b</td>
<td>9.72 0.63 c</td>
<td>2.13 0.25 a</td>
<td>2.33 0.23 a</td>
<td>3.72 0.64 ab</td>
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<td>range</td>
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<td>11.98 1.08 b</td>
<td>16.20 1.41 c</td>
<td>2.54 0.49 a</td>
<td>3.02 0.43 a</td>
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The Journal of Experimental Biology | Supplementary Material
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<tr>
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<td>max</td>
<td>429</td>
<td>157</td>
<td>b</td>
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<td>51</td>
<td>ab</td>
<td>196</td>
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<td>ab</td>
<td>74</td>
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<td>ab</td>
<td>191</td>
<td>90</td>
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<td>a</td>
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<td>0.05</td>
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<td>710</td>
<td>258</td>
<td>b</td>
<td>244</td>
<td>91</td>
<td>ab</td>
<td>325</td>
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<td>ab</td>
<td>115</td>
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<td>ab</td>
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<td>106</td>
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<td>19</td>
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<td>ab</td>
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<td>b</td>
<td>10</td>
<td>3</td>
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<td>29</td>
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<td>b</td>
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<td>207</td>
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<td>&lt;0.05</td>
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<td>ab</td>
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<td>216</td>
<td>79</td>
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<td>119</td>
<td>ab</td>
<td>235</td>
<td>62</td>
<td>ab</td>
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<td>115</td>
<td>b</td>
<td>290</td>
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<td>ab</td>
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<td>5</td>
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<td>5</td>
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<td>ab</td>
<td>58</td>
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<td>c</td>
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<td>13</td>
<td>ab</td>
<td>44</td>
<td>9</td>
<td>b</td>
<td>5</td>
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<td>a</td>
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<td>&lt;0.01</td>
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<td>MG (degree/s)</td>
<td>max</td>
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<td>248</td>
<td>b</td>
<td>264</td>
<td>73</td>
<td>ab</td>
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<td>ab</td>
<td>293</td>
<td>164</td>
<td>ab</td>
<td>317</td>
<td>136</td>
<td>ab</td>
<td>25</td>
<td>5</td>
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<td>248</td>
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<td>ab</td>
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<td>ab</td>
<td>290</td>
<td>164</td>
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<td>38</td>
<td>5</td>
<td>b</td>
<td>62</td>
<td>7</td>
<td>c</td>
<td>34</td>
<td>9</td>
<td>bc</td>
<td>50</td>
<td>8</td>
<td>bc</td>
<td>9</td>
<td>1</td>
<td>a</td>
<td>5.96</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
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<td>75</td>
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<td>b</td>
<td>39</td>
<td>9</td>
<td>ab</td>
<td>63</td>
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<td>b</td>
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<td>16</td>
<td>ab</td>
<td>46</td>
<td>10</td>
<td>ab</td>
<td>5</td>
<td>1</td>
<td>a</td>
<td>2.75</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

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)

<table>
<thead>
<tr>
<th>Prey types</th>
<th>Family</th>
<th>N</th>
<th>W (g)</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustaceans</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crabs</td>
<td>Portunidae</td>
<td>12</td>
<td>39.005</td>
<td>10</td>
</tr>
<tr>
<td>Xanthidae</td>
<td></td>
<td>4</td>
<td>2.82</td>
<td>4</td>
</tr>
<tr>
<td>Majoidae</td>
<td></td>
<td>1</td>
<td>0.08</td>
<td>1</td>
</tr>
<tr>
<td>Shrimps</td>
<td>Hippolytidae</td>
<td>8</td>
<td>6.555</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Alpheidae</td>
<td>1</td>
<td>1.02</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Unidentified</td>
<td>1</td>
<td>1.05</td>
<td>1</td>
</tr>
<tr>
<td>Fishes</td>
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<td>14</td>
<td>41.16</td>
<td>14</td>
</tr>
<tr>
<td>Pomacentridae</td>
<td></td>
<td>4</td>
<td>12.58</td>
<td>4</td>
</tr>
<tr>
<td>Labridae</td>
<td></td>
<td>1</td>
<td>10.47</td>
<td>1</td>
</tr>
<tr>
<td>Holocentridae</td>
<td></td>
<td>1</td>
<td>0.48</td>
<td>1</td>
</tr>
<tr>
<td>Pempheridae</td>
<td></td>
<td>1</td>
<td>4.5</td>
<td>1</td>
</tr>
<tr>
<td>Lutjanidae</td>
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<td>1</td>
<td>7.16</td>
<td>1</td>
</tr>
<tr>
<td>Unidentified</td>
<td></td>
<td>6</td>
<td>5.97</td>
<td>6</td>
</tr>
<tr>
<td>Others</td>
<td>Octopus</td>
<td>1</td>
<td>18.69</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Unidentified</td>
<td>1</td>
<td>18.69</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>42</td>
<td>110.38</td>
<td>33</td>
</tr>
</tbody>
</table>

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.

```r
######################################################################
## 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

templ = data.frame(abs(original$ax),
                   abs(original$ay),
                   abs(original$az))
original$max3 = apply(templ, 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))
}

The Journal of Experimental Biology | Supplementary Material
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(aapply(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
}
```r
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[, "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 = " ",
            append = TRUE)

write(out, file = ffname, append = TRUE)
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 ###