



## Using accelerometry to quantify prey attack and handling behaviours in piscivorous pike *Esox lucius*

Deurs, Mikael van; Andersson, A.; Vinterstare, J.; Didenko, A.; Persson, A.; Brönmark, Christer; Nilsson, P.A.

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1 BRIEF COMMUNICATION

2

3 TITLE: Using accelerometry to quantify prey attack and handling behaviours in piscivorous pike  
4 *Esox lucius*

5

6 AUTHORS: Mikael van Deurs<sup>1,2,\*</sup>, Arne Andersson<sup>1</sup>, Jerker Vinterstare<sup>1</sup>, Alexander Didenko<sup>3</sup>  
7 Anders Persson<sup>1</sup>, Christer Brönmark<sup>1</sup> and P. Anders Nilsson<sup>1,4</sup>

8

9 AUTHOR AFFILIATION:

- 10 1. Department of Biology, Ecology Building, Lund University, SE-223 62 Lund, Sweden.  
11 2. National Institute for Aquatic resources - Section for Marine Living Resources, Technical  
12 University of Denmark, Jægersborgs alle 1, DK-2920 Charlottenlund, Denmark.  
13 3. Institute of Fisheries of the National Academy of Agrarian Sciences of Ukraine, Obukhivska  
14 St. 135, 03164 Kiev, Ukraine  
15 4. Department of Environmental and Life Sciences - Biology, Karlstad University, SE-651 88,  
16 Karlstad, Sweden.

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18 \* Author to whom correspondence should be addressed: Mikael van Deurs, Tel: +45 51369380;  
19 email: [mikael.van\\_deurs@biol.lu.se](mailto:mikael.van_deurs@biol.lu.se) and [mvd@aqua.dtu.dk](mailto:mvd@aqua.dtu.dk)

20

21 KEY WORDS: accelerometer; *Esox lucius*; foraging; handling time; predation

22

23 ABSTRACT:

24 Predator-prey interactions play a central role in structuring aquatic food webs. Technical  
25 development that offers opportunities to observe predator behaviour also in the dark or in humic  
26 waters is therefore warranted. Here we use accelerometer technology to evaluate behaviours in the  
27 teleost ambush predator pike *Esox lucius* foraging on crucian carp. Automated rule-based estimates  
28 of prey-size determined handling time were obtained and are compared to video-recorded  
29 behaviours. Solutions to tag attachment and the limitations imposed by battery-time and data-  
30 logging capacities are evaluated.

31

32 MANUSCRIPT:

33 Piscivore predation plays a central role in structuring aquatic food webs (Kerfoot and Sih 1987,  
34 Carpenter and Kitchell, 1993). Predation is performed by individuals, and to bridge the order scales  
35 between individuals and systems, we need better identification of what factors and mechanisms  
36 influence behaviour and decision-making in individual predators (Fryxell and Lundberg, 1998).  
37 Fish are commonly apex predators in aquatic systems, but direct observation of their behaviour in  
38 nature is challenging (e.g. Jepsen et al. 2001). Studies are therefore commonly restricted to small  
39 scale laboratory settings (e.g. Nilsson et al., 2000), but even here the opportunity to make  
40 observations directly or by camera relies on sufficient visibility and proper light conditions (e.g.  
41 Jönsson et al., 2013). Studies on fish predator-prey interactions in darkness or in highly turbid or  
42 humic water are hence scarce for logistical reasons. Technical development however offers

43 opportunities to quantify predator behaviours also in the absence of visual signals. For example,  
44 conventional telemetry techniques can aid the collection of positional data (Marsac & Cayré, 1998),  
45 physiological telemetry techniques can monitor heart rate frequency (Priede, 1983), data storage  
46 tags can supply information on e.g. depths and temperature across visibilities and habitats  
47 (Stensholt, 2001), and accelerometers can measure and monitor behavioural activities (Broell et al.  
48 2013).

49 This study evaluates the use of accelerometer tags for indirect observation of piscivore-prey  
50 interactions using the ambush predator pike *Esox lucius* L. 1758 as model species (Craig, 1996,  
51 Forsman *et al.*, 2015). Accelerometers have previously been used for different applications in fish  
52 behavioural studies, such as the measurement of burst swimming performance (Franklin *et al.*,  
53 2003), activity patterns and energy expenditure (Murchie *et al.*, 2011; Wright *et al.*, 2014), fast start  
54 behaviour (Noda *et al.*, 2013), foraging behaviour (Broell *et al.*, 2013; Brownscombe *et al.*, 2014;  
55 Kawabata *et al.*, 2014), and mating and spawning behaviour (Tsuda *et al.*, 2006; Whitney *et al.*,  
56 2010). While previous studies have focused on distinguishing between different types of behaviour  
57 (i.e. foraging vs. escaping), the present work also evaluates the prospects of applying accelerometry  
58 to estimate handling time and prey size in situations where visual observation techniques are  
59 logistically impossible. Furthermore, as for pike, fast-start performance and prey capture dynamics  
60 have until now only been evaluated using video techniques (Webb & Skadsen, 1980; Rand &  
61 Lauder, 1981; Frith & Blake, 1991; Harper & Blake, 1991).

62 The accelerometer tag (2.3g (air), 25x12mm, 1.55V silver-oxide button cell (V389, Varta AG))  
63 contained a 3-axis MEMS (Micro-Electro-Mechanical-System) accelerometer sensor and a 2Mbit  
64 memory. The accelerometer was set in low-power, “wait-for-movement”-state, and data collection  
65 was triggered by an acceleration threshold at  $\pm 1.5g$  ( $g=9.82m\ sec^{-2}$ ) for more than 0.2 sec,  
66 indicative of attack behaviour. The threshold level was established when preparing for the study by

67 gradually increasing the threshold until activity events, that were not attacks, no longer triggered the  
68 data-logger (in total 5 preliminary trials without prey fish was made). The data logger then  
69 continuously recorded acceleration with 12-bit resolution at 100 Hz during 7 minutes. To avoid  
70 accidental triggering of data collection prior to or during tag attachment, the tag was pre-  
71 programmed with time of tag activation.

72

73 Two pikes (35 and 37 cm) were caught by electrofishing in the Lake Krankesjön, southern Sweden,  
74 and directly transported to the Ecology building, Lund University. Prior to and during the  
75 experiment, pike were individually held in a 200 × 50 × 50 cm aquarium (water depth: 15 cm)  
76 divided into two equally sized compartments by a sheet of grey PVC. Before each trial, a Velcro  
77 tape (15×7 mm) was glued (Loctite super attack) to the accelerometer tag, and the matching part of  
78 the Velcro was glued dorsally to the hard part of the pike head using veterinary glue (3M Vetbond,  
79 Fig. 1a) c. 24 hours before activation of the accelerometer tag. Attaching the tag to the head rather  
80 than the body allowed for detection of head shaking during prey handling. The accelerometer tag  
81 was then carefully attached to the pike by connecting the two matching Velcro parts. This was done  
82 approximately three hours prior to the pre-programmed tag activation time, and without any  
83 handling or removing of pike from the aquarium. To trigger natural attack behaviour in predatory  
84 fish, dead prey is often inadequate (see also Broell *et al.*, 2013). Therefore, an individual life  
85 crucian carp *Carassius carassius* L. 1758 (length: 7.2-12.0 cm) was placed under a non-transparent  
86 plastic container (14×10×20 cm) in one of the short ends of the arena five minutes before tag  
87 activation time. Ten minutes later, i.e. five minutes after tag activation, the prey was released by  
88 removing the container via a remote pulley system. Activity was monitored and recorded by a  
89 surveillance system (Timihillone H264) with a camera (Logitech C920HD) centrally located above  
90 the experimental arena. Experiments were performed under evaluation and permission from the

91 Malmö/Lund authority for ethics of animal experimentation (licence M36-14), and the use of live  
92 prey fish here, were comparable to Broell *et al.* (2013) and in Kawabata *et al.* (2014). Furthermore,  
93 in order to minimize the potentially harmful treatment of the prey fish, number of predators and the  
94 number trials was reduced as much as possible without compromising the conclusions. Also a novel  
95 and non-invasive (i.e. skin or flesh penetration) way of attaching the data-logger to the predator was  
96 applied.

97

98 Data from the accelerometer tag consisted of acceleration along the x, y, and z axes recorded at 100  
99 Hz. This three-dimensional data was translated to one-dimensional acceleration using vector norm  
100 calculations  $MA = \sqrt{x^2 + y^2 + z^2}$  according to Broell *et al.* (2013). The accelerometer-based  
101 handling time ( $h_a$ ) was computed as the time period (sec) between the start of the attack that  
102 triggered the data logger until  $MA$  fell below a threshold value ( $\tau$ ) of  $MA = 1.5$ . The accuracy of  $h_a$   
103 values were validated by comparison with video recorded handling times, where two definitions of  
104 handling time were applied when determining observed handling time: time from start of the attack  
105 until the pike completely stopped moving ( $h_1$ ) (this definition allowed unsuccessful attacks to be  
106 considered), and time from the start of the attack until the prey was completely engulfed ( $h_2$ , only  
107 applied to successful attacks). The sensitivity of  $h_a$  to  $\tau$  was evaluated for values of  $\tau$  from 1 to 2 in  
108 steps of 0.1. Sensitivity to data logging frequency was evaluated by comparing the  $h_a$  values  
109 derived from the original data sets to  $h_a$  values derived from modified data sets where only every  
110 tenth data point was included (simulating a data-logging frequency of 10 Hz).

111

112 The video recordings confirmed that the accelerometer tag was activated only when the pike  
113 attacked a prey, and no attacks took place without activating the tag. In total, eight successful trials

114 were completed (5 for pike-1 and 3 for pike-2). Trials were considered unsuccessful if the pike was  
115 uninterested in the prey, the video recordings failed, tag pre-programming was erroneous, or the tag  
116 detached prior to or during the trial. Video footage revealed that half of the successful trials resulted  
117 in a successful attack where the prey was swallowed (both pikes displayed successful and  
118 unsuccessful attacks). Unsuccessful attacks were either a single unsuccessful strike with no prey  
119 handling, or on two occasions, successful strikes was followed by unsuccessful attempts to hold or  
120 turn the prey. The accelerometer tag produced 3D data on movement that were readily transformed  
121 to one-dimensional *MA* for analyses (Fig. 1).

122 The computerized accelerometer-based handling time ( $h_a$ ) was significantly correlated to the  
123 observed handling time. The best correlation was found for  $h_a$  versus  $h_1$  (Linear regression:  $r^2 =$   
124  $0.93$ ,  $F_{1,7}=97.28$ ,  $p < 0.001$ ) and only slightly off the 1:1 relationship (i.e. small underestimation of  
125  $h_1$ ) (Fig. 2a). However, in the case of the observed handling time fulfilling definition 2 ( $h_2$ ,  
126 completely engulfed prey) the performance of the accelerometer was poorer. Even though the  
127 relationship was still highly significant (Linear regression:  $r^2=0.87$ ,  $F_{1,7}=47.1$ ,  $p < 0.001$ ), the  
128 computed  $h_a$  values were to a much larger extent underestimating the observed handling times (Fig.  
129 2b). The computation procedure of  $h_a$  was relatively insensitive to the selected threshold ( $\tau$ ) (Fig.  
130 2c) and to a reduction in data-logging frequency from 100 Hz to 10 Hz (Fig. 2d). Reducing the  
131 frequency did, however, result in loss of handling events lasting less than c. 1 s (i.e. failed to detect  
132 one successful and two unsuccessful attacks at 10 Hz). A previous study, differentiating between  
133 attack behaviour and other types of standard behaviours, also found that reducing the frequency is  
134 potentially problematic (Broell *et al.*, 2013). Lastly, it should be noted that in a few occasions a  
135 single brief *MA* spikes exceeding default  $\tau$  ( $MA = 1.5$ ) was observed long after completed prey  
136 capture and handling. However, these spikes never exceeded  $MA = 2$  and lasted less than 0.2 sec,  
137 and was therefore easily distinguished from unsuccessful attacks.

138 It was not possible to tell apart successful attacks on small prey from unsuccessful attacks, based on  
139 accelerometer output. For example, the geometric mean  $MA$  during periods of prey handling were  
140 negatively related to  $h_a$ , meaning that when unsuccessful attacks produced relatively high levels of  
141  $MA$ , this had to do with the relatively lower  $h_a$  of unsuccessful attacks (Fig. 3a,b). The geometric  
142 mean  $MA$  was highly correlated with average amplitude (i.e Pearson's correlation coefficient: 0.95;  
143  $t=7.63$ ,  $df = 6$ ,  $p < 0.002$ ). Hence, the same conclusion was reached when using  $MA$  amplitude  
144 instead of geometric mean  $MA$  as an explanatory factor.

145 It has previously been demonstrated that accelerometer tags can be applied to discriminate between  
146 escape, feeding, and routine behaviour (Broell *et al.*, 2013), determine swimming speed (Thiem *et*  
147 *al.*, 2015), and burrowing behaviour (Almeida *et al.*, 2013). Adding to this list, the potential of  
148 quantifying handling time and prey size enables important and interesting possibilities for studying  
149 predation and its consequences in aquatic systems.

150 Automated, numerical estimates of accelerometer-derived handling times ( $h_a$ ) allows for swift  
151 processing of large amounts of data, compared to e.g. video analyses. Estimates of  $h_a$  corresponded  
152 well with observed time from attack until the pike stopped moving ( $h_1$ ). The remaining part of prey  
153 handling was however not detected by the accelerometer, despite high gill movement, why handling  
154 time until complete swallowing of prey ( $h_2$ ) was poorly estimated.

155 The ability of accelerometry to discern between successful and unsuccessful attacks is limited. Half  
156 of the unsuccessful attacks in the present study lasted less than one second, consisting of missed  
157 strikes. However, one successful attack also lasted less than one second, involving the smallest prey  
158 (72 mm) used in the experiment. This prey was immediately swallowed. All other successful attacks  
159 lasted at least eight seconds. On the opposite side one unsuccessful attack lasted more than one  
160 second, as the prey was lost relatively late in the handling phase, and this attack could likewise not



161 be discriminated from the successful attacks. Failed strikes may thus be identified only in situations  
162 where the available prey items are relatively large and uniform in size.

163 In the majority of published accelerometer studies, the tag was attached to fish using invasive  
164 methods such as attachments through the dorsal musculature with different types of sutures or  
165 plastic wires (e.g. Franklin *et al.*, 2004; Broell *et al.*, 2013; Almeida *et al.*, 2013) or implanted into  
166 the abdominal cavity (e.g. Murchie *et al.*, 2011; Wright *et al.*, 2014; Landsman *et al.*, 2015). In the  
167 present study, tags were attached using surgical glue. This approach brought minimal harm to the  
168 fish, but the tag remained on the fish in general only 24-72 h (maximum 120h).

169 Limited data-logging capacity restricts the applicability of accelerometry to short-term  
170 measurements, in spite of the acceleration-triggered data recording used here. The high correlation  
171 between recordings at 100 Hz and the simulated estimates for 10 Hz, however, indicates the  
172 potential for lower recording frequencies. As long as handling times are not very short (Fig. 2d),  
173 recordings at 10 Hz should suffice for reliable measurements, thereby using less memory space.

174 In summary, the present study is the first to demonstrate how accelerometer technology can be used  
175 to study foraging behaviour in northern pike. The study further indicated that accelerometer  
176 technology can be applied to study handling times in settings where video-observation technology  
177 is inadequate. In doing so, this study has expanded what is already known about the use of  
178 accelerometer technology in studies of foraging behaviour in fishes (Broell *et al.*, 2013;  
179 Brownscombe *et al.*, 2014; Kawabata *et al.*, 2014). Although, the method comes with limitations  
180 (as discussed above), it still provides the potential for detailing studies of predation in e.g. highly  
181 turbid or humic waters, as well as detailed recording of exact acceleration behaviour during prey  
182 handling.

183

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189 REFERENCES:

- 190 Almeida, P. R., Pereira, T. J., Quintella B. R., Gronningsaeter A., Costa M. J. & Costa J. L. (2013).  
191 Testing a 3-axis accelerometer acoustic transmitter (AccelTag) on the Lusitanian toadfish.  
192 *Journal of Experimental Marine Biology and Ecology* **449**, 230–238.
- 193 Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J. F., Auclair, J. P., & Taggart, C. T.  
194 (2013). Accelerometer tags: detecting and identifying activities in fish and the effect of  
195 sampling frequency. *Journal of Experimental Biology* **216**, 1255–1264.
- 196 Brownscombe, J. W., Gutowsky, L. F. G., Danylchuk, A. J., Cooke, S. J. (2014). Foraging  
197 behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer  
198 biologgers. *Marine Ecology Progress Series* **505**, 241–251.
- 199 Carpenter, S. R., & Kitchell, J. F. (1993). *The trophic cascade in lakes*. Cambridge, UK: Cambridge  
200 University Press.
- 201 Craig, J. F. (1996). *Pike: biology and exploitation*. London: Chapman & Hall.
- 202 Forsman, A., P. Tibblin, H. Berggren, O. Nordahl, P. Koch-Schmidt & Larsson P. (2015). Pike  
203 *Esox lucius* as an emerging model organism for studies in ecology and evolutionary biology: a  
204 review. *Journal of Fish Biology* **87**, 472–479.
- 205 Franklin, C. E., Wilson, R. S., & Davison, W. (2003). Locomotion at  $-1.0^{\circ}$  C: burst swimming  
206 performance of five species of Antarctic fish. *Journal of Thermal Biology* **28**, 59–65.

207 Frith, H. R. & Blake, R. W. (1991). Mechanics of the startle response in the northern pike, *Esox*  
208 *lucius*. *Canadian Journal of Zoology* **69**, 2831–2839.

209 Fryxell, J. M. & Lundberg, P. (1998). *Individual behavior and community dynamics*. London:  
210 Chapman & Hall.

211 Harper, D. G., Blake, R. W. (1991). Prey capture and the fast-start performance of northern pike  
212 *Esox lucius*. *Journal of Experimental Biology* **155**, 175–192.

213 Jepsen, N., Beck, S., Skov, C., & Koed, A. (2001). Behavior of pike (*Esox lucius* L.) > 50 cm in a  
214 turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, *10*(1), 26-34.

215 Jönsson, M., Ranåker, L., Nilsson P. A. & Brönmark C. (2013). Foraging efficiency and prey  
216 selectivity in a visual predator: differential effects of turbid and humic water. *Canadian*  
217 *Journal of Fisheries and Aquatic Sciences* **70**, 1685–1690.

218 Kawabata, Y., Noda, T., Nakashima, Y., Nanami, A., Sato, T., Takebe, T., Mitamura, H., Arai, N.,  
219 Yamaguchi, T. & Soyano, K. (2014). Use of a gyroscope/accelerometer data logger to  
220 identify alternative feeding behaviours in fish. *Journal of Experimental Biology* **217**, 3204–  
221 3208.

222 Kerfoot, W. C. & Sih A. (1987). *Predation: direct and indirect impacts on aquatic communities*.  
223 Hanover, NH: University of New England Press.

224 Landsman, S. J., Martins, E. G., Gutowsky, L. F. G., Suski, C. D., Arlinghaus R. & Cooke S. J.  
225 (2015). Locomotor activity patterns of muskellunge (*Esox masquinongy*) assessed using tri-  
226 axial acceleration sensing acoustic transmitters. *Environmental Biology of Fishes* **98**, 2109–  
227 2121.

228 Marsac, F. & Cayré, P. (1998). Telemetry applied to behaviour analysis of yellowfin tuna (*Thunnus*  
229 *albacares*, Bonnaterre, 1788) movements in a network of fish aggregating devices. In

230 *Advances in Invertebrates and Fish Telemetry* (Lagardère, J.-P., Bégout Anras, M.-L. &  
231 Claireaux, G., eds.) pp. 155–171. Berlin: Springer.

232

233 Murchie, K. J., Cooke, S. J., Danylchuk, A. J. & Suski, C. D. (2011). Estimates of field activity and  
234 metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial  
235 accelerometer transmitters and intermittent-flow respirometry. *Journal of Experimental*  
236 *Marine Biology and Ecology* **396**, 147–155.

237 Nilsson, P. A. & Brönmark, C. (1999). Foraging among cannibals and kleptoparasites: effects of  
238 prey size on pike behavior. *Behavioral Ecology* **10**, 557–566.

239 Nilsson, P. A., Nilsson, K. & Nyström, P. (2000). Does risk of intraspecific interactions induce  
240 shifts in prey-size preference in aquatic predators? *Behavioral Ecology and Sociobiology* **48**,  
241 268–275.

242 Noda, T., Kawabata, Y., Arai, N., Mitamura, H. & Watanabe, S. (2014). Animal-mounted  
243 gyroscope/accelerometer/magnetometer: In situ measurement of the movement performance  
244 of fast-start behaviour in fish. *Journal of Experimental Marine Biology and Ecology* **451**, 55–  
245 68.

246 Priede, I. G. (1983). Heart rate telemetry from fish in the natural environment. *Comparative*  
247 *Biochemistry and Physiology Part A: Physiology* **76**, 515–524.

248 Rand, D. M. & Lauder, G. V. (1981). Prey capture in the chain pickerel, *Esox niger*: correlations  
249 between feeding and locomotor behavior. *Canadian Journal of Zoology* **59**, 1072–1078.

250 Sih, A., & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does  
251 it fail? *Animal Behaviour* **61**, 379–390.

252 Stensholt, B. K. (2001). Cod migration patterns in relation to temperature: analysis of storage tag  
253 data. *ICES Journal of Marine Science* **58**, 770–793.

254 Thiem, J. D., Dawson, J. W., Gleiss, A. C., Martins, E. G., Haro, A., Castro-Santos, T., Danylchuk,  
255 A. J., Wilson R. P. & Cooke, S. J. (2015). Accelerometer-derived activity correlates with  
256 volitional swimming speed in lake sturgeon (*Acipenser fulvescens*). *Canadian Journal of*  
257 *Zoology* **93**, 645–654.

258 Tsuda, Y., Kawabe, R., Tanaka, H., Mitsunaga, Y., Hiraishi, T., Yamamoto, K. & Nashimoto, K.  
259 (2006). Monitoring the spawning behaviour of chum salmon with an acceleration data logger.  
260 *Ecology of Freshwater Fish* **15**, 264–274.

261 Whitney, N. M., Pratt, H. L., Pratt, T. C. & Carrier J. C. (2010). Identifying shark mating behaviour  
262 using three-dimensional acceleration loggers. *Endangered Species Research* **10**, 71–82.

263 Wright, S., Metcalfe, J., Hetherington S. & Wilson R. (2014). Estimating activity-specific energy  
264 expenditure in a teleost fish using accelerometer loggers. *Marine Ecology Progress Series*  
265 **496**, 19–32.

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267

Figure 1. One-dimensional magnitude of acceleration ( $MA$ ). Example of a time line of  $MA$  values from a successful attack. The first 200 second of data is presented and the dashed horizontal line represents the threshold value  $\tau$  applied in the computerized extraction of handling times ( $h_a$ ). In the present example  $h_a$  was 22.3 sec. The imbedded graphs show the raw accelerations  $g$  in three dimensions ( $g$ :  $9.81 \text{ m sec}^{-2}$ ) before the transformation into the one dimensional vector norm.

Figure 2. Validating the accuracy of the accelerometer based handling time. (a & b) Comparing the computerized accelerometer based handling times ( $h_a$ ) to the observed handling times ( $h_1$  and  $h_2$ , see the definitions in Methods and Materials). Data points represent individual trials; successful attacks (*black*) and unsuccessful attacks (*grey*). Solid grey lines are regression lines (a:  $r^2=0.93$ ,  $h_1 = 1.25 \times h_a + 1.97$ ; b:  $r^2=0.87$ ,  $h_2 = 3.13 \times h_a - 5.64$ ) and dashed grey lines are the associated standard errors. The dotted black line is where the points should be aligned if  $h_a$  corresponded precisely to the observed handling times (i.e. the 1:1 relationship). (c) Sensitivity to  $\tau$ . For each threshold the Pearson's product moment correlation coefficient was calculated for the relationship between  $h_a$  and  $h_1$ . (d) Comparing  $h_a$  derived at 100 Hz and 10 Hz. The dashed line is where the points should be aligned if  $h_a$  values derived from 10 Hz recordings were identical to  $h_a$  values derived from 100 Hz.

Figure 3. Comparing successful and unsuccessful attacks. (a) Density distributions of  $MA$  values from all eight trials that was executed successfully, four successful attacks (*red*) and four unsuccessful attacks (*blue*). (b) Geometric mean  $MA$  plotted against the computerized handling time ( $h_a$ ); data include both successful attacks (*red*) and unsuccessful attacks (*blue*).









