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Short Title: Behaviour of ide Leuciscus idus

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Keywords: cyprinids; home range; migration; insectivores; lowland river.

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Abstract: 17 individuals of ide Leuciscus idus were radio-tracked weekly from September 2003 to September 2004 in the Elbe River, Czech Republic to examine migration patterns and the influence of environmental factors on the diurnal behaviour. Of the 10 environmental factors measured, ide were significantly influenced by turbidity, which increased diurnal movement and the home range size of the species. The peak of longitudinal movement occurred in the spring, indicating prespawning migration. Migrating fish moved downstream and later returned upstream to the vicinity of their original locations, displaying a homing behaviour.

* Manuscript

1	Factors influencing movement behaviour and home range size in ide
2	Leuciscus idus
3	
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INTRODUCTION

27 28

29 It has been suggested that the daily activity rhythms of fish are the result of a complex trade-30 off between growth and survival, which takes into account diel fluctuation in food 31 availability, food capture efficiency and predation risk (Metcalfe et al., 1999). Usually such 32 diel activity patterns are closely related to variations in the physical environment. For 33 example, a temperature-dependent shift in diel activity is supposed to be a consequence of 34 higher predation risk in cold water (Webb, 1978; Fraser et al., 1995). Changes in diel activity 35 patterns have been related to the light intensity and duration corresponding with the daytime 36 (Harvey & Nakamoto, 1999), season (David & Closs, 2003) or the moon phase (Horký et al., 37 2006). However, other environmental conditions, such as the influence of water turbidity 38 (Benfield & Minello, 1996; Sweka & Hartman, 2003) and water flow conditions, may have an 39 effect (Harvey & Nakamoto, 1999; Slavík et al., 2007).

40 Ide, Leuciscus idus (L.), is a species of benthopelagic, riverine cyprinid inhabiting 41 deeper, slower flowing reaches of lowland middle-sized rivers east of the Rhine basin in 42 Europe to Siberia (Maitland & Campbell, 1992). It achieves a maximum size of 53 cm total 43 length (L_T), a body mass of 2.0 kg, and a recorded age of 14 years. Ide are visually oriented 44 feeders and predominantly consumes insects, although coarse fish or plant material might be 45 occasionally consumed (Cala, 1970). Ide spawn in spring and belonging to the phyto-46 lithophilic spawning group (Balon, 1975). Their migratory pattern has been described as 47 potamodromous with a prevailing upstream migration (Cala, 1970; Müller, 1986). According 48 to Winter & Fredrich (2003), who observed migrations of ide in the middle reaches of the 49 River Elbe in Germany and the River Vecht in the Netherlands, ide is a flexible species 50 capable of adapting its movement pattern to different conditions of river systems. To 51 investigate within catchment variation in the migratory patterns of ide we tracked the

52 movements of individuals in a low stream order, upstream section of the Elbe River, closer to 53 the source than previous investigations (Winter & Fredrich, 2003). To assess which 54 environmental factors influence the migration and diurnal behaviour of ide, 17 specimens 55 were radio-tracked weekly from September 2003 to September 2004 in the Elbe River, Czech 56 Republic.

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MATERIALS AND METHODS

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60 STUDY AREA

61 The study was carried out on the upper part of the River Elbe, Czech Republic. The 62 river rises at 1383 m above sea level. It has a total length of 1091 km with a catchment area of 148,268 km². The Czech portion of the river is 368 km long and has a catchment area of 63 51,394 km². The primary river stretch studied was about 40 km long, from the weir at Střekov 64 (distance from the source 320 km; 50°38' N; 14°03' E) to the frontier with Germany (Fig. 1). 65 66 During spawning migrations, the stretch studied was extended as far as Meissen, Germany 67 (distance from the source 410 km; 51° 81' N; 13° 28' E) as fish were followed. The river 68 width in the area studied was 100 to 150 m, and the riverbanks have little aquatic vegetation 69 and are reinforced with rocks and concrete. The water was up to 6 m deep and no submergent 70 vegetation or floating plants were recorded. Across the whole study period, the average flow was 293 m³ s⁻¹, with the maximum in winter (748 m³ s⁻¹) and the minimum in early autumn 71 $(79 \text{ m}^3 \text{ s}^{-1}).$ 72

73

74 FISH CAPTURE AND TAGGING

Fish were sampled by electrofishing (650 V, 4 A, pulsed D.C.) and seventeen related at 5 km long river stretch

77 (Fig. 1). The individuals were measured to the nearest mm (mean standard length $378 \text{ mm } L_{s}$, 78 ranging from 285 to 450 mm) and weighed to the nearest g (mean fish body mass 755 g, 79 ranging from 450 to 1240 g). Fish were anaesthetized with 2-phenoxy-ethanol (0.2 ml l^{-1}). 80 Radio transmitters (MCFT 3B, 11 g in air, 14 x 43 mm, with an operational life estimated to 81 be 399 days; MCFT 3EM, 8.9 g in air, 11 x 49 mm, with an operational life estimated to be 82 278 days; Lotek Engineering, Inc., Canada) were implanted into the body cavity through a 83 midventral incision that was closed by three separate stitches, using a sterile, braided, 84 absorbable suture (Ethicon Coated Vicryl). The mass of the transmitter never exceeded 2 % of 85 the fish body mass in the air (Winter, 1983). Fish were held until they had recovered their 86 equilibrium and showed spontaneous swimming activity (c. 5 min. after surgery), then 87 released close to the site of capture. The transmitters had external antennae and their potential 88 range was approximately 300 m depending on the gain of receiver and tracking conditions.

89

90 SAMPLING PROCEDURES

91 All fish were tracked from a boat weekly during the period from 11 September 2003 to 92 21 September 2004. Once all the fish were positioned, one individual was randomly chosen 93 for a 24h tracking cycle. Fish positions were determined once in each three-hour period over a 94 diel cycle (0600 - 0859, 0900 - 1159, 1200 - 1459, 1500 - 1759, 1800 - 2059, 2100 - 2359, 2100 - 2359, 210095 2400 – 0259, 0300 – 0559 hours) using a GPS receiver. The interval between measurements 96 varied slightly depending on the tracking conditions (3 hours \pm 20 min.). The fish were 97 located using landmarks and positioned with the help of a GPS (GPS map 76S, Garmin Ltd., 98 USA) using two radio receivers (Lotek SRX 400 receiver firmware versions W5 and W31) 99 and three-element Yagi antennas equipped with a compass. The fish direction was determined 100 by the double lateral extinction technique (bearing on the bisecting line of the two extinction 101 axes; Winter et al., 1978). A computer program was developed to obtain fish position 102 coordinates and plot them on the map using the biangulation method proposed by White &103 Garrot (1990).

104

105 HABITAT MEASUREMENT

106 Water temperature (°C), dissolved oxygen concentration (mg l^{-1}), conductivity (μ S), pH, and 107 turbidity (NTU) were measured by microprocessors (Oxi 196; pH/Cond 340i/SET; TURB 108 355 T; WTW, Germany). Light intensity (Ev) was measured by a SECONIC Super Zoom 109 Master L-68 (Seconic, Tokyo, Japan) at the expected locations of individuals during each 110 positioning. Measurements of the atmospheric pressure and the moon phase were conducted 111 with help of the Remote Weather station BAR 928 H (Huger Electronics, Germany). The Elbe 112 River Authority measured water flow daily at a gauging station located within the study 113 stretch.

114

115 DATA ANALYSES

116 Short term movements were defined as the distance (m) between the fish positions determined 117 in two subsequent three-hour intervals over a 24 hour cycle and are henceforth referred to as 118 "diurnal movements". Although the fish were located every time, in several cases the signal 119 was so weak that triangulation could not be precise: These occasions were excluded from 120 further analysis. Longer term movements were determined from the difference (m) between 121 the locations of a fish in two successive week intervals and, henceforth, are referred to as 122 "longitudinal movements". Data on fish movements were analyzed using Map Source Version 123 5.3 (Garmin Ltd., USA). The sizes of home ranges were determined using the Minimum 124 Convex Polygon method (Mohr, 1947). Fish that were used for home range analyses were 125 suggested to occupy home range; i.e. fish could not move during two subsequent weeks in the 126 longitudinal direction more than its usual extent of diurnal movements across the twenty-four127 hour cycle. Furthermore, fish that moved for the whole twenty-four-hour cycle in only one 128 direction (upstream or downstream) was suggested to exhibit a mobile or emigration phase of 129 a home range shift and was subsequently excluded from the analyses. Data concerning light 130 intensity were first entered into the analysis as the absolute values of illumination (1 Ev \approx 5 lx; $y = 0.6211e^{0.6943x}$, where y = lx, x = Ev), referred to as 'intensity of illumination'. 131 132 Furthermore, three intervals with different light intensity were determined across the twenty-133 four-hour cycle: twilight (light intensity ranged between 1 - 6 Ev), day (above 6 Ev), and 134 night (below 1 Ev); in further analysis, these categories will be referred to as 'light intervals'.

135

136 STATISTICAL ANALYSES

137 Associations between the variables were tested using the Linear Mixed Model (LMM). 138 Separate models were applied for the following dependent variables: diurnal movements 139 (LMM I), home range size (LMM II) and longitudinal movements (LMM III). All of the data 140 were square root transformed to achieve normality before analyses. To account for the 141 repeated measurements of the same individuals across the period of observation, analyses 142 were performed using mixed model analysis with individual fish and date nested within 143 individual fish (LMM I, II) and individual fish and date nested within individual fish (LMM 144 III) as a random factors, using PROC MIXED (SAS, version 9.1).

PROC MIXED is the way to cope with repeated-measures experiments with people or animals as subjects, where subjects are declared random because they are selected from the larger population to which you want to generalize (SAS Institute Inc., 2004). For the LMM I model, fixed effect used were the classes 'moon phase' (8 levels), 'season' (spring, summer, autumn, winter), and 'light interval' (day, night, twilight), and the continuous variables were 'turbidity' (range 5.5 – 44 NTU), 'fish mass' (1293–3946 g), 'water temperature' (0–24 °C), 'water flow' (79–748 m³ s⁻¹), 'atmospheric pressure' (992–1033 hPa), 'conductivity' (332– 152 425 μ S), 'light intensity' (0 – 15.1 Ev), and 'dissolved oxygen' (5.5–12.9 mg l⁻¹). For the 153 LMM II - III models, fixed effects used were the same as for the LMM I model except for the 154 'light interval' (day, night, twilight) and 'light intensity' (0 - 15.1 Ev) that were excluded 155 from the analyses. The significance of each fixed effect (including interactions) in the 156 analyses was assessed by the F-test, upon sequential dropping of the least significant effect, 157 starting with a full model. Fixed effects and their interactions that were not statistically 158 significant are not discussed further. In unbalanced designs with more than one effect, the arithmetic mean for a group may not accurately reflect the response for that group, since it 159 160 does not take other effects into account. Therefore, the least-squares-means (LSMEANs) were 161 used. LSMEANs (further referred to as 'adjusted means') are, in effect, within-group means 162 appropriately adjusted for the other effects in the model. Adjusted means (Adj P) were 163 computed for each class; differences between classes were tested by the *t*-test. For multiple 164 comparisons, we used the Tukey-Kramer adjustment. Associations between the dependent 165 variable and other continuous variables were estimated by fitting a random coefficient model 166 using PROC MIXED as described by Tao et al. (2002). With this random coefficient model, 167 we calculated predicted values for the dependent variable and plotted them against the 168 continuous variable with predicted regression lines. The degrees of freedom were calculated 169 using the Kenward-Roger method (Kenward & Roger, 1997).

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RESULTS

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Final LMM models contained the fixed factors 'turbidity' for diurnal movements (LMM I), 'turbidity' and 'season' for home range area size (LMM II), and 'season' for longitudinal movements (LMM III). Details of the models are shown in Table I. Descriptive data of the extent of diurnal movements, longitudinal movements, total distance migrated during
spawning and home range per individual are provided in Table II. The other environmental
variables tested (water temperature, dissolved oxygen, conductivity, pH, atmospheric
pressure, moon phase and light intensity) were not found to have a significant effect.

181

182 DIURNAL MOVEMENTS AND HOME RANGE SIZE OF IDE

183 During the whole study fish did not remain at one exact position, however they occupied 184 defined home ranges between which they relocated (e.g. during spring migration). Mean home range size was $19,495.8 \pm 13,890.9 \text{ m}^2$ (Table II), but both diurnal movement and home 185 186 range size appeared to vary in a consistent manner. Repeated measurements indicated that 187 both diurnal movement [Fig. 2(a)] and the home range size [Fig. 2(b)] of ide increased with 188 increasing turbidity. The relationship between flow and turbidity was not statistically 189 significant; increased turbidity was a consequence of both surface run-off and phytoplankton 190 growth. Home range size was significantly smaller (Tukey-Kramer Adj. P < 0.05) during 191 winter than other seasons [Fig. 3(a)].

Final GLMM I model indicated the influence of the light interval nested within season on the diurnal movements of ide (Table I); however, differences among classes were insignificant, and hence the character of dependence was not possible to determine (Tukey-Kramer Adj. P > 0.05).

196

197 LONGITUDINAL MOVEMENTS OF IDE

Longitudinal movements of the ide were significantly larger (Tukey-Kramer Adj. P < 0.01) in the spring, with non-significant differences among other seasons [Fig. 3(b)]. Almost all individuals, with one exception, displayed downstream spring migrations, most of them remaining within Czech part of Elbe River (40 km long; Fig. 1). Six individuals moved to

202 near the confluence of the River Bílina at Ústí nad Labern, including one individual that 203 moved 19 km upstream to reach this spot (the only upstream migrating individual). Four 204 individuals moved downstream to near the town of Malé Březno and a further two to near the 205 border with Germany. Five individuals undertook longer migrations (68 - 100 km) to reach 206 spawning sites near Dresden and Meissen in the German part of River Elbe (Fig. 1). The 207 individuals that undertook longest migration started their run earliest, at the end of February. 208 All final destination of migration were shallower riffles with a gravel substrate. Later in the 209 season, ide displayed homing behaviour and returned to within 0.5 - 2 km of the starting 210 position.

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DISCUSSION

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214 Behaviour of visually oriented animals is known to be affected by visibility, as they rely on 215 visual cues for orientation and feeding. In aquatic ecosystems, the visibility is determined not 216 only by the light intensity but also by the water turbidity (Benfield & Minello, 1996). 217 Turbidity imposes a considerable environmental constraint with a potential to affect whole 218 fish communities (Colby et al., 1972; Diehl, 1988). It may shape the habitat choice patterns 219 (Miner & Stein, 1996), social interactions (Valdimarsson & Metcalfe, 2001) or reproductive 220 behaviour of the fish, in terms of reduced sexual selection (Järvenpää & Lindström, 2004; 221 Heubel & Schlupp, 2006). Increased turbidity influences visually-oriented fish by decreasing 222 their visual range (Utne-Palm, 2001), typically affecting foraging efficiency by reducing the 223 distance at which a predator detects prey (Benfield & Minello, 1996; Sweka & Hartman, 224 2003). Benfield & Minello (1996) evaluated the influence of turbidity on predation rates of 225 gulf killifish, Fundulus grandis Baird and Girard, and that significantly fewer prey were 226 consumed in tanks containing turbid water. Brook trout, Salvelinus fontinalis L., become

227 more active in higher turbidity, thus increasing the chance of encountering potential prey by 228 enlarging the total volume of water searched (Sweka & Hartman, 2001a). Hence, we suggest 229 that ide extend their diurnal movements and home range size as a result of the reduced 230 foraging success in turbid water.

231 In riverine systems, increased turbidity is usually associated with increased flow 232 during hydrologic events (Sahoo et al., 2006). However, low discharge may have the opposite 233 effect: increased water residence time during low water flow may allow the buildup of 234 phytoplankton biomass (Lane et al., 2007). Here there was no significant relationship between 235 discharge and turbidity, suggesting both potential sources and that the behaviour of ide was 236 influenced by the water turbidity per se. Home range size varied consistently with season and 237 turbidity. The influence of turbidity is likely to due to its effect on visibility. Reduced diurnal 238 movement in winter may be due to lower food availability and/or temperature related 239 metabolism.

The winter season is a period of reduced activity in cyprinid fish (Bauer & Schlott, 2004). They tend to remain in areas with the most appropriate conditions for wintering, as was shown for example in bream *Abramis brama* L. migrating into lentic refugia (Molls & Neumann, 1994). A restricted home range may be a direct consequence of a reduced metabolic rate linked to low temperatures as well as a result of efficient energy conservation or the use of locally restricted refuge during harsh conditions (Brown & Mackay, 1995; Hiscock *et al.*, 2002).

Many freshwater fish species, including cyprinids, undertake long distance migrations during the breeding season (Baras & Cherry 1990; Lucas 2000). Previous reports of ide indicated an upstream pre-spawning migration followed by downstream movement after spawning (Cala, 1970; Müller, 1986), including studies in the middle reaches of the River Elbe (Winter & Fredrich, 2003). In contrast, we observed that ide undertook similar long

252 distance migrations in spring but in the opposite direction, i.e. downstream during spring and 253 returning upstream towards formerly occupied areas later in the season. These findings are 254 partly consistent with Cala (1970) from Kävlingeån in Sweden, where ide also displayed large 255 downstream migration in spring. However, the latter case is more complicated as the fish 256 migrated downstream to coastal waters in the spring, where they remained for the consecutive 257 summer, only returning to the river in autumn (Cala op. cit.). Such inconsistency in the 258 direction of migration may indicate that the movements of fish are shaped by multiple factors 259 that vary even within river systems. An obvious constraint is the presence of lateral 260 obstructions that hamper fish migration (Lucas & Frear, 1997; Horký et al., 2007), although 261 in our study no fish were observed to move to the vicinity of the weir at Strekov during spring 262 migration. The location of suitable spawning areas (Pollux et al., 2006) and channel 263 morphology (Lau et al., 2006) may also be essential.

264 Although ide are declining in numbers, classified as vulnerable by IUCN Red List 265 criteria (2001) and protected as an endangered species (Lusk et al., 2004), few references 266 regarding its behaviour exist (Cala 1970; Winter & Fredrich 2003). Our data demonstrate that 267 the turbidity may substantially influence the movement patterns of this species. As turbidity is 268 influenced by both eutrophication and changes in land-use (Duchrow & Everhart, 1971), and 269 increased turbidity has a negative effect on foraging success and growth of fish (Sweka & 270 Hartman 2001a; Sweka & Hartman 2001b), eutrophication of the river catchment could be an 271 important negative influence on ide abundance and distribution.

Our findings further indicate that their migratory behaviour is shaped by multiple factors that vary even within river systems. Whilst encouragingly this may indicate a degree of plasticity in the species, more work is needed to understand the factors influencing these migrations and hence direct conservation efforts to improve the breeding success of the remaining populations.

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283	
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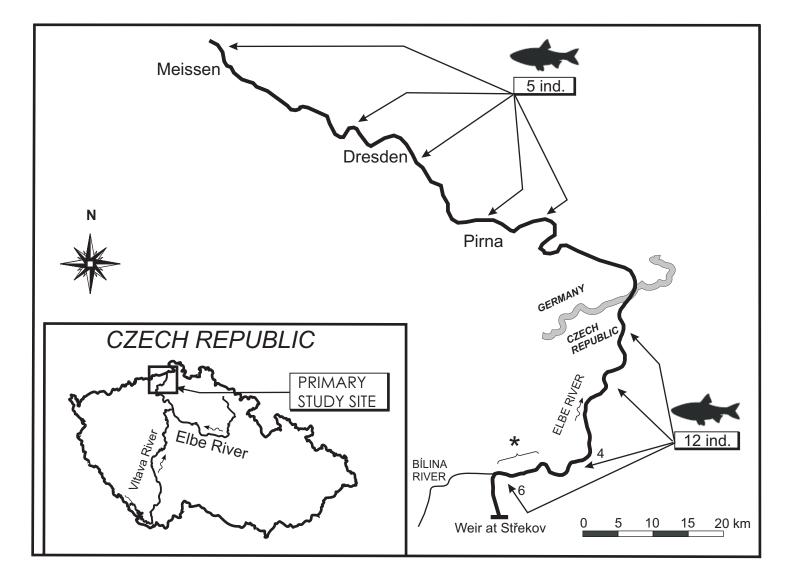
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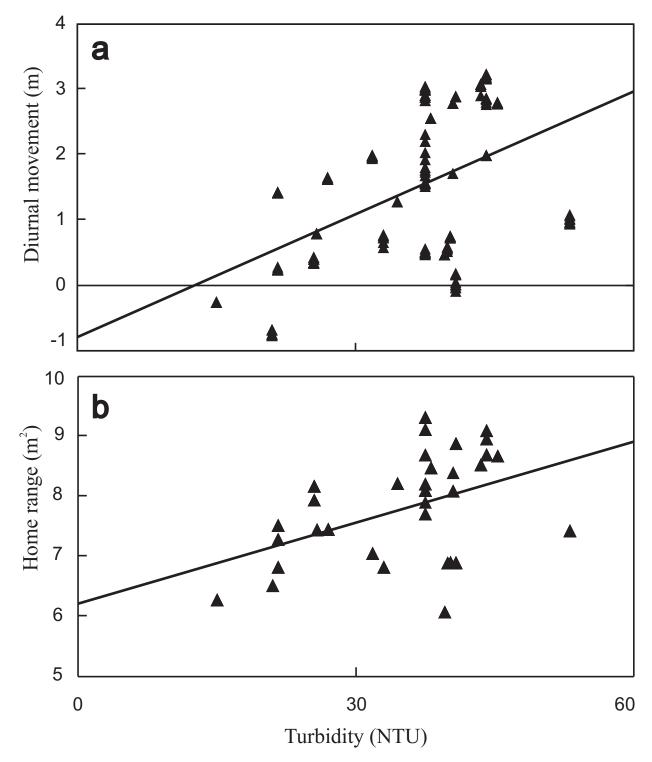
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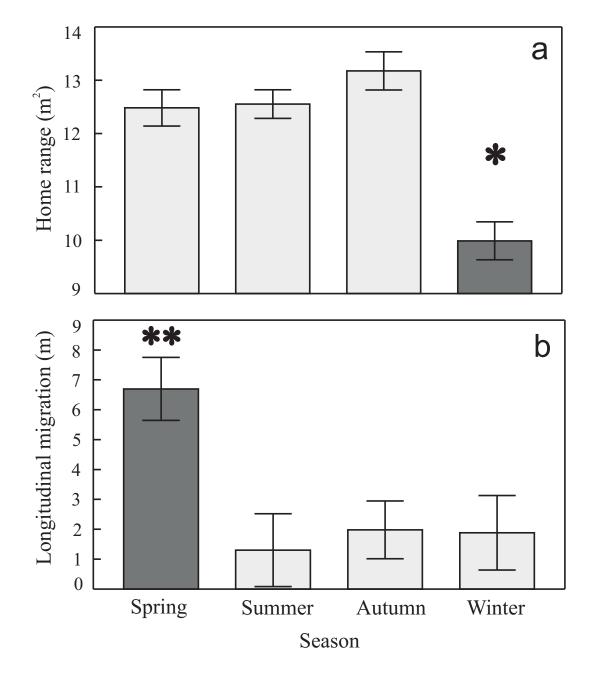
1	FIG. 1 Map showing the location of the study site with highlighted distances of spring
2	downstream migrations and number of individuals (ind.) migrating within Czech and
3	German part of River Elbe. Bracket with asterisk indicate the river stretch where the fish
4	were caught and released after tagging. Arrow ($\neg \rightarrow$) indicates the direction of river
5	flow.
6	
7	FIG. 2 Relationship between diurnal movements (a) and home range size (b) of ide and
8	turbidity. Predicted values are from square root transformed data. The curves were fitted
9	by: $y = 0.0188x - 0.0395$, ($r^2 = 0.38$) for diurnal movements and $y = 0.0189x + 7.4581$,
10	$(r^2 = 0.34)$ for home range size.
11	
12	FIG. 3 Home range size (a) and longitudinal movements (b) of ide across seasons. Asterisks
13	indicate significant differences between groups (* P < 0.05; ** P < 0.01). Values are
14	adjusted means \pm S.E. of square root transformed data.







Figure



Table

- 1 TABLE I. Type 3 tests of fixed effects for diurnal movements, home range area size, and
- 2 longitudinal movements.
- 3

Effect	Num DF	Den DF	F	P<
LMM I (diurnal movement)				
turbidity	1	256	7.82	0.0056
light interval(season)	11	256	3.20	0.0004
LMM II (home range size)				
turbidity	1	255	68.37	0.0001
season	3	255	56.12	0.0001
LMM III (longitudinal movement)				
season	3	255	5.79	0.0008

4

5 TABLE II. Tagged individuals of ide with mean (\pm S.D.) of their recorded diurnal movements,

6 longitudinal movements (LM), total distance migrated during spawning (TD) and

7 home range (HR).

Individual code	DM (m)	LM (m)	TD (m)	HR (m ²)
12	50.1 ± 100.5	$1\ 824.8\pm 5\ 168.2$	13 649	$29\ 817.6 \pm 23\ 924.05$
14	24.8 ± 68.2	4 908.7 ± 13 711.2	99 729	19 506.4 ± 14 325.2
16	39.4 ± 89.7	6 372.6 ± 6 803.6	13 284	23 465.8 ± 12 698.7
17	15.6 ± 24.2	135.6 ± 361.8	3 882	$7\ 400.4 \pm 4\ 441.02$
18	45.7 ± 95.8	5 510.2 ± 10 119.3	54 160	11 342.1 ± 8 432.6
24	32.8 ± 84.3	1 447.8 ± 3 193.4	18 633	36 157.5 ± 22 001.1
28	77.8 ± 120.1	6 238.5 ± 13 801.3	85 505	24 158.2 ± 17 325.8
40	21.1 ± 54.3	$1\ 710.7 \pm 1\ 909.6$	2 908	8 352.1 ± 5 368.3
43	65.7 ± 118.6	2 811.3 ± 5 122.2	18 284	25 931.0 ± 18 963.2
44	34.3 ± 40.5	5 517.6 ± 12 024.6	37 406	$13\ 700.2 \pm 7021.4$
45	38.1 ± 81.6	982.5 ± 3 421.7	4 145	27 536.5 ± 19871.8
46	20.4 ± 53.8	1 628.1 ± 4 236.9	9 380	23 658.8 ± 21 879.6
47	43.2 ± 94.4	2 874.3 ± 3 465.5	26 089	$17\;502.3\pm13\;468.2$
48	37.3 ± 71.1	1 382.4 ± 2 678.6	4 332	19 875.4 ± 13 489.7
49	19.2 ± 52.9	1 348.2 ± 1 825.1	3 546	26 849.7 ± 21 487.2
50	28.4 ± 65.3	2 949.5 ± 8 236.4	67 946	13 672.3 ± 9 237.4
51	30.2 ± 41.5	2 131.4 ± 5 628.5	13 680	2 502.7 ± 2 030.6

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