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<sup>3</sup> Bedload transport in rivers: size matters but so does shape!

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## 15 ABSTRACT

Bedload transport modelling in rivers, which defines the threshold for pebble movement, takes 16 into account the size and density of pebbles, but does not formally consider particle shape. The 17 18 lack of analyses evaluating the influences of shape and density on particle mobility presents a major deficiency. To address this issue and to compare the relative roles of the density and 19 shape of particles, we performed original sediment transport experiments in an annular flume 20 21 using molded artificial pebbles equipped with a radio frequency identification tracking system. The particles were designed with four distinct shapes and four different densities while having 22 the same volume, and their speeds and distances traveled under constant hydraulic conditions 23 24 were analyzed. The results show that particle shape has more influence than particle density on the resting time between particle displacement and the mean traveling distance. For all densities 25 investigated, the particle shape systematically induced differences in travel distance that were 26 strongly correlated ( $R^2 = 0.94$ ) with the Sneed and Folks shape index. Such shape influences, 27

although often mentioned, are here quantified for the first time, demonstrating why and howthey can be included in bedload transport models.

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### 31 INTRODUCTION

Sediment transport is a key process in fluvial geomorphology, being important for 32 sustainable management of navigable channels, designing engineering projects, predicting 33 morphological changes and associated hydraulic risks, interpreting sedimentary archives and 34 restoring rivers <sup>1</sup>. It involves three phases of particle mobility: (1) entrainment  $^{2-6}$ ; (2) motion 35 <sup>7–9</sup>; and (3) deposition <sup>10,11</sup>. Sediment transport at the particle scale is a stochastic phenomenon 36 <sup>7,12,8,13,14,9</sup>, which mostly arises from the complex interactions between particle collisions and 37 highly variable friction, drag, and lift forces due to fluid turbulence. Thus, for practical 38 considerations, empirically calibrated sediment transport functions widely use Shields stress 39 40 number ( $\tau^*$  or  $\theta$ ) to quantify the balance of the forces exerted on the channel bed particles, and the critical Shields number  $(\tau^*c)$ , which is the threshold value necessary to set particles in 41 motion, to determine the moments at which drag forces exceed stabilizing forces ( $\tau^* > \tau^*_c$ ) and 42 particles can be entrained <sup>15–21</sup>. Such approaches have been used to estimate particle stabilizing 43 forces from median pebble size and submerged density <sup>16</sup>. At the river reach scale, sediment 44 45 transport estimates generally encapsulate a relation depending on the Shields stress, and therefore also include the median grain size <sup>20,22–27</sup> of the transported sediment. 46

Published bedload transport datasets from rivers with similar flow conditions, morphologies, and median grain sizes, may show different transport rates, with large variations in the threshold for setting particles in motion <sup>28</sup>, variations that can be up to 10-fold <sup>29</sup> around the mean empirical Shields curve <sup>30–32</sup>. To explain such dispersion, many studies have focused on the role of mixed grain size, hiding effects <sup>33–36</sup>, macro-roughness, channel steepness, or bed roughness relative to channel depth <sup>37</sup>. However, fewer studies have qualitatively related pebble

shape to bedload transport through the influence of pebble angularity <sup>38,39</sup>, pebble imbrication 53  $^{34,35,40}$ , or bed roughness  $^{34,40,41}$  (i.e. the *D/K* ratio, where *D* is the diameter of the particles to be 54 moved and K is the bed-particle diameter). In environments with smooth-beds (D > K) and 55 during low to moderate flood events, coarse particles of spherical or ellipsoid shape were 56 observed <sup>42</sup> to be more likely to experience entrainment and transport than flatter shapes. 57 Conversely, in rough-bed rivers (D < K), Demir and Walsh<sup>1</sup> found that displacement of flatter 58 shapes (i.e. discs and blades) seems to be promoted. Overall, selective shape entrainment and 59 travel length both decrease as flood magnitude increases and/or particle size decreases <sup>43</sup>. 60 Whereas these previous studies have emphasized that robust deterministic expression of initial 61 62 motion should encapsulate the role of particle shape and bed roughness in particle motion modelling <sup>38,39,44,45</sup>, the scarcity of field and experimental data has prevented a quantitative 63 account of this role. 64

To partially fill this gap, we designed a parametric study based on experiments run in 65 an annular flume in which the displacements (encapsulating onset motion, travel length and rest 66 periods) of artificial pebbles of various shapes and densities were tracked for several hours. 67 Particle shape has been quantified by many different parametrizations <sup>46-52</sup> expressing 68 69 angularity, surface roughness, or departure from sphericity. As the latter directly impacts on inertial moments and pivoting angle, we investigated the influence of shape in terms of the 70 departure from sphericity, examining various ellipsoid particle shapes (from plate to blade 71 72 types).

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### 74 **RESULTS**

The number of revolutions made by the monitored particles ranged between 439 laps for an elongated blade and 2270 laps for a sphere, making the lap duration observations were taken from large sample sizes. Although the lap durations within the annular flume displayed large variations (from 3 seconds up to a few minutes; see example in Figure 1) over the total
run duration, the cumulative travel distances of the particles (Figure 2) displayed a fairly
constant slope that permitted the average traveling velocities of the different artificial pebbles
to be defined.



Figure 1. Example of the distribution of lap durations (shape = disc; density = 2.4 g.cm<sup>-3</sup>)

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The slight increases observed in the slopes of the cumulative distance curves over time for all shapes and densities reflect the progressive augmentation of the particles' velocities caused by a decrease in the mixing load due to abrasion (relative mass loss of 1.2% per kilometer traveled). As this was moderate and affected all tagged particles in a similar manner, we consider that it had very little impact on the first-order estimates and results of the experiments.



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#### density (B).

The four particle shapes investigated exhibited clear differences in cumulative travel length, with variations in the particle densities also demonstrating effects (Figure 2). The spherical particles traveled the farthest and fastest (mean velocities ranging from 0.44 to 0.60 m.s<sup>-1</sup>), with their mean virtual velocities displaying an inverse relationship with density (Figure 3). The compact blade-shaped particles were the second fastest, exhibiting mean velocities ranging from 0.25 to 0.44 m.s<sup>-1</sup>, again displaying an inverse relationship with density, although to a lesser extent than that of the spherical particles. In contrast, the mean virtual velocities of the disc- and elongated blade-shaped particles were minimally influenced by their densities: the mean velocities were clustered within a narrow range from 0.14 to 0.17 m.s<sup>-1</sup> and 0.19 to 0.21 m.s<sup>-1</sup> respectively. Within the density classes, the distances traveled by the particles clearly showed a high variability in relation to their shapes (Figure 2B and Figure **3**A). The experiments clearly indicate that the variability in velocity associated with pebble shape is substantially higher than that associated with particle density (~100% compared with ~30%).

106 To explore the influence of particle shape on mobility in a more quantitative way, we 107 used the sphericity index,  $\Psi_p$  (1), of Sneed and Folks (1958):

108 
$$\Psi_p = \sqrt[3]{\frac{S^2}{Ll}}$$
 Equation (1)

109 where *L*, *I*, and *S* are the longest, intermediate, and shortest axes of the pebbles.

110 The sphericity index  $\Psi_p$  shows a remarkable positive relationship with the mean 111 traveling velocity (Figure 3B). Moreover, the mean velocities increased from 0.52 to 0.85 m.s<sup>-1</sup> 112 <sup>1</sup> for decreasing densities from 2.6 to 2.0 g.cm<sup>-3</sup>. These results suggest that it is possible to 113 estimate differences in the mean virtual velocities and mobilities of particles according to their 114 sphericity.



116 Figure 3. Mean velocity as function of density (A) and Sneed and Folk spherical index (B).

The lap-scaled average travel velocities measured integrate the duration of motion 117 phases and the resting periods in between. However, the pebble shape and density can 118 potentially impact each of these two phases differently. The lap duration distributions are 119 characterized by a first peak at around 3 s in all experiments (Figure 1), which corresponds to 120 a revolution speed of  $\sim 1.2 \text{ m.s}^{-1}$ . For experimental conditions similar to those used in this study, 121 high speed camera viewing<sup>56</sup> previously indicated a mean hop velocity of  $1.2 \pm 0.2$  m.s<sup>-1</sup> for 122 123 pebbles in an annular flume. This modal lap duration of ~3 s therefore represents a continuous succession of hops over a full lap, without any resting time. These modal values decrease 124 slightly with increasing density (Figure 4A), as expected from the larger inertial effects after 125 the pebble is set in motion. More importantly, they are almost independent of the pebble shape, 126 as was also observed in a straight flume study<sup>63</sup>. This implies that the impact of shape on the 127 mean traveled distance is mostly caused by its influence on the resting time between 128 movements, i.e. on the immobilization conditions and on the threshold for setting pebbles in 129 motion. To illustrate this inference, a simple calculation of the mean resting time fraction, or 130 immobility ratio (I<sub>r</sub>), can be estimated through 131

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$$I_r = \frac{T - N_l t_m}{T} , \qquad \text{Equation (1)}$$

with *T* being the total duration of the runs,  $N_l$  the number of achieved flume revolutions during *T*, and  $t_m$  the modal lap duration (first mode on the distribution of Figure 1) corresponding to a continuous succession of hops over a full lap.



Figure 4. (A) mean hop velocity and (B) time fraction of immobility of the 16 different artificial pebbles.

Except for spherical pebbles that display a slight increase, the immobility ratio (Figure 4B) is only weakly or not affected by the particle density. In contrast, the shape of a pebble deeply impacts its mobility, with the immobility ratio raging from  $\sim$ 50% for the spherical shapes up to  $\geq$ 85% for the elongated blades.

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#### 144 **DISCUSSION**

The greater velocity of the spherical and compact-blade-shaped particles relative to the 145 elongated-blade and disc-shaped particles is in good accordance with the literature <sup>1,39,64</sup>, given 146 that the flatness of the flume bottom constitutes a low roughness bed surface, despite clustering 147 of temporary resting pebbles. As most lithologies of the pebbles present in rivers show a density 148 close to 2.7 g.cm<sup>-3</sup>, very similar to the highest value used in this study, we expect their mean 149 velocities to be more strongly influenced by their shape than by their density. On a quantitative 150 basis, this supports the claimed need to include a particle shape parameter in the sediment 151 transport equation <sup>34,41,65</sup>. 152

To do this, we focus on the conditions for setting a particle in motion, because pebble shape has a major influence on virtual velocity through resting periods. Following Komar and Li's (1986)<sup>41</sup> description, balancing of the moments of tractive and resisting forces for the critical stress yields:

157 
$$au_c \propto \frac{l_W \Delta \rho g S I L}{l_D A_a}$$
 Equation (2)

158 where  $A_a$  is the apparent section exposed to the flow, and  $l_D$  and  $l_w$  the respective moment 159 arms of the drag force and submerged weight respectively. Assuming that pebbles tend to lie 160 with their *S*-axis vertically oriented, the moment arms of the drag force  $l_D$  approximately scales 161 with the *S*-axis. As a pebble can orient either longitudinally or transversally, we use the 162 intermediate variable  $\sqrt{LI}$  to account for the apparent section exposed to the flow ( $A_a \propto S\sqrt{LI}$ ) 163 and the moment arm of the submerged weight  $l_w$ . Therefore:

164 
$$\tau_c \simeq k \frac{\sqrt{LI} \Delta \rho g^3 \sqrt{(SIL)^2} \widetilde{D}}{S^2 \sqrt{LI}} = k \sqrt[3]{\frac{(IL)^2}{S^4}} \Delta \rho g \widetilde{D} = k \frac{1}{\Psi_p^2} \Delta \rho g \widetilde{D} \qquad \text{Equation (3)}$$

165 where k is a function of the particles' Reynold number considered as a constant,  $\tilde{D} = \sqrt[3]{SIL}$ , the mean pebble size, and  $\Psi_P = \sqrt[3]{\frac{S^2}{IL}}$ , the Sneed and Folk's index. Here,  $\frac{1}{\Psi_P^2}$  corresponds 167 more or less to the term tan  $\phi$  in Komar and Li (1986): when particle flatness increases (i.e. 168  $\Psi_P$  decreases), the pivoting angle increases and mobility is reduced. Suppressing the unknown 169 k, the threshold can be expressed as:

170 
$$\tau_{c} \simeq \left(\frac{\Delta \rho}{\Delta \rho_{ref}}\right) \left(\frac{\Psi_{P_{ref}}}{\Psi_{P}}\right)^{2} \tau_{c_{ref}}$$
 Equation (4)

171 where  $\tau_{c_{ref}}$  is the critical Shields stress of a reference pebble of similar size.

172 The non-dimensional critical threshold is expressed as:

173 
$$\tau_c^* \cong \frac{\tau_c}{\Delta \rho g^{\sim}} = \frac{k}{\Psi_P^2} = \left(\frac{\Psi_{P_{ref}}}{\Psi_P}\right)^2 \tau_{c_{ref}}^* \qquad \text{Equation (5)}$$

174 where  $\tau^*_{c_{ref}}$  is the critical Shields stress of a reference pebble of similar size.

175 Representing the mean travel velocity of the particle as a function of the critical stress 176  $\tau_c$  shows an inverse trend between the two variables (Figure 5): both density and departure from 177 sphericity decrease the ratio of tractive over resistive moments and favor particle immobility.



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Figure 5. Mean velocity of the 16 artificial pebbles vs. their critical shear stress normalized to that of the spherical artificial pebble with a submerged density of 1.6 ( $=\frac{\tau_c}{\tau_{c_{ref}}} = \left(\frac{\Delta_p}{1.6}\right) \left(\frac{1}{\Psi_p}\right)^2$ ).

181 Most bedload transport capacity formulae are functions of the excess Shields stress and 182 follow two general forms: (1)  $\Phi = K(\tau^* - \tau_c^*)^{\alpha}$ , and (2)  $W^* = (\tau/\tau_c)^{\alpha}$ , where  $\Phi$  and  $W^*$  are two 183 distinct non-dimensional expressions of the bedload transport rate, and  $\alpha$  and K two constant 184 terms <sup>66</sup>. To account for the role of pebble shape in a transport capacity relationship, one could 185 introduce into the formula the modified expression for critical shear stress (eq. 4), or the critical 186 Shields stress (eq. 5) that includes the Sneed and Folk Index. To explore this hypothesis, we built on the fractional transport rate model developed for transport of a mixture of grain sizes (e.g. Parker et al., 1982<sup>67</sup>). This choice was motivated by the fact that such a relation already proposes a similarity collapse for heterogeneous sediment, which is the case in our experiments with particles of variable shapes and densities mixed with a natural pebble load. We arbitrarily considered Wilcock and Crowe's (2003)<sup>68</sup> relation for fractional transport rate, in which the form of the similarity collapse is:

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$$W_i^* = 14 \left(1 - \frac{0.894}{\phi^{0.5}}\right)^{4.5}$$
 when  $\phi = \frac{\tau}{\tau_{ci}} \ge 1.35$  Equation (6)

where  $\tau$  is the bed shear stress,  $\tau_{ci}$  the critical shear stress for incipient motion of a specific pebble *i* (more exactly it corresponds to the minimum shear stress required to achieve a small reference transport rate of  $W_i^* = 0.002^{-67}$ ), and  $W_i^*$  the dimensionless transport rate  $W_i^* =$  $\frac{Rgq_{bi}}{F_i(\frac{\tau}{\rho})^{3/2}}$ , with  $R_i = \frac{\Delta \rho_i}{\rho}$  being the ratio of the submerged sediment (of type *i*) density to water density, *g* being gravity,  $q_{bi}$  the volumetric transport rate per unit width of the particle of type *i* (i.e. of similar shape, size, and density), and  $F_i$  the proportion of the pebble type being of the class *i*.

Following our simplified analysis of the force moment balance, we defined the critical (or reference) shear stress as a function (eq. 7) of the mean characteristics of the transported sediment load (i.e. mean gravel size  $D_m$ , mean shape factor  $\psi_{Pm}$ , and mean density  $\Delta \rho_m$ ) according to:

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$$\tau_{ci} = \left(\frac{\Delta_{\rho_i}}{\Delta_{\rho_m}}\right) \left(\frac{\Psi_{Pm}}{\Psi_{Pi}}\right)^2 \tau_{cm}$$
 Equation (7)

with  $\tau_{cm}$  being the critical shear stress for the mean gravel load. Here,  $\tau_{cm} = \Delta \rho_m g D_m \tau_c^* \cong 28 \ Pa$  considering that  $\Delta \rho = 2600 \ \text{kg.m}^{-3}$ ,  $D_m \approx 5 \ \text{cm}$  for the mean gravel diameter of the 65 kg of limestone pebbles, and  $\tau_c^* \cong 0.036^{-68}$ . Within the flume, provided that not all of the particles are in full motion, the conditions of alluvial rivers prevail, i.e. the sediment flux  $q_{si}$  is equated by the transport capacity  $q_{bi}$ . In our experiments, the mass sediment flux per unit width of the pebble class *i* can be expressed from the mean traveling velocity through:  $q_{si} = \frac{F_i M}{A} V_{gi}$ , with A being the surface of the flume bottom, *M* the mass of sediment introduced into the flume, and  $V_{gi}$  the mean displacement velocity of particles of type *i*. It follows that a virtual mean velocity can be derived for particle *i* from the above fractional transport rate equation:

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$$V_{gi} = \frac{AM\rho_{si}}{R_i g} \left(\frac{\tau}{\rho}\right)^{3/2} W_i^* \left(\frac{\tau}{\tau_{ci}}\right)$$
Equation (8)

with  $\tau_{ci}$  derived from equation (7) and a mean shape factor  $\Psi_{Pm} = 0.7 \pm -0.08$  for the 65 kg of limestone pebbles.

The virtual velocities derived from the bedload transport relation show a well-defined 219 correlation with the measured virtual velocities (Figure 6). However, the slope of the correlation 220 line is larger than unity, and our modified version of the bedload transport tends to 221 underestimate the observed transport for the densest elongated-blade or disk-shaped pebbles. 222 Despite these slight discrepancies from the observations, these results suggest that the role of 223 pebble shape on bedload transport can be predicted, and that the inclusion of pebble shape 224 225 characteristics in the modelling of bedload transport offer much promise for improving bedload transport predictions. 226



Figure 6. Comparison between the mean measured velocities of particles of various shapes and densities and the theoretical particle velocity derived from a fractional transport rate relation adapted from Wilcock and Crowe's (2003) relation <sup>68</sup>.

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In terms of sediment dynamics, pebbles travel in the flume following an alternating 231 pattern of resting and motion periods, as generally observed in a natural stream<sup>8</sup>. We therefore 232 233 consider that our experiments succeeded in capturing the first order behavior of the bedload, and that the introduction of a shape factor into critical Shield stress and bedload transport 234 models might be transposed to rivers. However, the experimental conditions are slightly distinct 235 from those of natural rivers, in particular the use of a monodispersed sediment load and a low-236 roughness bottom. Additional experiments exploring distinct bottom conditions, grain size 237 distributions, and using straight channels are probably necessary to strengthen our initial results 238 and resolve the slight discrepancies between the model and observations. Similarly, 239 experiments using pebbles with a unique and defined type of particle shape (for example, only 240

platy particles, as expected in sediment derived from the erosion of schist-rich lithologies), instead of a single particle mixed with a large population of pebbles of distinct shapes, should help to derive a more universal relationship. Nevertheless, this study represents a preliminary and promising step towards addressing the role of particle shape in bedload transport.

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#### 246 CONCLUSION

These experiments, based on innovative tools (artificial pebbles of controlled density 247 containing RFIDs) offer new perspectives for studying sediment transport mechanisms. The 248 comparative analysis of the shape and density of particles on their mobility highlights the 249 crucial influence of particle shape. Furthermore, it also indicates that the sphericity index ( $\Psi_P$ ) 250 of Sneed and Folks (1958)<sup>69</sup>, which correlates with mean velocity, is relevant for including 251 shape parameters in sediment transport formulae. The method developed in this study can be 252 reproduced to investigate how bed roughness (changing D/K ratio) and/or a tracer's grain-size 253 can change the balance between the effects of shape and density on particle velocity. It allows 254 investigation of whether bed roughness promotes the transport of flat-shaped particles, as 255 reported in the literature, and whether particle density can mitigate this effect. Repeating the 256 257 experiments with smaller particle sizes (maintaining a constant D/K ratio) would also allow investigation of whether size mitigates the influence of shape and density on particle transport. 258

259

#### 260 METHODS

We designed four differently-shaped particle models within the grain-size class of 45– 64 mm (5.5–6.0  $\Psi$ -units), with all models having the same volume (*i.e.* 49.3 cm<sup>3</sup>) but exhibiting differences in the sphericity index <sup>53</sup> (Figure 7A ; Table 1). After creating silicon molds (RTV 120) for these four models, we manufactured 16 artificial pebbles using a mixture of resin and corundum powder in variable proportions, creating pebbles of four different densities (2.0, 2.2, 266 2.4, and 2.6 g.cm<sup>-3</sup>) for each mold shape <sup>54</sup>. We equipped these artificial pebbles with 267 transponders of Radio Frequency Identification, RFID, (model RI-TRP-WR2B of Texas 268 Instrument, Dallas Texas USA, also known as PIT Tags) to monitor their displacements within 269 an annular flume<sup>55</sup> (Figure 7B). A detection antenna located on the outside of the flume, along 270 a lateral window, enabled tracking of the number of laps achieved by the RFID-equipped 271 pebbles and the time for each revolution.



272 273 274

Figure 7. The four particle shapes investigated (A) and the annular flume equipped with the RFID system (B).

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Table 1. Shape characteristics of the artificial particles tracked in the flume.

SHAPE	<i>a</i> -axis (mm) L	<i>b</i> -axis (mm) I	c-axis (mm) S	Vol.(cm <sup>3</sup> )	Sphericity index (Sneed and Folks, 1958)
<b>Compact Blade</b>	68.1	46	30	49.3	0.66
Sphere	45.5	45.5	45.5	49.3	1
Disc	65	63	23	49.3	0.51
Elongated Blade	97.2	46.1	21	49.3	0.46

In an attempt to reproduce bedload transport conditions, these artificial pebbles were 278 mixed with 65 kg of limestone pebbles of a similar grain-size (i.e. class 45–64 mm) and were 279 run within an annular flume <sup>56</sup>. A set of experiments were run following the designs of previous 280 studies <sup>54,56,57</sup> for which the sediment dynamics have been characterized<sup>56</sup>, i.e. with a low 281 roughness bottom and a monodispersed grain size distribution. During the experiments, the 282 pump discharge sustaining the fluid injection into the flume was maintained at 240 m<sup>3</sup>.h<sup>-1</sup>, 283 which for the introduced sediment mass corresponds<sup>56</sup> to a shear stress of  $\tau = 135$  Pa at the base 284 of the flume according to Euler theorem applied to the moments, a Shield stress of  $\tau^* = 0.16$ , a 285 mean transit velocity for pebbles of  $\approx 0.4 \text{ m.s}^{-1}$ , and a sediment flux of  $\sim 24 \text{ kg.m}^{-1}.\text{s}^{-1}$ . Under 286 these conditions, high speed camera viewing<sup>56</sup> indicated that the pebbles were transported in 287 the annular flume in a similar manner to that observed<sup>8</sup> in rivers, with alternating transport 288 phases with rolling and saltation, and resting times caused by temporary blockage and piling of 289 particles. 290

Each experimental run lasted for 45 minutes. To avoid superpositioning of radio-291 frequency signals and missed RFID transponder detections<sup>54,58,59</sup>, only the four particles of the 292 same density were simultaneously present in the flume, thereby also limiting to four the number 293 of transponders. A total of six runs were achieved for the densities of 2.6 and 2.4 g.cm<sup>-3</sup>, and 294 five runs for the densities of 2.0 and 2.2 g.cm<sup>-3</sup>. For each artificial pebble, the combined runs 295 provide a long duration of almost 4 hours and a large cumulative traveled distance, from which 296 the mean traveled velocity (or virtual velocity as defined by Haschenburger and Church<sup>60</sup>) can 297 be computed and the distributions of the lap times estimated. Finally, we compared the virtual 298 velocities and lap distributions of the 16 artificial pebbles, to investigate the effects of the 299 different shapes and densities on bedload transport. In this study, the use of an annular flume 300 enabled the acquisition of a relatively long time series compared with typical straight flume 301 experiments <sup>61</sup> and the sampling of a population of practically uncensored particle trajectories 302

303	without the limitations induced by a limited detection window or flume length <sup>62</sup> . This ensured
304	that the ranges of traveled distances under conditions of continuous movement were well
305	represented in the experiment. We also made sure that the duration of the experiments (45
306	minutes) was much longer than the maximum resting time recorded (~5 minutes), to avoid time
307	censorship effects on the distributions of the resting periods and lap times, and to be sure of the
308	statistical significance of the distributions.
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# 480 Author contributions

- 481 M.C., H.P., and J.L. contributed to the design of the experiment. M.C., J.L., and H.P. analyzed
- 482 experimental results; J.L., H.P., M.C., A.R., and J-R.M. wrote the manuscript.

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## 487 **Competing Interests**

488 The authors declare no competing interests.