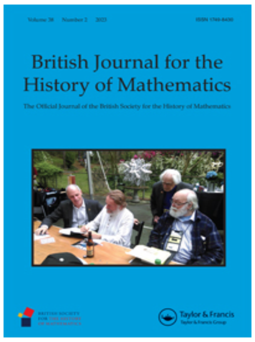

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D'Arcy Thompson on flight

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D'Arcy Thompson (1860–1948) is most remembered for his influential book *On Growth and Form* (1917), which looked to maths to explain why biological creatures take the shapes that they take. In January 1917, a few months before this book was released, Thompson had a letter to the editor published in *Nature* titled 'Stability in Flight'. Using this paper, and the response to it, as a basis, this article will investigate Thompson's relationship with mathematics, uncovering his ideas on an ideological hierarchy of subjects, where mathematics informs biology, but the reverse case is not true. It will also explore the ideas of flight Thompson discusses in the article, from the aeronautical physics paper which inspired Thompson, to the ideas on modern ornithology which agree with his work.

1. Introduction

D'Arcy Wentworth Thompson (1860–1948) was a biologist interested in the applications of mathematics to biology. On January 17th, a letter to the editor written by Thompson was published in *Nature*, titled 'Stability in Flight' (Thompson 1917b). This short paper featured a call for discussion from his fellow scientists, which was answered on February 25th 1917, with a letter to *Nature* by Herbert Maxwell under the same 'Stability in Flight' title.

Using this exchange as a basis, this article will investigate Thompson's relationship with mathematics, uncovering his ideas on an ideological hierarchy of subjects, where mathematics informs biology, but the reverse case is not true. It will also explore the ideas of flight Thompson discusses in the article, from the aeronautical physics paper which inspired Thompson, to the ideas on modern ornithology which agree with his work.

2. D'Arcy Thompson

D'Arcy Thompson was born in Edinburgh in 1860. The son of a Classics scholar and grandson of a veterinarian, Thompson grew up fluent in Greek and Latin, and with access to animals in an academic light (Thompson 1958). After three years studying medicine at Edinburgh University, Thompson moved to a zoology course at Trinity College, Cambridge, which he graduated from in 1883. The next year, he successfully applied for the position of Professor of Biology at the newly founded university in Dundee. More details on Thompson, particularly his childhood, can be found in

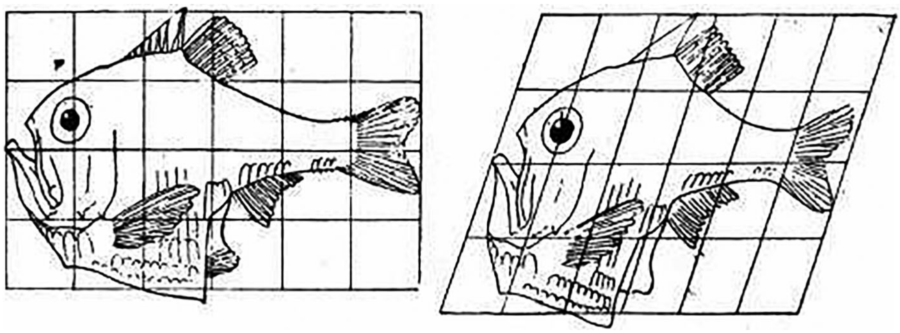

Figure 1. Diagram of *Argyropelecus Olfersi* (left) and *Sternoptyx diaphana* (right) from *On Growth and Form*, D'Arcy Wentworth Thompson, Public domain, via Wikimedia Commons.

the biography his eldest daughter, Ruth D'Arcy Thompson, wrote after his death (Thompson 1958).

Along with his role as professor, Thompson also worked on the Board of Fisheries for Scotland, on top of attempting to establish a natural history museum for the university (Wolfram 2018). As a result, Thompson was very busy, and his publication rate was slow. One thing he did put out was *A Glossary of Greek Birds*, a compilation of ancient Greek avian knowledge. This glossary, along with several of his other publications, earned Thompson a fellowship of the Royal Society in 1916 (Royal Society 1916).

In secondary literature, Thompson is most often explored from the perspective of biology, with his mathematics taking a back seat. There are, however, several papers which bring the mathematics to the fore.

Matthew Holmes discusses Thompson's relationship to physics via experiment (Holmes 2019), characterizing Thompson as an experimentalist, who looked to physicists to assist him in the completion of *On Growth and Form*. This help came in the form of setting up experiments and providing Thompson with mathematical explanations of the results, which Thompson then applied to his biology. One example of this is when Thompson contacted Charles Darling, a physicist working on water droplets, to help in investigating a potential link between the forms of sea urchins and the forms of water droplets (Holmes 2019). Here, Thompson wanted help not only setting up an experiment to create urchin forms from water, but also in finding mathematical expressions for this; this is a very literal example of Thompson looking to mathematics to inform biology.

Thompson's relationship with mathematics is also discussed in an article by Wolfram (2018). Wolfram characterizes Thompson as 'first and foremost a collector' (Wolfram 2018, 45), and frames his interest in mathematics as an interest in data collection. This is most evident in his collection of data related to the tides and fishing, but is also seen in pure mathematics; Wolfram describes Thompson's work on number theory as 'collecting properties of numbers' (Wolfram 2018, 47).

The year after gaining his fellowship, 1917, was an important one for Thompson. It was the year he was appointed as Professor of Natural History at St Andrews, and the year he published *On Growth and Form* (Thompson 1917a). This book is often seen as Thompson's magnum opus.

It was described in one contemporary review as 'one of the strongest documents in support of the mechanistic view of life that has yet been put forth' (McMurrich 1917, 513), and is still held in high esteem today. The centenary celebration of the book's release was held in St Andrews and Dundee and sparked several new articles on the book. One of these claims that *On Growth and Form* 'pioneered the science of biomathematics', as well as influencing many other fields (Jarron 2018, 30). In this book, Thompson discussed biology under mathematical constraints; he looked to, often rather basic, concepts in physics to explain the way various organisms grow. This comes in contrast to the prevailing Darwinistic views at the time, that species were changed over time by natural selection, and as such growth had little to do with the form of any being. The most well-known example of Thompson's ideas is the diagrams found in chapter 17 of the first edition, 'On the Theory of Transformations'. These use transformations on grids to change the proportions of one species to match another, most memorably with fish.

3. Stability in flight

1917 is also the year in which our episode takes place, though several months before Thompson's ideas would reach a wider audience through the release of *On Growth and Form*. On January 25th, Thompson's first letter on flight was published in *Nature* (Thompson 1917b), taking up only one column's worth of space. As its length suggests, the paper doesn't go into much detail, instead presenting a rather simple idea and giving a few examples.

The idea Thompson suggests is that birds with 'small tails and comparatively small and narrow [to the bird's body] wings' are better suited for flight at high winds, being more 'skilful, or agile' under these conditions. A few examples of such birds are provided, such as seagulls, swallows, and albatrosses. Also mentioned are those birds which are considered by Thompson to be less adapted for flight at high winds; pigeons, robins, and magpies. These latter birds are characterized as having round wings.

The letter finishes off by inviting discussion, and briefly bringing up a separate point; Thompson wonders whether the heron has long legs to compensate for its long neck. This idea is based on centre of gravity; having more mass in the legs would help to keep the centre of gravity of long-necked birds like the heron close to the wings.

In this paper, as in *On Growth and Form*, which at this point was being prepared for publication, Thompson has taken a mathematical concept and applied it in biology. Bird flight and human flight have long been intertwined, with humans learning from the example of birds. This was true long before humans conquered the skies, as seen in Leonardo Da Vinci's diagrams of potential flying machines, as well as in the development of the first aeroplanes (Bossoh 2021).

In this way, Thompson's combination of birds and planes is not unusual. Here, though, Thompson is using knowledge originally used in human flight and applying it to birds, in a neat twist on the expected order of things.

4. Thompson and Brodetsky

While the letter is entirely based on observations that Thompson made, the idea behind it came from mathematical principles set out in a theoretical paper published a few months previously by Dr Selig Brodetsky, which concluded that the equivalent conditions of Thompson's birds in aeroplanes would make the machines safer and more stable in flight at high winds (Brodetsky 1916).

According to a letter Thompson sent to the mathematician George Greenhill (Thompson 1917f), the reason Thompson published in *Nature* was because he had been encouraged to do so by Brodetsky. The two had indeed been in correspondence on the topic, with Brodetsky sending Thompson a copy of his paper in 1916. Thompson responded with his thoughts on its application to flight, which Brodetsky suggested writing up for a journal (Brodetsky 1917). These letters do not have any more content than what is discussed in *Nature*; in fact, several passages of the *Nature* letter are lifted straight from Thompson's response to Brodetsky (Thompson 1917d).

Selig Brodetsky was born in 1888, a Jewish Russian who immigrated to England as a child (Mestel 2004). Like Thompson, Brodetsky studied at Trinity College, though he studied mathematics, being bracketed senior wrangler in 1908. 'Bracketed' here indicates that he shared the title, given to the highest scorer in the Cambridge mathematical tripos exam. He received a doctorate from the University of Leipzig in 1913, and returned to England as a lecturer at Bristol shortly before WW1 broke out.

In the outbreak of war Brodetsky paired up with GH Bryan, a lecturer at Bangor, to work on the physics of aeroplanes. The paper which Thompson referenced in his letter to *Nature* came about as a result of this collaboration. This work is a relatively early one in the field of aviation, with one of the first major works on the subject having only been published in 1911, by Bryan, titled *Stability in Aviation* (Boyd 2017; Bryan 1911).

Brodetsky created a simplified model of the effect of various wind speed changes on an aeroplane, restricting the dimensions in his calculations by not taking vertical changes into account. Brodetsky truncates approximations at the squared term, in order to limit the number of coefficients he needs to calculate: 'there is, of course, no limit to the number of coefficients that can be calculated in this way, but after the first two the algebra is very heavy' (Brodetsky 1916, 144).

Starting with an initial rudimentary diagram of a plane, and using the equations of motion, Brodetsky was able to work out what was needed in each of the variables he set out in order to ensure a minimum of disturbance. Disturbance is measured as curvature, or the change in angle of the plane, when wind hits it.

The variables relevant to Brodetsky's first case, where wind speed changes once and then remains stable, are as follows:

S_1,S_2 are the area of the main plane, and its tail
K_1,K_2 are the resistance coefficients of the respective areas
M,Mg are the mass and weight of the plane
I is the moment of inertia
H_0,V_0 and a_0 are the initial airscrew thrust, velocity, and angle of attack, respectively.

Brodetsky also gives the velocity of the wind, with u moving horizontally backwards, and v vertically upwards.

The curvature is given by dθ ds, where θ is the 'the angle… between the velocity V and the forward horizon' (Brodetsky 1916, 142), and s is the distance that the plane moves. Brodetsky does not express this explicitly, but we can see that

$$s = \int V \, \mathrm{d}t$$

Brodetsky finds an estimate for dθ ds by using

$$\frac{\mathrm{d}\theta}{\mathrm{d}s} = \frac{\frac{\mathrm{d}\theta}{\mathrm{d}t}}{\frac{\mathrm{d}s}{\mathrm{d}t}}$$

and substituting in equations for θ and s found through use of the equations of motion for the plane:

$$V = V_0 + a_1 t + a_2 \frac{t^2}{2!} + \ldots$$

$$\theta = c_1 t + (b_2 + c_2)\frac{t^2}{2!} + \ldots$$

Here, a_1,a_2,b_2,c_1, and c_2 are all unknown constants, and both equations are truncated at the t^2 term for simplicity.

With these substitutions, Brodetsky gets

$$\frac{\mathrm{d}\theta}{\mathrm{d}s} = \frac{c_1}{V_0}\left\{1 + (\frac{b_2 + c_2}{c_1} - \frac{a_1}{V_0})t\right\}$$

The initial curvature is seen as the most important factor in this equation, since 'after a short time it may be safely left to the pilot to adapt the course to the altered conditions' (Brodetsky 1916, 140). Thus, we concentrate on the $\frac{c_1}{V_0}$ term.

With careful use of algebra and substituting terms which stem from the initial equations of motion, Brodetsky eventually finds

$$\frac{c_1}{V_0} = -\frac{1}{V_0}\left\{\frac{2K_1 S_1 \sin a_0 \cos a_0}{M} u + \frac{K_1 S_1 \cos^2 a_0 + K_2 S_2}{M} v\right\} + \ldots$$

The important terms here with regards to D'Arcy Thompson's work on birds are those involving S_1, S_2 and M; we see that M must be maximized, and S_1 and S_2 minimized, which is what gives the condition 'the ratio of the total area to the total mass, shall… be as small as possible' (Brodetsky 1916, 146). The inference about the relative size of the tail is found in a similar manner.

Armed with various estimations both of initial curvature and its changes over time, Brodetsky concluded that the safest aeroplanes were those with 'large velocity, small angle of attack, small ratio area/load, [and] small tail fairly far behind the main plane' (Brodetsky 1916, 156). It is easy to see that this is where Thompson drew his inspiration for his *Nature* letter.

This inspiration was drawn only from the conclusions Brodetsky presented, rather than the mathematical content of the paper; Thompson describes it as 'rather too hard for' him (Thompson 1917d). This is in line with other assessments of Thompson's mathematical ability, both from comments by Thompson, and in the literature. Wolfram comments that 'he never learned' calculus (Wolfram 2018, 41), which would explain why Thompson could not follow the solving of a differential equation here.

5. Public criticism

On February 22nd, *Nature* published a response to Thompson's paper. Of Thompson's theory on the qualities that best equip a bird for stability in flight, the author, Herbert Maxwell, says that 'no such generalisation can stand in the face of facts' (Maxwell 1917). Maxwell argues his case by way of counter-example, claiming in one case that D'Arcy's assessment of a pigeon's agility is incorrect, as is the claim that their wings are rounded rather than narrow: 'no species of pigeon known to me has rounded wings' (Maxwell 1917).

Who was Maxwell, to be taking such a strong stance against Thompson here?

Maxwell was born in 1845, and inherited a baronetcy from his father in 1877 (Smith 1938). He had no formal qualifications to show from his time in education, of which some were spent at Eton, and one at Christ Church, Oxford. After inheriting his title, Maxwell entered the world of politics, holding the position of MP for Galloway for seven consecutive terms, and holding various titles and responsibilities in parliament over that time.

In his later years, Maxwell turned back to intellectual pursuits, becoming an avid writer of academic books. His works touched on historical figures from Scotland, as well as more scientific texts which ventured into fishes, plants and insects. He was elected a fellow of the Royal Society in 1898, though no reason for this is cited on his election certificate other than his own wish to be a member (Royal Society 1898).

Both being fellows of the Royal Society interested in biology, Maxwell and Thompson would have orbited the same academic spheres. There is no evidence of correspondence between the two, though they do seem to have met; in a letter to mathematician George Greenhill (Thompson 1917f), Thompson describes Maxwell as 'an industrious person (not to say a busy-body)', and wonders whether Maxwell's criticisms are him 'paying off a very old score'.

6. Thompson's response

This letter to Greenhill was sent on 19th February, one of many in a long series of friendly correspondence between Thompson and the mathematician. More than a hundred of these exist in the archives at St Andrews, ranging in date from 1915 to 1925. Greenhill himself had worked on flight (Nicholson 1929); he wrote a paper in 1910 titled *Theory of Stream Lines with Applications to an Aeroplane*, and one in 1912 called *Dynamics of Mechanical Flight*. In the letter, Thompson tells Greenhill of the upcoming *Nature* letter from Maxwell, describing his own initial *Nature* paper as 'small and inoffensive'. In contrast, Maxwell's response is seen as Thompson 'being skinned alive for it'.

As a result of being tipped off, Thompson was able to produce a response which was published as the letter immediately after Maxwell's (Thompson 1917c). This was not too unusual at the time; several letters to the editor in this era of *Nature* take the same form.

In his response, Thompson seems quite defensive, pointing out that he was 'suggesting an inquiry, not laying down the law' (Thompson 1917c). This is interesting in comparison with Wolfram's description of *On Growth and Form*; Thompson is said to be asking constantly why creatures are the shape they are, and 'over and over again the answer that's given is: "because it's following such-and-such a physical phenomenon, or mathematical structure"' (Wolfram 2018, 40). Thompson follows this structure in his original *Nature* paper. He does ask for input, but this only comes at the end of the paper; it is easy to read the rest as ‘laying down the law’.

Thompson’s defensiveness is especially evident when he addresses Maxwell’s criticism of his heron observations; Thompson insists that, having grown up near a heronry and ‘having seen the birds nearly every day of [his] life’ (Thompson 1917c), he is aware of how they fly. He also accuses Maxwell here of having ‘gone out of his way for the sake of fault-finding’.

There is an interesting line in Thompson’s response, where he is divorcing himself from the basic idea of comparing tail and wing sizes to flight stability. He says that ‘certain learned mathematicians’ (Thompson 1917c), here referring to the papers he used in his original letter, had proven the advantage of a shorter tail, despite these not making any comparison of aeroplanes to birds. Then he says that ‘the naturalist has no right to dispute such abstract and theoretical demonstrations’ (Thompson 1917c).

This suggests almost a hierarchy of subjects in Thompson’s mind, where mathematics is informing biology, and, at least in this case, the reverse case is not possible.

Holmes presents Thompson’s use of physics as a way of simplifying his biological problems: ‘divorced from the complexity of biology, the workings of these laws could now be seen with greater clarity’ (Holmes 2019, 7). This could be seen as biology working as an application of physical laws, again implying the hierarchy.

Thompson defends this position with a reference to Galileo, and his work ‘show [ing] the mechanical advantages of a hollow pillar’, stating that although there exist examples in nature, like trees and feathers, which go against this, naturalists do not have ‘sufficient right to question it’ (Thompson 1917c).

Thompson also made reference to Galileo in this way a few years previously in a paper for the *Transactions of the Royal Society of Edinburgh*, ‘Morphology and Mathematics’ (Thompson 1916).

7. Repercussion

Though the use of mathematics to inform biology as seen here is present in Thompson’s other works, the actual ideas about flight discussed here are not present elsewhere. They did not, for example, make it into the second edition of *On Growth and Form*, published in 1942, though other mentions of wings and flight did.

These take the form of a section about flight in his chapter on magnitude, where he explains that larger birds must fly at a higher speed to be able to stay in the air, whereas smaller birds can afford to be slower. There is also a section in the chapter on the form of tissues where Thompson discusses the shapes of dragonfly wings, but this is less related to flight and more to the shapes inside the wings.

It is possible that this is because Thompson had no new material to present, having explained all his thoughts in the *Nature* article. However, Thompson was not afraid to repeat himself - his paper ‘Morphology and Mathematics’ (Thompson 1916) is almost word for word what he later published in the chapter of *On Growth and Form* on the theory of transformations. Instead, it could be that the negative experience Thompson had with his *Nature* letter was something that put him off exploring this further.

Further to this, Thompson’s letters also show signs that he was affected by Maxwell’s criticism. The correspondence between Thompson and Brodetsky was a short one, which conspicuously ended when Thompson did not respond to a letter from Brodetsky sent only a few days after the Maxwell letter was published in *Nature*.

Looking at the evidence here, it suggests that Thompson held some sort of grudge against Brodetsky as a result. Further, he brings the man up in a later letter to Greenhill (Thompson 1924), where he indicates not wanting to communicate with him.

This letter reveals a potential bias Thompson has against Brodetsky unrelated to the *Nature* letter; his wording is 'don't make me have to go to the Jew Brodetsky' (Thompson 1924). Thompson also referenced Brodetsky's religion in his 1917 letter to Greenhill, calling him 'that little spawn of Abraham' (Thompson 1917f).

8. Thompson's legacy in the study of bird flight

The study of birds can be traced back thousands of years, but it is only relatively recently that understanding of their flight was achieved. Bossoh describes George Campbell, 8th Duke of Argyll, as 'one of the first to popularize the theoretical principles of bird flight' (Bossoh 2021, 1). He held a lifelong interest in the topic and assisted in the founding of the Aeronautical Society in 1866. Argyll firmly believed in the possibility of mechanical flight, and further that it would become possible if and only if humans gained understanding of the flight of birds.

Argyll believed that birds moved forwards in the air by nature of tilting themselves downwards, and that the shape of the wings and feathers were the key to their ability to stay in the air. He was aware of the importance of weight to a bird's flight, knowing that 'flight speed depended on an inverse relationship between a bird's wing size to its body weight' (Bossoh 2021, 2). Like Thompson, Argyll may have found this by observation, though he does not seem to have turned to mathematics for explanation.

Another man working on the flight of birds prior to Thompson was James Bell Pettigrew, the Professor of Medicine and Anatomy at St Andrews from 1875 till his death in 1908 (Anonymous 1908). Bell Pettigrew was particularly interested in the movement of wings, especially those of birds. Unlike Argyll's ideas, Bell Pettigrew proposed the idea that a bird's wings move in a figure of eight motion, which is what, along with the flexibility of wings, allowed birds to move both horizontally and vertically (Pettigrew 1873).

Bell Pettigrew was also very interested in mechanical flight. He discussed his ideas on this in his book on animal locomotion, which described walking, swimming, and flying, then concluded with a chapter on aeronautics. Bell Pettigrew believed that the key to artificial flight lay in the replication of bird flight. He dismissed the idea of lighter than air flight having potential, but also held distaste for the idea which ended up working, describing fixed wing 'rigid' planes as 'in some respects quite as irrational as the ballooning model' (Pettigrew 1873, 211).

Pettigrew also commented on the interplay between the weight and wing area of flying creatures; 'still it appears from the researches of M. de Lucy that there is a general law, to the effect that the larger the Volant animal the smaller by comparison are its flying surfaces' (Pettigrew 1902), here also demonstrating that it was known to at least one other scientist.

Neither Argyll nor Bell Pettigrew looked the other way round, using mechanical flight to explain the natural. However, both men were too early to do so; Argyll died three years before the first successful flight by the Wright brothers, and Bell Pettigrew died only a few years after. That Thompson was one of the first to explore birds in such a manner may simply be a coincidence of the timing with which he came upon the subject. By 1917, the first world war had prompted a rapid increase in study into aeroplanes, giving Thompson material that he could work with.

After Thompson's *Nature* letter, many others have taken up the study of birds with respect to mechanical flight. Thompson's name does not come up as a pioneer in this regard in modern texts, and as such it seems likely that his small exchange with Maxwell did not have any great effect.

Despite this, as seen from the ideas Argyll and Pettigrew shared with Thompson, the connection between area and weight was known about. It seems odd that Maxwell took a stance against this idea, especially as it shows up in modern ornithology; a recent book by Taylor and Thomas (2014) on mechanical biology with respect to bird flight discusses various qualities which can be attributed to the ratio of the area of a bird's wings to its weight, known as 'wing loading'.

The area of a bird's wings versus its weight is implied by Thompson in his 'comparatively small and narrow wings' (Thompson 1917b), and is explicitly stated as important for aeroplanes by Brodetsky.

Taylor and Thomas do not discuss birds in high wind conditions specifically, but there is a match with Thompson's ideas on bird migration – he singles out robins as birds which are 'poor fliers', i.e. have more rounded wings, as being good for migration. Taylor and Thomas confirm this: migratory birds should have lower wing loading, meaning a less weight and more wings, fitting Thompson's description.

Thompson's claims about herons, however, seem to be in error. Herons do fly with their neck tucked in, as pointed out by Maxwell, and thinking for a moment about the effects of levers and moments in physics, you can see that this would reduce the effect the neck had on centre of gravity quite a bit. It is quite possible that Thompson really did forget that herons fly like this, given that several other birds with long necks, like the goose, fly with them outstretched, demonstrating his point much better. After all, centre of gravity *is* very important in flight.

From this it could also be argued that Thompson had poor observation skills, although this would not match up well with Holmes' categorisation of Thompson as an experimentalist. Thompson was indeed aware of the ability of the heron to tuck its neck in, saying as much in one of his letters to Brodetsky (Thompson 1917e) before publishing the *Nature* paper. As such, it is curious that he chose the heron example, rather than a more appropriate option.

9. Conclusion

D'Arcy Thompson saw mathematics as a guiding light to inform biology, as seen in his response to Maxwell's criticism of his use of Brodetsky's work on aerodynamics. The incident of the *Nature* letter provides an example of the tendency that Holmes pointed out, of Thomson often relying on physicists like Brodetsky to provide him with results, both of experiments and the mathematics underpinning them.

Thompson's idea of using aerodynamics to inform ornithology was similar to the modern ideas of the study, though his actual work was somewhat underdeveloped. Perhaps if he'd continued his study, Thompson could have worked out some of the finer details we know today. Instead, the only reference to Thompson in Taylor and Thomas's book on the subject is found in some diagrams which are a reference to the coordinate grids Thompson is most known for.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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