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NOTES ON THE BEHAVIOR AND MECHANICS OF SCOOPING OVIPOSITION IN *LIBELLULA COMPOSITA* (HAGEN) (ANISOPTERA: LIBELLULIDAE)

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Females were observed ovipositing, both alone and in tandem, in Chaves County, New Mexico, United States. The ♀ oviposits by scooping water droplets into the air with the tip of her abdomen. This mode of oviposition is common in many Libellulinae, but this is the first report of a ♀ using it in tandem as well as in solo oviposition. The ♀ *L. composita* also grips the ♂ abdomen with her legs during post-copulatory oviposition flight, a behavior previously reported only in subfamilies Trameinae and Zygonychinae. Possible functional significance of this flight behavior is discussed based on observations and analyses of the mechanics of the oviposition process that are evident in photographs.

INTRODUCTION

Libellula composita (Hagen) is found in the western United States from California to Oregon and east to Kansas and Texas (NEEDHAM et al., 2000). DUNKLE (2000) notes that its occurrence is "scattered and rare". Little has been published on its biology. KENNEDY (1917) reported catching "A single female of this rare species...while she was perched on the top of a greasewood bush" in the Humboldt River valley in Nevada. He stated that it was the only one of the species he had seen alive, though he later notes that during 1915 he found the species common in the Owens Valley in California. DUNKLE (2000) noted that "Males at water patrol much of the time, occasionally resting on reed tips. Pairs lay eggs in tandem, flying wildly between dips to the water". The species is often found at hot springs in Oregon and California (D.R. Paulson, pers. comm., 2003) and can tolerate alkaline or saline waters (DUNKLE, 2000; R. Larsen, pers. comm., 2003). In July 2001, while on a post-meeting trip after the Dragonfly Society of the Americas' annual meeting, I had an opportunity to briefly observe the species and to photograph single females and pairs in tandem, in flight and ovipositing.

DESCRIPTION OF SITE

The location of these observations was the Bureau of Land Management (BLM) Overflow Wetlands Wildlife Habitat Area adjacent to Bottomless Lakes State Park in Chaves County, New Mexico. The Park is bounded on the west by the Pecos River. Groundwater from the Sacramento Mountains, far to the west, flows beneath the area, producing springs which feed lakes such as Lea Lake, the largest water body in the vicinity. In spite of intensive irrigation in the region, the water table is very shallow in this immediate area (ANONYMOUS, 2002). The Overflow Wetland itself has spring fed shallow streamlets and some areas of sheet flow. Oviposition by *Libellula composita* was in these small streams and areas of shallow flowing water where there was much emergent vegetation, predominantly grass. R. Larsen (pers. comm., 2003) has identified the grass species in the Overflow Wetlands as Salt Grass, *Distichlis stricta*. Other Odonata species in the wetland included *Argia alberta, Ischnura barberi, Anax junius, Erpetogomphus designatus, Erythemis collocata*, and *Libellula saturata*.

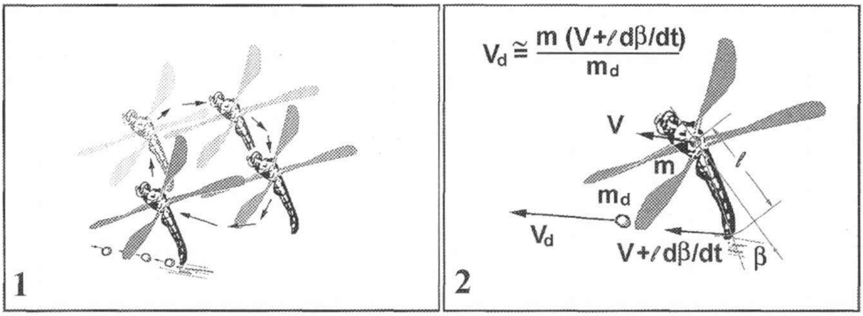
SCOOPING OVIPOSITION IN ODONATA

CORBET (1999) surveyed modes of oviposition in Odonata, and identified as his oviposition mode FC7: "Female Flying Contact oviposition onto water, with subsequent scooping". Typically this involves the female flying forward, dipping the tip of her abdomen into the water is such a way as to scoop droplets of water from the surface and flinging them (presumably with eggs washed off the abdomen and carried in the droplets) onto plants or other nearby substrates. After this she flies up and backwards in a small closed circular or elliptical path, repeating the process (shown schematically in Figure 1). During the portion of the maneuver in which she approaches the point where water is scooped, the female may also begin curling the abdomen ventrally, thus using muscular contraction to add to the speed of the abdomen as it breaks the surface of the water. If all the momentum of the flying female were transferred to the water droplet, the droplet would be propelled with a velocity greater than that of the abdominal tip by a factor equal to the ratio of the mass of the female to that of the water droplet (Fig. 2). S.W. Dunkle (pers. comm., 2003) has indicated that he has observed scooping oviposition taking place with the abdomen flexed forward prior to entering the water so that only the forward flight momentum was available to propel the water droplets. In either case, the abdominal flexure would provide a spring-like energy absorption mechanism to reduce the impact force of the initial contact of the abdomen with the water.

CORBET (1999) listed the following taxa as having been documented in the literature as having species that use oviposition mode FC7: Corduliidae: Corduliinae: *Procordulia, Somatochlora*; Libellulidae: Brachydiplacinae: *Tyriobapta*; Libellulinae: *Hadrothemis, Libellula, Lyriothemis, Nesciothemis, Orthemis, Orthetrum, Potamarcha, Sympetrum*; and Tetrathemistinae: *Eothemis*.

Subfamily classifications throughout this paper follow DAVIES & TOBIN (1985) to maintain consistency with the referenced works.

DUNKLE (1989) has noted that "Females of all our species [of *Libellula*] have lateral flaps on the margins of abdominal segment 8 which can be used as a scoop to throw drops of water containing eggs onto the bank." MILLER (1989) also associated this



Figs 1-2. Elements of scooping oviposition: (1) a schematic representation of the typical flight sequence that comprises "scooping oviposition" in Libellulidae: In the lower left image, the dragonfly is just completing the process of flipping up a jet of from one to several water droplets. Next the insect flies in a closed path, up (upper left image), backwards (upper right image) and then down and forward (right image). In the forward flight phase the female may also flex the abdomen ventrally to add to the momentum of the abdomen tip as it enters the water; – (2) scooping oviposition involves the transfer of momentum from the dragonfly to the water. V_d = velocity of water droplet, m_d = mass of water droplet, V = velocity of dragonfly, m = mass of dragonfly, β = angle of flexure of abdomen, dβ/dt = angular velocity of abdomen with respect to center of mass of dragonfly, ℓ = distance from center of mass to tip of abdomen.

oviposition behavior with the presence of these bilateral foliations, and reported scooping oviposition in "4 species of Tetrathemistinae and in 23 spp. of Libellulinae". Specific detailed accounts of scooping oviposition have been given by GLOYD (1958) for *Libellula saturata*, WILLIAMS (1977) for *Libellula croceipennis*, and NOVELO-GUTIERREZ & GONZALEZ-SORIANO (1984) for *Orthemis ferruginea*. Most libelluline females using scooping oviposition appear to oviposit in solo flight, often with males guarding them by flying nearby. DUNKLE (2000) said of the *Libellula* that "Males usually hover-guard egg-laying females, nearly all of which splash eggs onto the bank". None of these authors mentioned scooping oviposition being associated with tandem flight. I observed *L. composita* using this mode of oviposition both singly and in tandem.

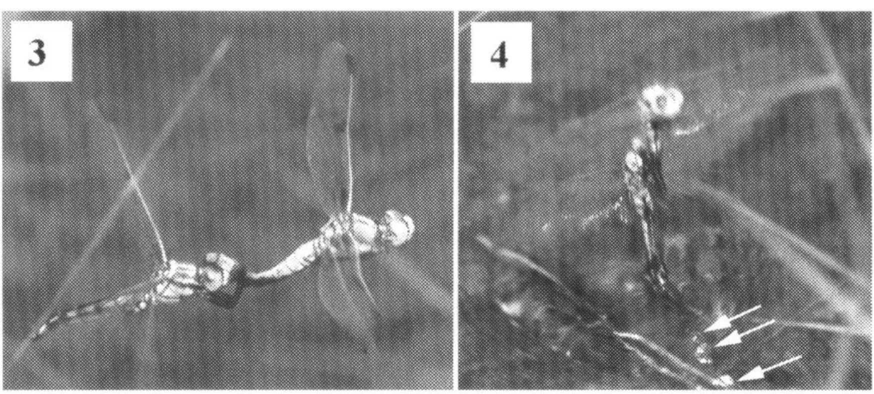
TANDEM OVIPOSITION IN LIBELLULIDAE

MARTENS et al. (1997) listed tandem oviposition in Libellulidae in five subfamilies: Leucorrhiniinae (*Celithemis*); Sympetrinae (*Diplacodes, Erythrodiplax, Indothemis, Sympetrum*); Urothemistinae (*Macrodiplax, Selysiothemis, Urothemis*); Trameinae (*Hydrobasileus, Idiataphe, Miathyria, Pantala, Tramea*); Zygonychinae (*Zygonyx*). They noted that "While it is typical in Anisoptera for the female to grasp the male's abdomen during copulation...such behaviour following copulation is exceptional". They stated that post-copulatory tandem flight with the female holding the male's abdomen with her legs was "only known from" the Trameinae (4 species of *Tramea*) and Zygonychinae (*Zygonyx natalensis*). As noted above, DUNKLE (2000) reported *Libellula composita* to oviposit in tandem. In my observations of the species in tandem flight, I noted that the female grasped the male's abdomen both in horizontal flight and during tandem oviposition.

MARTENS et al. (1997) speculated on the possible phylogenetic significance of female grasping as a reproductive behavior characteristic, noting that Trameinae and Zygonychinae shared this trait as well as certain similarities in advanced wing venation characteristics. This is the first report of this behavior in the Libellulinae; it is obviously rare in this subfamily, so its presence in one species does not negate its possible value in studies of systematic relationships. MARTENS et al. also listed a number of hypotheses regarding the adaptive significance of the trait, and the observations reported below show the behavior to be of definite functional significance to tandem oviposition in *L. composita.*

OBSERVATIONS OF TANDEM FLIGHT AND SCOOPING OVIPOSITION IN *LIBELLULA COMPOSITA*

While collecting and observing Odonata in the BLM Overflow Wetlands, I noted that pairs of *Libellula composita* in tandem appeared regularly on the shallow, clear stream along which I was working. They flew rapidly and rather wildly, occasionally stopping briefly in vegetated areas to oviposit. After collecting a pair, I began attempting to take photographs of the oviposition activity. I used a Nikon N90S camera equipped with a 200 mm Micro-Nikkor ED f4 macro lens, an SB28 strobe flash unit and Fuji Provia 100 transparency film. The day was bright and clear, but the dragonflies were moving very rapidly, and it was difficult, even with automatic focusing, to track and photograph them. While thus lacking somewhat in clarity, the resulting photographs do show some interesting characteristics of the species' oviposition behavior.



Figs 3-4. *Libellula composita* (Hagen) in tandem flight: (3) post-copulatory flight between oviposition bouts. The female is grasping the male's 7th abdominal segment with her mid and hind legs, an exceptional behavior previously documented only in Trameinae and Zygonychinae; — (4) female engaging in scooping oviposition in tandem with male. She continues to grasp his abdomen with her legs. White arrows point to water droplets, a sequence of three resulting from this bout.

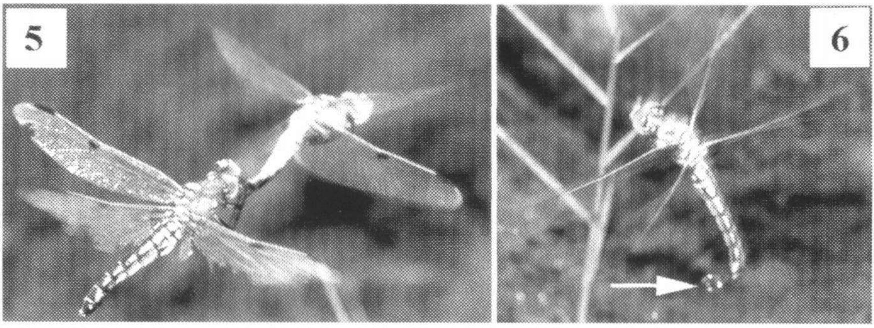
Figure 3 shows a pair in tandem flight. The female is gripping the anterior half of segment 7 of the male's abdomen with her middle and hind legs, thus pulling segments 8 through 10 of the male's abdomen down into close contact with her head. This contact is also maintained during tandem oviposition as shown in Figure 4. White arrows have been added to the photograph to show the locations of the water droplets propelled by the female. There are three fairly large droplets visible, indicating the female has scooped up a rather substantial jet of water.

In Figure 4, as in all the photographs I took, the trajectories of the droplets scooped up by female *L. composita*, whether alone or in tandem, were fairly shallow. This is different from the observations of GLOYD (1958), who indicated that the *L. saturata* "flipped up small water droplets as high as six or eight inches" (15-20 cm), and WILLIAMS (1977), who included a picture of *L. croceipennis* showing a droplet trajectory which I estimate to reach a height of 4.5 cm and a horizontal distance of 22 cm. The amount of abdomen flexure and the ratio of horizontal to vertical speed of the dragonfly during the time its abdomen is in the water would both influence the shape of the water trajectory.

While most of the ovipositing *L. composita* I observed were in tandem, I did see two separate females ovipositing singly. PAULSON (1969) has noted that "... females of many species oviposit first in tandem and then alone at the same site. As there are important advantages to oviposition in tandem ... it is clear that there should be strong selection for these patterns of behavior, yet individual females in many cases behave otherwise, as if the tendency to utilize alternative pathways of behavior has been of equal advantage". Perhaps this behavioral plasticity helps to offset whatever factors are responsible for the scattered and uncommon distribution of this species. M. May (pers. comm., 2003) notes that release of the tandem may very well be initiated by the male rather than by the female, the benefit of an opportunity to mate with a second female outweighing that of remaining with the ovipositing female while she finished laying the remainder of her mature eggs.

In all scooping oviposition by *L. composita* that I observed, either by tandem pairs or by single females, the eggs were being flung towards clumps of vegetation. R. Larsen (pers. comm., 2003), who lives near the Overflow Wetlands and makes frequent observations of the Odonata there, notes that, over open water, numbers of Pecos Pupfish (*Cyprinodon pecosensis*) follow ovipositing Odonata and take the eggs as they enter the water. He adds that eggs would be more likely to survive predation by pupfish when oviposited away from open water in the Salt Grass vegetation of the Overflow Wetlands.

Larsen (pers. comm., 2003) also observed that "pupfish will leap from the water and grab the tandem female just behind the hind wing triangle. If only one fish grabs her wing the male can lift the female to safety and the fish will drop off...leaving a rectangle notch in the wing". Figure 5 is a photo of a tandem pair showing the female to have tattered hind wings, with notches that could have been made by fish. The grip of the female on the male abdomen while in tandem would certainly help to make it more difficult for predatory pupfish to pull her from the male. Larsen also noted that "Lone



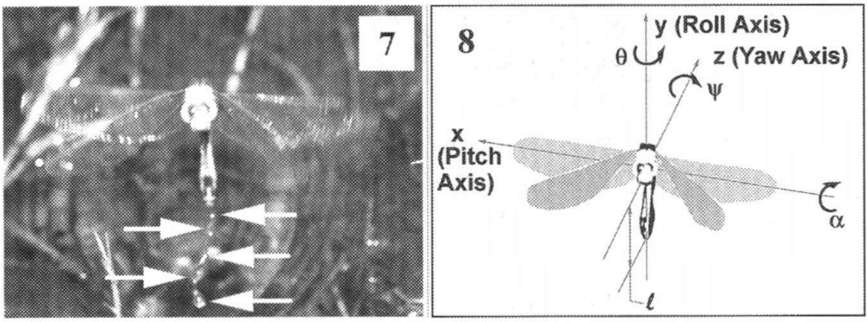
Figs 5-6. *Libellula composita* (Hagen) in flight: (5) male and female in tandem flight showing the damage to the hind margin of the female's hind wings. There is also a notch in the hind margin of her left fore wing. Some of this damage may be from predation attempts by pupfish during oviposition. Such events have been observed by R. Larsen (pers. comm., 2003); – (6) lateral view of female engaging in scooping oviposition. The white arrow indicates a water droplet scooped up by the dragonfly. Droplet is about 4 mm in diameter. If there were no air bubbles entrained in the droplet, it would have a mass of about 10 to 15% that of the dragonfly.

composita females ovipositing rarely survive an attack by Pupfish ..."

Figure 6 is a lateral view of a solo female ovipositing, and shows quite clearly the size of the water droplet being scooped from the water. This photograph allows an estimate of the mass of the water droplet, since the droplet and insect are in roughly the same plane, and perspective errors are minimized. The diameter of the droplet appears to be about the size of one of the dragonfly's eyes, and measurements indicate the drop to be about 4 mm in diameter (head width at the eyes of a female *L. composita* is about 7 mm), giving it a volume of about 0.045 cm^3 and a mass of 45 mg, assuming that no air has been entrained in the droplet. I have not weighed *L. composita*, but based on other similarly sized Libellulidae species that I have weighed, I would estimate a mass of between 300 and 400 mg. This indicates that the water droplet is somewhere between 10 and 15 percent of the total mass of the dragonfly, a significant amount. It is worth noting that the flanges on the eighth segment of *L. composita* are small compared with those of some FC7 species such as *Libellula saturata* and *Orthemis ferruginea*. One would expect the latter species to scoop up even larger water droplets.

Appendix 1 contains several figures showing the results of a simple analysis of momentum transfer and droplet trajectories together with the flight velocities that would be required to produce them.

The scoop-like area formed by the flanges on the ventral abdomen of *L. composita* can be seen quite well in Figure 7, which shows a front view of a single female. The picture catches the end of an abdomen flick, with a long jet of water droplets visible. It is very interesting to see that in this case the droplets are not in a straight line, but follow a sinuous path. This could only be the result of the female's abdomen tip oscillating in a rolling motion about the axis running lengthwise through her abdomen while the abdomen tip was traversing the water. One full cycle of oscillation occurred, and measurements of the angle between tangents to the stream show the rotation to have had an amplitude of



Figs 7-8. *Libellula composita* (Hagen) female engaging in solo oviposition: (7) front view showing a sinuous jet of water droplets scooped into the air. The non-linear path of the water indicates that the insect was experiencing rolling oscillations during the time the tip of her abdomen was passing through the water; — (8) sketch of the female shown in Fig. 7, with axes shown for reference in discussing the mechanics of the oviposition process. The axes are assumed to pass through the center of mass of the dragonfly. x = Pitch Axis, y = Roll Axis, z = Yaw Axis. α = Pitch rotation (positive when abdomen moves toward the viewer, out of plane of picture), θ = Roll rotation (positive when right wing moves forward and left wing backward), ψ = Yaw rotation (positive when right wing moves up and left wing down). l = distance (parallel to y axis) from center of mass to center of water droplet being propelled by tip of abdomen.

36° on the first half cycle and 28° on the second. Since all the other photographs show straight paths for the water droplets scooped up in oviposition, it is of interest to explore how the unusual sinuous droplet trajectory of Figure 7 might occur.

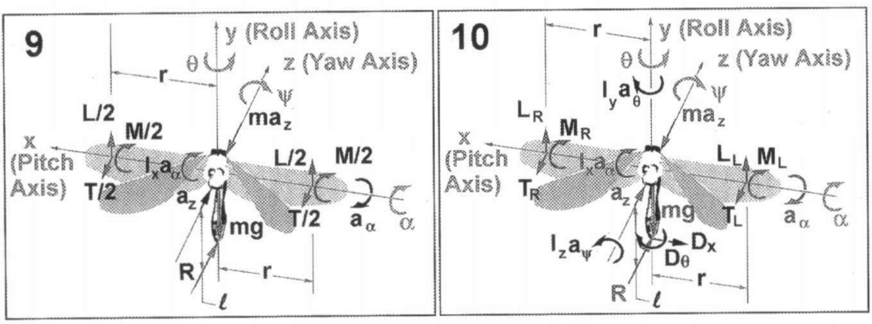
MECHANICS OF SCOOPING OVIPOSITION

Figure 8 is sketch based on the photograph of Figure 7. A coordinate system superimposed on the sketch will be used in analyzing the forces acting on an ovipositing female. The axis system passes through the insect's center of mass, and it is assumed for simplicity that the center of mass is also coincident with the point where the wing aerodynamic forces would be applied to the thorax. The plane formed by the x and z axes is assumed to be parallel to the water, so that the y axis is perpendicular to the water. Rotations about the x axis (α) are called pitching motions, rotations about the y axis (θ), rolling motions, and rotations about the z axis (ψ), yawing motions. The distance between the tip of the abdomen and the center of mass is denoted as ℓ.

When the female is ovipositing, the aerodynamic forces of flapping flight that provide lift to keep her in the air and thrust to move her forward must also overcome the inertial forces imposed at the abdomen tip by the water as it is scooped up. Figure 9 is a simple, schematic, "free body diagram" of the dragonfly pictured in Figure 7. We assume, again for simplicity, that the female is not actively flexing her abdomen, so that all momentum is due to forward motion.

Free body diagrams picture an object with all external forces that act on it shown as vectors. We assume that the left and right hand wing pairs are each producing half the total aerodynamic forces. The wings provide horizontal thrust forces (shown as "T/2") that balance the reaction force of the water ("R", acting at the abdomen tip) and the reverse inertia force ("ma_z", equal to the product of the mass of the dragonfly multiplied by its acceleration, but pointing in the opposite direction from the acceleration vector. The reverse inertia force is an artifact that allows us to rewrite Newton's Second Law from the conventional "F = ma" to read "F-ma = 0", so that the "forces" on the diagram are shown in equilibrium). We assume here that while the abdomen is in the water, the dragonfly is decelerating since R effectively reduces the thrust that is maintaining forward motion.

The wings must also provide a torque or moment (shown as "M/2") to oppose the couple ("$R\ell$") that tends to rotate the dragonfly in a nose-down direction about the Pitch Axis. We assume that M does not completely balance $R\ell$, so we show a reverse inertia couple ("$I_x a_\alpha$", equal to the product of the mass moment of inertia of the dragonfly about the x axis times the angular acceleration, but opposite in direction to the acceleration). Figure 6 also shows the lift forces ("L/2") on each wing that balance the weight



Figs 9-10. Schematic free body diagrams of forces involved in scooping oviposition: (9) a simplified representation of the forces acting on the dragonfly of Fig. 7 assuming symmetry of the aerodynamic forces. r = distance (parallel to x axis) from center of mass to spanwise center of aerodynamic forces, L = aerodynamic lift, T = aerodynamic thrust, M = aerodynamic pitching moment, R = reaction force acting on abdomen due to acceleration of water droplet, m = mass of dragonfly, g = acceleration of gravity, mg = weight of dragonfly, a_z = deceleration of dragonfly caused by water, a_α = pitching acceleration caused by water, I_x = pitching mass moment of inertia of dragonfly. The insect's weight is balanced by lift forces developed by the wings. The thrust forces generated by the wings move the insect forward and partially balance the reaction force of the water on the tip of the abdomen (R). The arrow marked ma_z called the "Reverse Inertia Force", is the product of the mass of the dragonfly and its acceleration, but points in the opposite direction from the acceleration vector. Since the insect is decelerating while its abdomen is in the water, this "force" is shown pointing forward. The circular arrows representing the moments produced by the wings offset the couple (R l) that tends to rotate the insect in a nose-down direction about the pitch axis; — (10) forces acting on the dragonfly assuming slight asymmetry of the aerodynamic forces generated by the wings. This would result in short duration imbalances in the lift and thrust forces. Assuming the aerodynamic forces produced by the right wings are slightly greater than those produced by the left wings, the dragonfly would receive positive yaw and roll accelerations (a_ψ and a_θ, respectively). D_x = drag force of water on abdomen due to yawing motion, D_θ = drag moment on abdomen due to rolling motion, I_y = rolling mass moment of inertia of dragonfly, I_z = yawing mass moment of inertia of dragonfly.

of the dragonfly ("mg", the product of the mass of the dragonfly and the acceleration of gravity). I have shown L/2, T/2 and M/2 as net forces acting at a point near the wing tip (distance "r" from the center of mass) and on the pitch axis for simplicity. These forces are assumed to be in balance, that is, we can sum the horizontal forces, the vertical forces, and the moments about the center of mass and assume that they add up to zero in each case. (The resulting equilibrium equations are summarized in Appendix 2). The impact of the force of the water on the tip of the abdomen causes a deceleration of the dragonfly and tends to rotate it in a nose-down pitch movement.

In Figure 9 we assumed the right and left aerodynamic forces were equal. However, because dragonflies' wings flap independently, it is likely that there will be slight differences at any instant in time. These differences could come about, for example, in response to a gust of wind, or as a reaction to some other disturbance. These differences would result in short duration imbalances in the aerodynamic forces. In Figure 10 we consider the free body diagram of the ovipositing female dragonfly under the assumption that there are imbalances in the right and left aerodynamic forces.

Suppose for illustrative purposes that the right wing is producing slightly greater forces than the left wing (i.e. $L_R > L_L$, $T_R > T_L$, $M_R > M_L$). In the case of the lift forces, the imbalance would tend to rotate the insect (left wing down) about the Yaw Axis. This would result in an angular acceleration, a_ψ, and a reverse inertia moment, $I_z a_\psi$. There would also be a resistance force, due to drag of the water on the abdomen, opposing this rotation, shown as D_x. In the case of the thrust forces the imbalance would tend to rotate the insect (right wing forward) about the Roll Axis. This would result in angular acceleration a_θ, and corresponding reverse inertia moment $I_y a_\theta$. The drag of the water in this instance would appear as a resisting moment, shown as D_θ. We note that the damping effect of the water would provide significant resistance to lateral movement of the tip of the abdomen, but very little damping of rolling movements. Thus the most visible outcome of these short duration disturbances would be the rolling displacements, exactly the motions made evident by the sinuous water droplet trajectory.

The major factors contributing to the dynamics of the sinuous water jet captured on film in Figure 7 thus appear to be: (1) slight differences in aerodynamic forces between left and right sides of the flapping wings and (2) high damping (caused by drag of the abdomen tip in the water) of pitch or yaw motions and low damping of roll motions. Apparently these factors can sometimes combine to produce a rolling oscillation of the abdomen as it passes through the water, resulting in a wavy trajectory of the stream of water droplets thrown by the female. Exact analysis of the mechanics of this phenomenon is not possible without high-speed movie or video footage, but I believe that this qualitative explanation captures the essential physics of the situation.

IMPACT OF THE MECHANICS OF SCOOPING OVIPOSITION

The practical significance of what we see in these photos lies in the insight they give us into the mechanics of oviposition. The process of scooping produces forces on the female's abdomen that induce movements of the head that include backward displacement, nose-down pitch rotation, and sometimes roll or twisting rotation. For a solo female these motions would not be significant (the head simply moves along with the rest of the body), but for a female in tandem, the male's grip on her head would tend to resist these movements. The male-female tandem provides greater inertial and aerodynamic resistance to the water-scooping inertial reactions, but only if the connection between them is secure.

Odonata have a unique head-to-neck joint, the head essentially resting on the narrow tip of the sharply tapering neck. This provides extreme mobility of the head about all axes, an essential aspect of the insect's flight control system (MITTELSTAEDT, 1950), but results in a very fragile head-to-neck connection. To compensate for the fragility of this joint so that it remains functional in situations in which the head must be held rigid, Odonata have a unique head-arresting system (GORB, 2001). The arrester system would certainly help to stabilize the female's head, but with the large moment arms involved here (i.e. the distances between the head and abdomen tip of the female and the distance from her head to the male's thorax) the head-to-neck joint would be subject to large forces and would remain the weak link in the chain. The female's grasp on the male's abdomen with her legs would provide bracing against rolling or pitching movements, and would provide a load transmittal path around the relatively weak neck joint. The extra support of her legs is probably essential to the ability of the species to perform scooping oviposition in tandem without damage to the female.

CONCLUSIONS

The little known species *Libellula composita* has been observed to use scooping oviposition (oviposition mode FC7 of CORBET, 1999), both in solo and in tandem flight. While this mode is widely used in the genus *Libellula*, no other species is known to use it in tandem egg laying.

L. composita is the first of the Libellulinae (*sensu* DAVIES & TOBIN, 1985) reported to employ female gripping of the male abdomen in post-copulatory flight. MARTENS et al. (1997) point out the possible adaptive significance of this behavior in Trameinae and Zygonychinae as a means to resist damaging forces being exerted on the female head in highly maneuverable tandem flight. In the case of *L. composita*, resisting the forces encountered in tandem scooping oviposition may be an equally important adaptation. Finally, the female's grip certainly improves the chances of her surviving the pupfish predation attacks that were noted by R. Larsen (pers. comm., 2003).

The sinuous path of scooped water droplets visible in a photograph of an ovipositing solo female (Fig. 7) provides strong evidence of the complexity of the flight mechanics in Odonata that use scooping oviposition. The everyday actions of Odonata in flight entail marvelously complex functioning which we see only occasionally in fleeting glimpses. Figure 7 provides such a glimpse.

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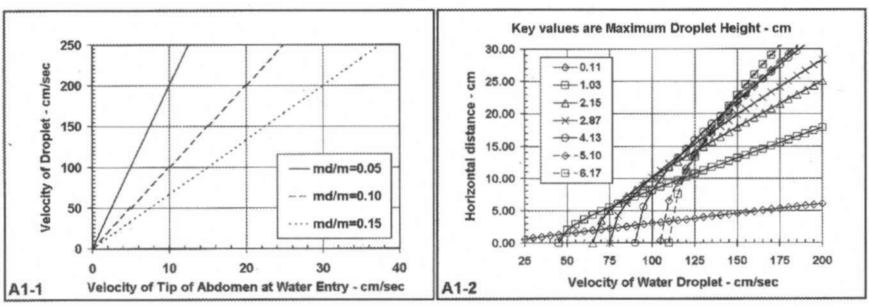
Appendix 1

RESULTS OF A SIMPLE ANALYSIS OF THE KINEMATICS OF SCOOPING OVIPOSITION

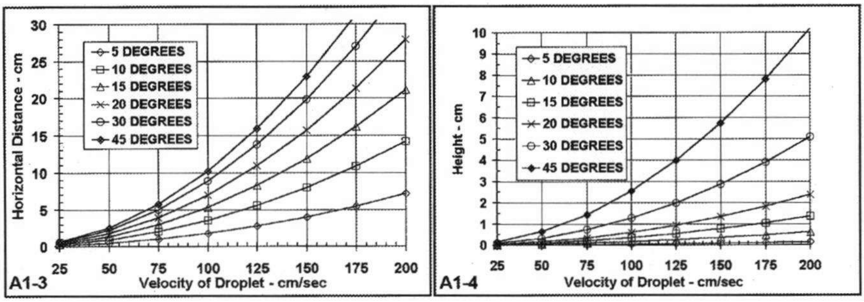
By neglecting aerodynamic drag on the water droplet and assuming complete momentum transfer between the dragonfly and the water droplet, we can predict the velocity of the water based on the velocity of the dragonfly's abdomen. Figure A1-1 graphs this information for three values of the ratio of droplet mass to dragonfly mass. For example, to impart a velocity of 150 cm/sec to a water droplet with a mass of 15% of that of the dragonfly, the insect would have to have been traveling at 15 cm/s.

Figure A1-2 is a plot of horizontal distance traveled by the scooped water droplet versus velocity of the droplet for various values of maximum trajectory height. The photograph of *Libellula croceipennis* taken by WILLIAMS (1977) showed a droplet that had traveled about 11 cm at the halfway point (22 cm horizontal distance) and was at a maximum height of 4.5 cm. Using Figure A1-2, we can estimate the velocity of the drop at a little less than 150 cm/s.



Figs A1-1,2. Trajectories of scooped water droplets: (A1-1) velocity of scooped water droplet versus velocity of dragonfly for various ratios of water droplet to dragonfly mass. m_d = droplet mass, m = dragonfly mass. Units in cm/sec. Complete momentum transfer assumed; – (A1-2) water droplet horizontal distance traveled (cm) versus velocity of droplet (cm/sec) for various values of maximum droplet height (cm).

Figures A1.3 and A1.4 show the maximum height reached by the water droplet and the total horizontal distance it travels as a function of the velocity imparted to it and the angle of inclination of the velocity vector from the horizontal. That is, we assume that the droplet is not flipped horizontally, but at an angle so that it has an upward velocity component. Using the WILLIAMS (1977) data of 4.5 cm height and 22 cm horizontal distance, we can estimate the angle of inclination for this trajectory to have been about 40 degrees.



Figs A1-3,4. Distance traveled by scooped water droplet as function of velocity of droplet and angle of inclination of velocity vector to the horizontal. Distance in cm, velocity in cm/sec. Based on simple particle mechanics and zero aerodynamic drag: (A1-3) horizontal distance traveled; — (A1-4) maximum height reached by droplet — maximum height is reached at half the horizontal distance.

Appendix 2

THE EQUILIBRIUM EQUATIONS OF A DRAGONFLY DURING SCOOPING OVIPOSITION

Figure 9 depicts the forces assumed to be acting on the dragonfly as it engages in scooping oviposition. Summing forces in the y direction yields:

Eq. 2.1: $R - T - m\,a_z = 0$

Summing forces in the z direction, we obtain:

Eq. 2.2: $L - m\,g = 0$

And summing moments about the x axis yields:

Eq. 2.3: $M - R\,\ell + I_x a_\alpha = 0$

These equations still hold for the condition shown in Figure 10 if we note that $T = T_R + T_L$, $L = L_L + L_R$, and $M = M_R + M_L$. We also have additional equations that result from the imbalance in the right and left aerodynamic forces. Summing moments about the z axis yields:

Eq. 2.4: $r\,L_R - r\,L_L - \ell\,D_x - I_z a_\psi = 0$

Finally, we sum moments about the y axis:

Eq. 2.5: $r\,T_R - r\,T_L - D_\theta - I_y a_\theta = 0$