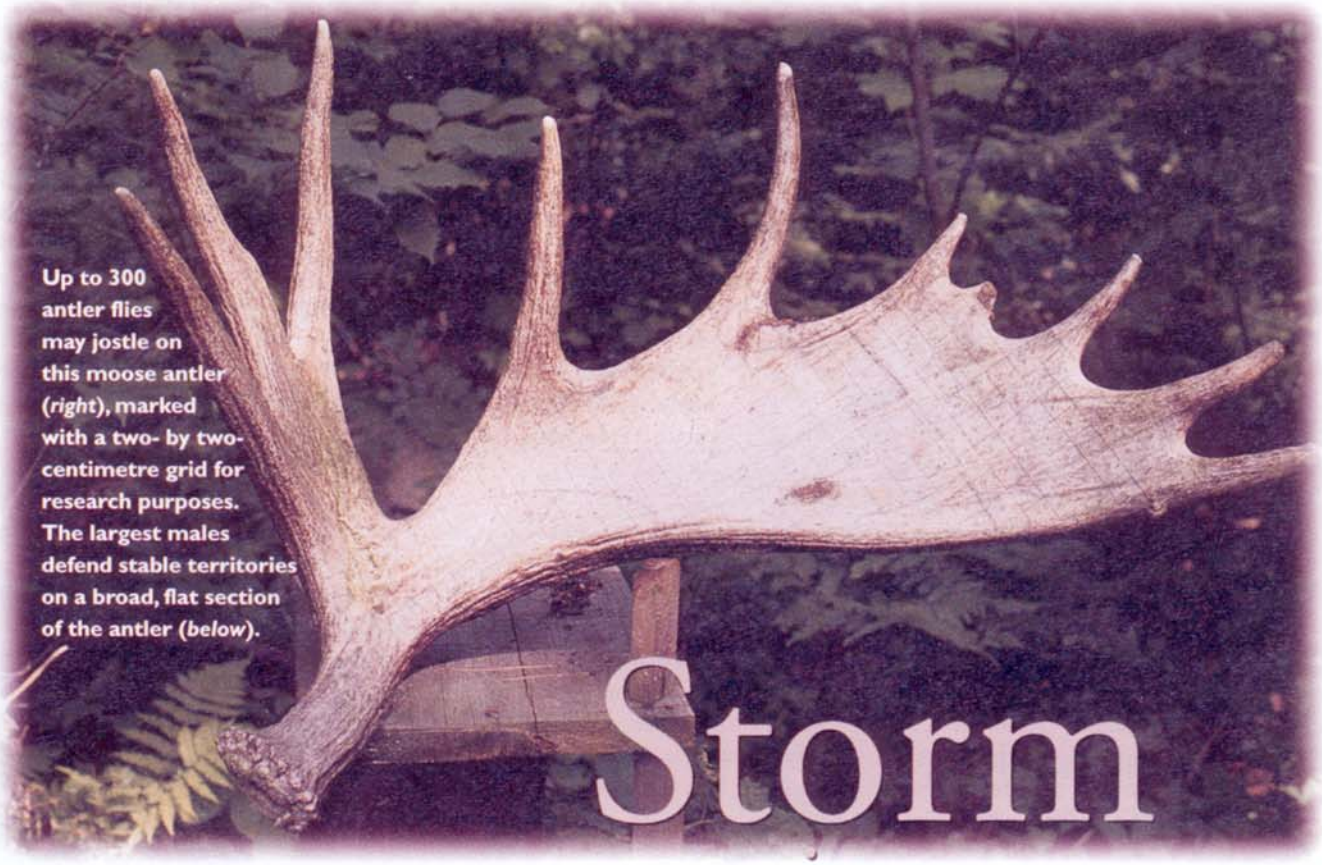


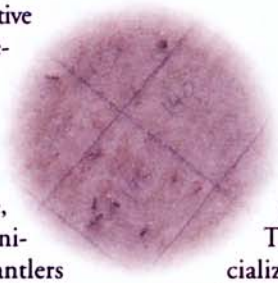
Up to 300 antler flies may jostle on this moose antler (*right*), marked with a two- by two-centimetre grid for research purposes. The largest males defend stable territories on a broad, flat section of the antler (*below*).

# Storm in a Teacup

## *The passionate life of the antler fly*

BY RUSSELL BONDURIANSKY

Melting snow leaves the discarded moose antler—a bizarre, spiky apparition —to settle, lifeless, into soggy Algonquin leaf litter. If you resist the urge to haul the antler away, but come back on a hot day in early summer, you might glimpse a biological marvel that few people have ever noticed. Look closely at the antler's broad surface and you will see dark, diminutive animals strutting aggressively over the sweet-smelling brown bone. The antler's second life has begun.



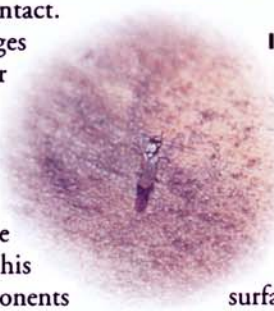
As most people know, the mighty male moose, among the world's largest animals, grows a new rack of antlers each year. Having served their purpose in the fierce battles of fall rutting season, the heavy appendages are shed in winter. Few people realize that the antlers, though discarded, have yet to witness fiery scenes of battle and romance. For this is the story of a beast that makes up in passion for what it lacks in brawn: the tiny antler fly (*Protopiophila litigata*), which makes its home exclusively on the rock-hard weapons cast off by moose and deer.

The antler fly is a highly specialized member of Piophilidae, an obscure family comprising mainly carrion flies. Although currently known only from parts of Ontario and Nova Scotia, this species may eventually be found across a much wider geographic range. After three summers (1993–95) of research in Algonquin Park, University of Guelph professor Ron Brooks and I have gained some insight into the private life of this minute scavenger.

On warm days in early June, the first winged pioneers appear out of nowhere to claim last winter's crop of antlers. The larger males establish territories, and sally forth on brisk patrols within their invisible boundaries. Spotting movement, the male orients and charges at the intruder, be it another antler fly or an unsuspecting insect of a different species. Even large bluebottle flies (as big as elephants, relatively speaking) are not spared his wrath. Hence, we named this species *litigata*, Latin for "one who picks fights".

Russell Bondurianksy (top); R. J. Brooks

If the intruder is another male antler fly, the attacker will stop a few centimetres away, rotate one wing horizontally to a 90° angle with his own body, and trot sideways in a semicircle. Two males, facing off, spin counterclockwise about an invisible axis between them, always maintaining eye contact. Then each contestant lunges forward and jabs the other with his front legs. Normally, this fierce boxing match is over in a few seconds, when the winner (usually the larger fly) chases the loser away and returns to his domain. But when the opponents are evenly matched, the fight may last a full minute and even escalate into a wrestling event. Locked in a furious embrace, the grappling males sometimes roll off the antler—right off the edge of the world.



**In three seasons of research, over 1,800 flies were marked with an individual code by means of a physical restraining device. This is male 110, who lived in 1994.**

Should the intruder be a female, the male's response is, understandably, rather different. The male leaps onto the female's back and performs rapid and complicated stimulatory motions against the tip of her abdomen, using his mid- and hind legs and genital appendages. This early stage in the relationship ("courtship") apparently enables each partner to assess the desirability of the other. Females seem to prefer larger males, whereas males prefer fatter females, which carry more mature eggs. Such choosiness is not surprising, since copulation represents an investment of eggs and sperm, both of which are energetically costly for flies to produce. Mating also requires 2.5 hours of valuable time, a substantial portion of a fly's life. If the male finds the female unacceptable, he will simply hop off and walk away. If the female dislikes her partner, she may try to shake him off, or curve her abdomen out of his reach, or simply remain unresponsive to his stimulatory efforts. If both parties are in favour, the female extends the tip of her abdomen for the male to grasp, and he establishes genital lock.

**Antler flies mate on the underside of the antler, or in other areas where they are less likely to be attacked by searching males.**

Russell Bonduriansky (top and bottom); R. J. Brooks

While the flies integrate their astonishingly complicated genitalia, the female (carrying her partner) escapes the bedlam on the antler's crowded upper surface, and makes her way to the shade and relative peace on its underside. The two surfaces clearly serve different functions: fighting above and mating below. If you flip the antler over, the flies quickly relocate to the appropriate side.

By now, you may be wondering how we learned all this. To be sure, tiny flies don't surrender their intimate secrets without a struggle. We use a dissecting microscope for lab work and concoct tiny scalpels and probes out of pins and razors. Fortunately, for once, it actually *helps* to be nearsighted. But the main challenge is to distinguish individuals among the hordes of tiny flies on the antler. For this, we must paint an individual code on the back of each fly—without injuring it in the process. No mean feat, when the "canvas" is a nervy animal 2.5 millimetres long. We solved this problem by constructing a device that could keep a fly gently restrained under the microscope, allowing us to mark it with a tiny number, letter or other symbol. Beyond that, it's only a matter of crouching for hours over an antler, notebook in hand, beneath a dense cloud of mosquitoes, blackflies, deerflies and no-see-ums. All for the sake of science.

But let's return to the mating pair on the underside of the antler. After more than 1.5 hours of sitting very still to avoid being detected and attacked by wandering males, the pair has completed sperm transfer. The male now performs a peculiar dance on the female's back and gradually reels in his penis (which is almost as long as his body), but does not dismount. The female extends her ovipositor and deposits a small droplet of cloudy liquid on the antler surface, then immediately spins around and sucks it up. She appears to be making use of excess sperm, perhaps from previous copulations, as a supplementary source of food and water!

After this, the female wanders back to the boxing tournament on the antler's upper surface and searches for suitable egg-laying sites in the bony landscape. Her partner, still hitching a ride, now makes himself useful by pushing away attacking males with his wings. Once the female has located a suitable crack or pore in the bone, she inserts her tubular ovipositor and lays several eggs. She will deposit eggs into several cracks after each copulation, and return to the antler a couple of days later to mate again.

**A large crack serves as the primary egg-laying site and attracts the highest density of flies. Ovipositing females—carrying their mates—disappear into the subterranean darkness of the crack in search of the best environment for their eggs.**

The eggs hatch into minute larvae, which feed on organic matter inside the porous bone between the antler's surfaces. A full year later, during heavy rain, mature larvae will leave this dark world of subterranean tunnels. This brief, secretive migration is among the most fascinating and cryptic chapters in the life of the antler fly. Pale, delicate, shy in the light, the larvae squirm to the surface through tiny openings and wiggle anxiously to the tips of the antler's finger-like projections. Here, they perform an astonishing feat: the

*Continued on page 31*

**Antler Flies** (*continued from page 28*) thin wormlike animals stand up, coil into C-shapes and spring off the antler. They land up to 50 centimetres away on the leaf litter and burrow, once again, out of sight. Now they spin puparia—little brown cocoons—inside which an amazing transformation takes place. Two weeks later, fully adult flies emerge to dry their wings and return to the antler.

Although the activity on the antler's upper surface resembles a jumble of frenzied scuffling, the impression of chaos is misleading. Here's a simple road-map. If the antler boasts a sizeable crack, it will be the most important egg-laying site. Ironically, this legacy of violence from the antler's former career also attracts the highest density of males and becomes a seething cauldron of aggression. But the *largest* males defend territories on a broad, flat part of the antler. This "arena" is less crowded, and fights are less frequent. The smallest males, who are quickly expelled from either of these areas, wander over the rest of the antler's surface without establishing stable territories. Since the largest males—who are able to defeat most rivals—should be able to "choose" where they will be on the antler, we predicted that males on the arena would achieve more matings over their lifetimes than males elsewhere. To our surprise, the pattern appears to be far more interesting. Males around the large crack mate more frequently than those on the arena, but perhaps because they fight so often, their life spans are reduced. This produces a kind of balance: average lifetime mating success appears to be the same for males on the arena as for those around the crack. But losers still abound: small males, excluded from either option, achieve fewer matings.

Our main conclusion: for an antler fly, life is especially unfair. For females as well as males, reproductive success—the objective, if there is one, of a fly's travails—depends primarily on body size. The largest females lay at least four times as many eggs as the smallest ones. For males, the difference is far more drastic. Because they achieve more matings and mate with females that carry more eggs, the largest males sire at least 23 times as much progeny as the smallest males. But adult body size may depend largely on the quality and quantity of food available to a larva during its development—in other words, pure luck. Since bigger is better, you might expect that antler flies are increasing in size over evolutionary time—a terrifying prospect, given their pugnacious disposition. No need to worry: the advantages of large size in reproduction are counterbalanced by disadvantages in larval development—recall the narrow tunnels inside the antler. No doubt, this is small consolation for a runty antler fly adult.

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