Why do male antler flies (*Protopiophila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers

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The antler fly *Protopiophila litigata* Bonduriansky (Diptera Piophilidae) forms large mating/oviposition aggregations on discarded moose (*Alces alces*) antlers, where the strikingly aggressive males engage in frequent combat. According to theory, costly fighting behaviour will be maintained by selection only if winners sire more progeny than losers. Through a field study of individually marked flies, we addressed the question "Why do male antler flies fight?" by investigating what resources males compete for on antlers, whether or not large male body size and resulting advantage in agonistic encounters confers positional advantage in the mating aggregation, and whether the successful males experience greater survivorship or greater mating frequency. As expected, most agonistic contests were won by the larger male. Large males tended to live longer, mate more frequently, and achieve more matings over their lifetimes than small males. Males fought and defended territories primarily on the upward-facing ('upper') surfaces of antlers. The main oviposition site attracted the highest density of single males, and mean body size of single males was largest in this region. Males mate-searching near the main oviposition site achieved the highest mean lifetime mating success on the upper surface. Multiple regression analysis indicated that the main oviposition site was the only region where mate-searching tended to increase male mating frequency and, on average, males mated nearly twice as frequently when mate-searching there as they did when mate-searching elsewhere. These results suggest that male antler flies fight for opportunities to search for females in areas where they will mate more frequently and thus achieve more matings over their lifetimes.

KEY WORDS: mating system, intrasexual competition, body size, agonistic success, mating success, *Protopiophila litigata*, Piophilidae.

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INTRODUCTION

Intrasexual competition is an important component of sexual selection in many insect mating systems (Baker 1983, Alcock 1987). It is usually most intense among males, because male fecundity tends to be limited by availability of fertile females (Trivers 1972, Parker 1979, Gwynne 1991). When intrasexual competition among males involves agonistic contests (combat), body size is often an important factor (Wilkinson 1987, Miyatake 1993). Male body size is correlated with male mating success in a variety of insect species (e.g. McLachlan & Allen 1987, Droney 1992, Carroll & Salamon 1995), but the selective processes involved are often poorly understood (Alcock 1989, Boake 1989), especially in complex mating aggregations and in wild populations.

In many insect species, males are highly aggressive and engage in frequent combat (e.g. Parker 1970, Sigurjonsdottir & Parker 1981, Otronen 1984a). Typically, larger individuals defeat smaller ones (e.g. Dow & von Schilcher 1975, Boake 1989). As a result, large males may be able to search for mates in the most advantageous locations, such as areas where female encounter rate is highest (Thornhill 1980, Alcock 1996) and thereby achieve higher mating success (e.g. Partridge & Farquhar 1983, Moore 1990; but see Boake 1989). However, in some systems, small males may achieve higher mating success than large males, perhaps because they are quicker or more agile (e.g. McLachlan & Allen 1987, Neems et al. 1990). Because territory defense is costly in both time and energy (Hoffmann & Cacoyianni 1990, Koenig 1990), males are expected to defend territories in sites providing best access to females, and territory holders are expected to achieve higher mating success (Hoffmann 1987, Moore 1990). Females of many species are attracted to resources found at oviposition sites, and males therefore compete for and defend these sites to gain mating opportunities (e.g. Mangan 1979, Waage 1988, Papaj 1994).

Differences among males in lifetime mating success may arise either from differences in survivorship (e.g. Banks & Thompson 1985) or mating frequency (e.g. Koenig 1990, Jarvis & Rutledge 1992, Papaj 1994, Carroll & Salamon 1995). Thus, a particular site or region in the mating aggregation may be advantageous for mate-searching because it augments male survivorship (e.g. via lower risk of predation), or because it augments male mating frequency (e.g. via higher female encounter rate). The high energetic costs and risk of injury associated with territorial defense make it unlikely that territory holders would experience higher survivorship. Thus, the positional advantage experienced by territory-holding males is likely to be higher mating frequency.

This study addresses the relation between body size, agonistic success, position at the mating site and mating success in the complex mating aggregations of antler flies, *Protopiophila litigata* (BONDURIANSKY 1995). This small necrophagous fly mates and oviposits exclusively on discarded cervid antlers. Males engage in frequent and vigorous 'boxing matches' and sometimes defend territories (BONDURIANSKY 1996). At the start of copulation, coupled flies emigrate from the antler's upward-facing surface, where density of aggressive single males is high, to other parts of the antler. Immediately following copulation (approx. 2 hr duration), females oviposit into cracks or pores in the antler and males remain in tandem and 'guard' them by pushing away single males with their wings (BONDURIANSKY & BROOKS 1998a).

Using longitudinal data on a wild population, we investigated the structure of antler fly mating aggregations in order to understand how fighting might enable a male antler fly to increase its fitness. Specifically, we asked which parts of the antler are contested by males, whether males able to mate-search in these areas achieve higher lifetime mating success, and whether this advantage results from higher survivorship or higher mating frequency. We expected that advantage in agonistic contests enables large males to search for mates in advantageous locations and thus achieve higher mating success than small males. Preliminary observations also suggested that the main oviposition site on each antler was the most strongly contested region and, hence, the most advantageous region for mate-searching.

METHODS

Study site, antlers and fly population

This field study was carried out at the Wildlife Research Station, Algonquin Park, Ontario, Canada, in 1994 and 1995. Algonquin Park contains mixed forest and wetlands supporting moose (*Alces alces*) and antler flies (*Protopiophila litigata*). We collected 9 discarded moose antlers, set them on 0.8 m high wooden stands 5-15 m apart in the forest near the Station, and studied the *P. litigata* attracted to them. The extremely high site fidelity of *P. litigata* (BONDURIANSKY 1996) enabled us to obtain longitudinal data on wild, unconstrained flies.

Sexing, measuring and marking of flies

We sexed, measured and marked with individual codes (5 June to 10 August 1994) 609 males and 231 females, using the technique of BONDURIANSKY & BROOKS (1997). Body length (BL), from tip of abdomen to tip of antennal flagellum, measured to 0.01 mm with Mitutoyo calipers under a dissecting microscope, was used as an index of body size. BL exhibits good repeatability ($r = 0.94$) and is strongly correlated ($r = 0.89$) with hind femur length (BONDURIANSKY & BROOKS unpublished). Each fly was captured by covering it with a small jar, and released at the same antler approx. 1 hr after capture. Of 609 males marked, 534 (88%) were seen at least once after release. More than 50% of marked individuals remained on the same antler throughout their lives, suggesting that very few individuals left the study site. The proportion of unmarked individuals varied from 25-70% over the season.

Agonistic contests and territorial behaviour

To determine the relationship between body size and success in agonistic encounters, we recorded (10 June-14 August 1995) the outcomes of 246 agonistic contests among 40

marked males. After each contest, the winner was identified as the male chasing his opponent. To investigate territorial defense, we demarcated a 2 × 2 cm grid on the surface of an antler and recorded (every 10 sec, for 30 min) the locations (grid square number) of several males defending territories.

Ethogram records

The analyses described below were performed using data from a series of ethograms (i.e. cross-sectional records of the location on the antler and activity of each marked individual on an antler at a given time). We constructed ethograms between 5 June and 25 August 1994, at intervals of approx. 2 hr, starting between 09:00 and 11:00 hr and ending between 16:00 and 20:00 hr each day (3-5 ethograms per day). At each ethogram, we recorded the activity (i.e. single, copulating, ovipositing, mate-guarding, defending a territory) and the location (region) of each marked individual on each of the 8 antlers, thus obtaining a total of 5878 separate observations.

Four antlers (M1, M2, M3 and M4) each yielded enough data for analysis of the mating aggregations (M1: n = 115 ethograms; M2: n = 67 ethograms; M3: n = 63 ethograms; M4: n = 143 ethograms). On the basis of preliminary observations, the surface of each of these antlers was subdivided into 13 regions delineated in pencil (Fig. 1). On each antler, the pedicel (area of attachment to the skull) was labelled PD, regions on the upward-facing surface ('upper surface') were labelled A1-A5, and corresponding regions on the downward-facing surface ('underside') were labelled B1-B5. The most heavily damaged area on each antler (on M1, a reddish, pungent, porous area; on M2 and M3, a tip gnawed by rodents; on M4, a large crack) was encompassed in a region labelled C. The finger-like protrusions of each antler (Fig. 1) were combined into region PR.

Male mating frequency, survivorship and mating success

We used ethogram data to construct a longitudinal biography for each individual male and calculate its lifetime mating success (LMS) (total number of copulations observed over individual's lifetime), survivorship (S) (number of days a male was observed after the marking date), and mating frequency (MF). MF (copulations per day) was calculated as MF = LMS/S, for males (n = 276) with S > 4 days. Analyses of LMS and S were performed using males (n = 433) with S > 1 day, to exclude males possibly injured during measurement and marking.

Characteristics of regions on antlers

The surface area of each region on antlers M1, M2, M3 and M4 was calculated from dimensions obtained with a tape-measure. For each region on each of the four antlers we calculated a weighted mean male BL using each observation of each male in a region as 1 data point. Most males were observed several times in 1 or more regions. For the largest antler (M4), which yielded 59% of total ethogram observations, we also calculated weighted means (as for BL, above) for male MF, S, and LMS for each region. Multiple regression analysis of the effects on MF of male BL and number of observations in each region on antler M4 was performed using the "backward elimination of variables" method (Zar 1996) for males that had been observed at least 10 times on antler M4.

To determine whether mating frequency was higher at the main oviposition site (region C) than elsewhere on antler M4 we subdivided the total mate-searching time of each male that had mated both in region C and elsewhere into time spent in region C and time spent elsewhere, and calculated separate mating frequencies (cop. per hr searching, assuming 1 observation = 2 hr search time in the region) for each component. Because pairs emigrate at
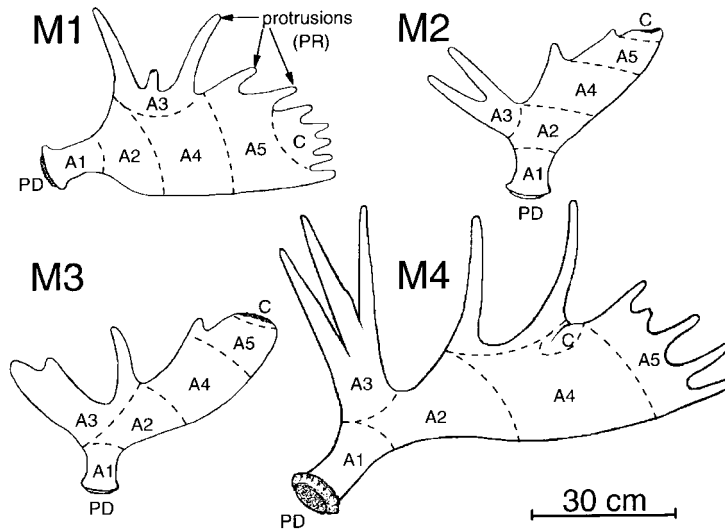
Fig. 1. — Region boundaries (dotted lines) demarcated on the upward-facing surfaces of discarded moose antlers M1, M2, M3 and M4 (see text).

the start of copulation (BONDURIANSKY & BROOKS 1998a), we were seldom able to record the site of initial encounter. Instead, a coupled male was assumed to have achieved the copulation in the region where he was observed mate-searching in the previous ethogram on the same day. Statistical analyses were performed using STATISTICA (Release 5.0, © StatSoft, Inc., 1984-1995).

RESULTS

Male agonistic contests and territory defense

We observed four types of agonistic contests (listed from most to least frequent): (1) both males oriented, charged and engaged in a 'boxing match', pushing and pummelling each other with their forelegs; (2) one or both males oriented, rotated one wing horizontally to 90° with its body and sidestepped in a semicircle about its opponent, then charged and boxed the other male; (3) one male charged, while the other attempted to run away; (4) one male charged and mounted the other for approx. 2 sec, after which either male could be the winner. Following each contest, the winner chased the loser (up to 20 cm), then stopped and turned. Coupled pairs and insects of other species (including large calliphorid and muscid flies) were also attacked. As expected, most of the 246 agonistic contests observed were won by the larger male (Fig. 2; Wilcoxon test; n = 246 contests; T = 4420; z = 8.9; $P < 0.0001$). A similar result was obtained when each combination of males

was used only once in the analysis (Wilcoxon test; n = 87 contests; T = 565; z = 5.3; P < 0.0001). Hence, large males are agonistically dominant over small ones.

Some males defended territories, mainly on the upper surfaces of antlers (Fig. 3). A typical territory (Fig. 4) included a small core area where the male rested and from which he charged other males (which he attacked), females (which he mounted) or coupled pairs (from which he sometimes attempted to dislodge the coupled male) up to 15 cm away. Single males not defending territories either wandered over the antler surface, or rested nearly motionless on the underside.

Male survivorship and mating success

As expected, male lifetime mating success (LMS) was an increasing function of male body size (n = 433; r = 0.16; F = 11.6; P = 0.0007). Male survivorship (S) also increased with body size (n = 433; r = 0.11; F = 5.1; P = 0.0248), as did male mating frequency (MF) (n = 276; r = 0.15; F = 6.1; P = 0.0145). These patterns did not result from the decrease in mean body size over the season (BONDURIANSKY 1996): although male BL was a decreasing function of order of first capture (males 1-528 of known BL, 5 June to 10 August 1994; r = – 0.40; F = 101.3; P < 0.0001), LMS (n = 433; r = – 0.01; F = 0.07; P > 0.5), S (n = 433; r = – 0.07; F = 2.2; P > 0.1) and MF (n = 276; r = 0.00; F = 0.00; P > 0.5) did not covary with order of first capture. Hence, large males tended to achieve more matings because they lived longer and mated more frequently than small males.
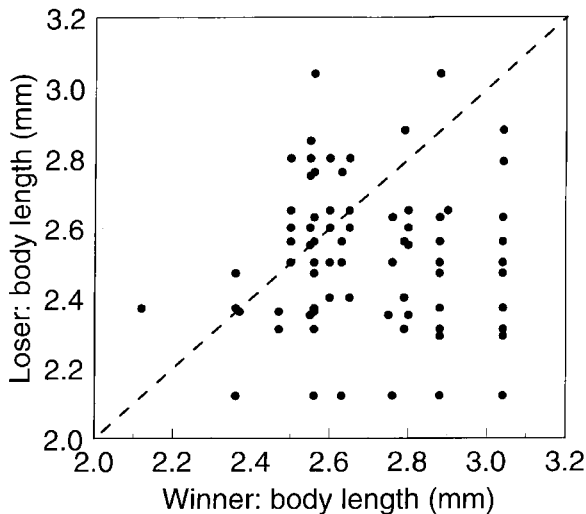

Fig. 2. — Body lengths of winners and losers in 246 agonistic contests among 40 *P. litigata* males, showing that larger males were more likely to be winners.
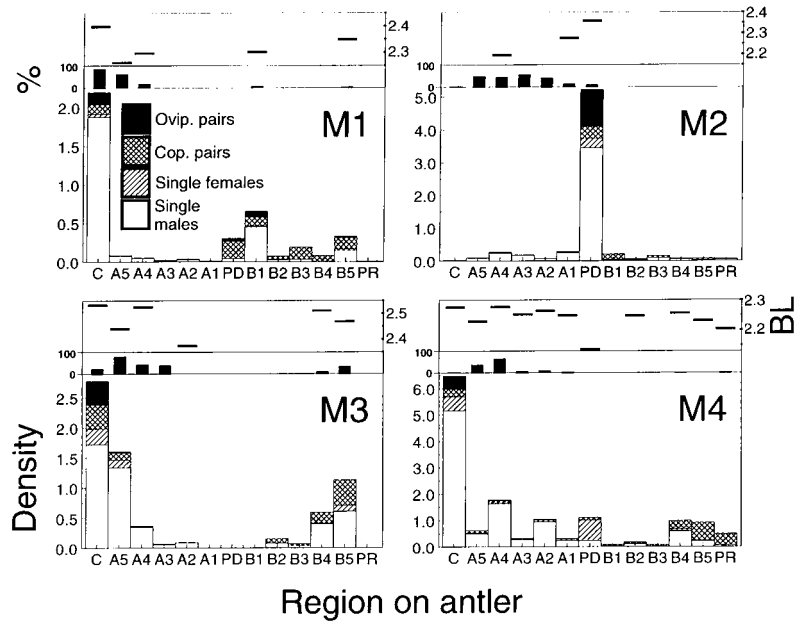
Fig. 3. — For each region on the surfaces of discarded moose antlers M1, M2, M3 and M4, the density (individuals or pairs/100 cm²/ethogram) of *P. litigata* single males, single females, pairs copulating and pairs ovipositing/mate-guarding (stacked bars), proportion (%) of single males (where n > 9 single males) observed defending territories (solid bars), and mean body length (mm) of single males (where n > 9 single males) (horizontal lines) during the summer of 1994.
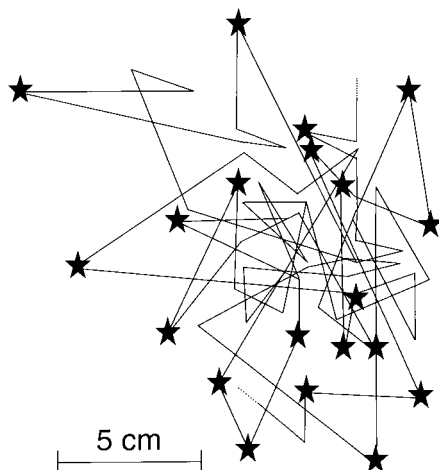

Fig. 4. — A typical pattern of territory defense by a *P. litigata* male on a discarded moose antler over 30 min; lines indicate the territory-holder's movements (walking); stars indicate agonistic contests with other males, all of which were won by the territory holder.

Male competition and mating success at the main oviposition site

The most heavily damaged part (region C) was the main oviposition site on antlers M1 (16/28 observed ovipositions), M3 (15/17 observed ovipositions) and M4 (43/65 observed ovipositions), but the pedicel (region PD) was the main oviposition site on antler M2 (12/13 observed ovipositions). Variation among antlers in the location of the main oviposition site (Figs 1, 3) could not be explained by the relative surface areas of regions C and PD. However, areas where adults oviposited and grazed were reddish and emitted a sweet scent, suggesting that location of oviposition sites may depend on the distribution of a microbial culture on the antler.

Two observations indicate that the main oviposition site was the region most strongly contested by males. First, density of single males was much higher in the region containing the main oviposition site than elsewhere on each of the four antlers (Fig. 3). Second, mean body length of single males was largest in the region containing the main oviposition site on antlers M1, M2 and M3, and a very close second-largest (after the region containing the secondary oviposition site) on antler M4 (see Discussion) (Fig. 3). We consider mean BL of single males in a region to reflect the intensity of male-male competition there because large, agonistically dominant males who are able to 'choose' their location on the antler will constitute a greater proportion of the single males in a more intensely contested region. Because the main oviposition site was the most contested region, we expected it to be the most advantageous for mate-searching.

Two observations suggest that the main oviposition site was the most advantageous region for mate-searching. First, this region contained the highest density of single females on antlers M1, M2 and M3, and the second-highest density on antler M4 (see Discussion) (Fig. 3). Second, among upper surface regions on antler M4 (i.e. contested regions, where males defended territories), the main oviposition site (region C) yielded the highest mean male LMS. Mean male BLs were not equal among regions on the upper surface of antler M4 (ANOVA, $F_{(5,1786)} = 2.71$; $P = 0.0191$), and the intensity of competition for an upper surface region on antler M4 (operationalized as mean male BL in the region) was correlated positively with mean male LMS in that region (Fig. 5I; n = 6; r = 0.99; F = 134.4; $P = 0.0003$). Hence, on antler M4, more strongly contested upper surface regions were more advantageous for mate-searching. The main oviposition site was the most advantageous mate-searching region on the upper surface.

Positional advantage: increased survivorship or mating frequency?

As expected, mate-searching at the main oviposition site appeared to augment male LMS via increased MF rather than increased S. The intensity of competition for an upper surface region on antler M4 (operationalized as mean male BL in the region) was not correlated with mean male S in that region (Fig. 5II; n = 6; r = 0.19; F = 0.15; $P > 0.5$), suggesting that males mate-searching in highly contested regions did not tend to experience higher survivorship than males mate-searching elsewhere. In contrast, males mate-searching near the main oviposition site achieved higher mean MF than males mate-searching in any other upper-surface region (Fig. 5III). The intensity of competition for an upper surface region was not correlated significantly with mean MF in that region (Fig. 5III; n = 6; r = 0.75; F = 5.29; $P = 0.0830$). However, multiple regression analysis of the effects of BL and number

of observations in each region (excluding PD) on antler M4 on MF of individual males (adjusted r^2 = 0.14; $F_{(13,57)}$ = 1.90; P = 0.0492) indicated that only the number of observations at the main oviposition site (region C) affected MF (n = 71; r = 0.26; F = 4.87; P = 0.0307). Moreover, of the 37 males that mated both near the main oviposition site (region C) and elsewhere on antler M4, 29 (78%) experienced higher MF in region C (n = 37; mean = 0.23 cop./hr searching; SD = 0.15) than elsewhere on the antler (n = 37; mean = 0.13 cop./hr searching; SD = 0.12) (Student t test for dependent samples; $t_{(36)}$ = 3.77; P = 0.0006). Of these 37 males, those that spent 50% or more of their time mate-searching near the main oviposition site (n = 5; mean BL = 2.41 mm) were significantly larger (Mann-Whitney U = 15.0; P = 0.0039) than the other males (n = 32; mean BL = 2.21 mm). These results suggest that the advantage associated with mate-searching near the main oviposition site was higher MF than elsewhere, and that large males experienced higher LMS, in part, because they were able to spend more of their time mate-searching near the main oviposition site. Mean LMS was also high in regions B4 and B5 (Fig. 5I), but this may be an artifact of the sampling regime (see Discussion).
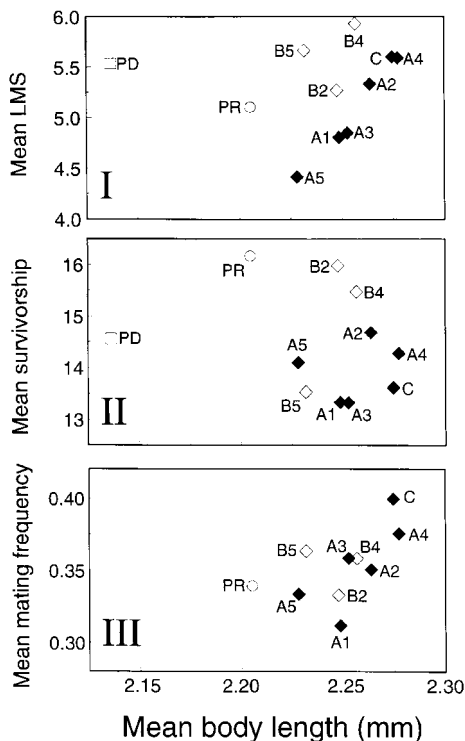

Fig. 5. — Weighted mean body length (mm) and weighted mean lifetime mating success (total number of copulations observed over male's lifetime) (I), survivorship (d) (II), and mating frequency (copulations per day) (III) of *P. litigata* males in each region (where n > 9 single males observed) on the surface of discarded moose antler M4 (□ = region PD; ◆ = regions on the antler's upper surface; ◊ = regions on the antler's underside; ○ = region PR).

DISCUSSION

The main conclusion of this paper is that male antler flies fight for opportunities to search for mates near the main oviposition site because mate-searching there enables males to mate more frequently than elsewhere on the antler. Large males achieve more matings over their lifetimes than small males because they survive longer and mate more frequently. These findings are important because few other field studies of insects have been based on longitudinal data, and have elucidated the fine structure of complex mating aggregations. Our results support the predictions of theory, and are broadly consistent with results from cross-sectional studies showing that males compete most intensely for sites providing best access to females (e.g. MANGAN 1979, THORNHILL 1980, PAPAJ 1994, ALCOCK 1996).

Male body size, agonistic success and mating success

Most agonistic contests were won by the larger male. Large male agonistic dominance is expected when contests are settled by fighting, and has been observed in many other insects (e.g. SHELLY 1987, 1989; GOLDSMITH 1989; FORSYTH & ALCOCK 1990; CHOE 1994a, 1994b; ALCOCK 1996). Agonistic behaviour of *P. litigata* males resembles that of some sympatric piophilid species such as *Protopiophila latipes* and *Liopiophila varipes*, but *P. litigata* males appear to engage in a greater repertoire of agonistic interactions (BONDURIANSKY 1996).

Males defended territories primarily on the upper surfaces of antlers, and especially in regions close to the main oviposition site (Fig. 3). It seems clear that these territories serve as a claim to a prime mate-searching region of the antler. The strongly contested regions, where both costs and benefits of territoriality are greatest, contained the larger males, many of them defending territories. Less contested regions, where both costs and benefits are lower, contained smaller males, few of them defending territories (Fig. 3). Territory defense may be energetically costly (KOENIG 1990) and large males may be more successful as territory holders in contested regions because they are better able to bear the energetic costs and more likely to win many consecutive agonistic contests.

Large males tended to achieve greater lifetime mating success than small males, apparently as a result of both greater survivorship and greater mating frequency. The tendency for large males to survive longer may have resulted from lesser vulnerability to the small predators (spiders and empidid flies) found on antlers (BONDURIANSKY 1996), and from better overall condition. Large males mated more frequently because they were able to spend more time mate-searching at the main oviposition site (see below) and, perhaps, as a result of female preference for large males as mates (BONDURIANSKY & BROOKS 1998b). Large males achieve greater mating success in many species of Diptera (e.g. MANGAN 1979; PARTRIDGE & FARQUHAR 1983; OTRONEN 1984b; PARTRIDGE et al. 1987; TOFT 1989a, 1989b; DRONEY 1992), although some exceptions are observed (e.g. BOAKE 1989, ALCOCK 1990, 1993). Mating success is an important factor of male fecundity (PAYNE 1979, WADE 1979, ARNOLD & WADE 1984).

Body size explained only 2.5% of the variance in lifetime mating success of *P. litigata* males. The residual variance probably reflects both noise in the data set and dependence of mating success on additional factors not considered in this study.

For example, if small males enjoyed an advantage in scramble competition, this would partly compensate for their disadvantage in agonistic contests and weaken the overall effect of body size on mating success. Small males enjoy a mating advantage resulting from greater speed, agility or metabolic efficiency in some insects (e.g. MᴄLᴀᴄʜʟᴀɴ & Aʟʟᴇɴ 1987, Nᴇᴇᴍs et al. 1990). An interesting alternative possibility is that much of the remaining variance reflects stochastic factors in the mating system.

Characteristics of oviposition sites

The most heavily damaged area served as the main oviposition site on three antlers, while the porous pedicel served as the main oviposition site on the fourth antler (Fig. 3). This variation may have resulted from differential distribution on the antlers of the microbial cultures on which adults and larvae feed. In the closely related fly *Piophila casei*, oviposition may be induced by contact with a specific microflora (Jᴏɴᴇs et al. 1971), and *P. litigata* females might use a similar cue. Porous parts of antlers offer access to the interior bony canals for oviposition and seem to emit stronger scent, which suggests the presence of a microbial culture. Thus, females may use scent to locate oviposition and feeding sites, and males may use it to locate advantageous areas for mate-searching.

The main oviposition site was the most contested region on each antler. It attracted the highest density of single males on each of the four antlers, and the largest males on antlers M1, M2 and M3 (Fig. 3). On antler M4, the mean body size of males at the main oviposition site (region C) was slightly smaller than that of males in the adjoining flat upper surface region (A4) containing the secondary oviposition site. This pattern may have come about because the curved topography and very high density of single males in region C (Fig. 3) prevented males from defending stable territories there.

Advantages of mate-searching near the main oviposition site

The main oviposition site on each antler appeared to be the most advantageous mate-searching region for males. This region contained the highest density of single females on antlers M1, M2 and M3, and the second highest density of single females on M4 (see below). On antler M4 the intensity of competition for an upper surface region was positively correlated with mean male lifetime mating success in that region, and the main oviposition site yielded the highest mean male lifetime mating success (Fig. 5I). Hence, as predicted by theory, males competed most intensely for the most advantageous regions in which to search for mates.

The advantage of mate-searching near the main oviposition site appears to be greater mating frequency rather than greater survivorship. In principle, mate-searching in a contested region may augment male survivorship: for example, the region's topography may facilitate predator avoidance. In practice, this is unlikely because the high density and large mean body size of single males in such regions (Fig. 3) tend to result in intense combat that may cause physiological wear and injury (Bᴏɴᴅᴜʀɪᴀɴsᴋʏ unpublished observation). We detected no correlation between mean male body size in a region and mean male survivorship there, and

males searching near the main oviposition site experienced average survivorship (Fig. 5III). In contrast, the main oviposition site yielded the highest mean male mating frequency of all regions on the upper surface. Although the correlation among regions of mean male body size and mean male mating frequency was not quite significant (P = 0.08), other tests indicated that only the number of observations at the main oviposition site affected mating frequency, and that individual males mated almost twice as frequently when mate-searching near the main oviposition site as they did when mate-searching elsewhere.

Males may have experienced high mating frequency near the main oviposition site because density of single females was high in this region (Fig. 3). In addition, it is possible that a greater proportion of females near the main oviposition site were gravid (i.e. had eggs ready for oviposition) and thus were more receptive and/or attractive to males. Because females risk injury in male-male brawls (Bonduriansky & Brooks 1998a), non-gravid females may benefit by feeding away from areas where aggressive single males are densely aggregated, perhaps resulting in a higher proportion of gravid females near the main oviposition site than elsewhere. Because males often reject non-gravid females and females sometimes reject small males (Bonduriansky & Brooks 1998b), a high proportion of gravid females and large males near the main oviposition site would result in a high frequency of mating there. This may also explain why the pedicel (region PD) on antler M4 had the highest density of single females but a very low density and small mean body size of single males (Fig. 3): most of the females in that region may have been feeding, and non-gravid.

In our analyses, we assumed that only the regions on the upper surface of antler M4 were contested by males because territory defense was confined almost exclusively to the antler's upper surface (Fig. 3), and even non-territorial males there were more active and aggressive than males on the underside (Bonduriansky unpublished observation). On the undersides of antlers, males fight only in areas adjacent to oviposition sites, such as in region B5 on antler M3 (Figs 1, 3). However, the conclusion that agonistic success determines mating success leaves unexplained the very high mean mating success in some underside regions of antler M4 (Fig. 5). It is possible that males on the underside of the antler employed an alternative, non-agonistic mate-acquisition tactic, as occurs in some insects (e.g. Forsyth & Montgomerie 1987, Thornhill 1987, Forsyth & Alcock 1990). A simpler explanation is that the tendency of males to rest on the underside of the antler after mating (Bonduriansky unpublished observation) may have resulted in a positive correlation between mating success and the proportion of observations as a single male on the underside, even if most mating partners were actually encountered elsewhere.

Thus, male-male agonistic competition for access to advantageous mate-searching locations may suffice to explain the structure of antler fly mating aggregations on moose antlers. Male antler flies defend territories near oviposition sites because these resources attract females, a form of resource-defense polygyny (Emlen & Oring 1977) that appears to be common in Diptera (e.g. Mangan 1979, Papaj 1994). Another apparently common insect mating system is female-defense polygyny (Emlen & Oring 1977), where males compete for access to female emergence sites (e.g. Thornhill 1980; Alcock 1989, 1996). One interesting question remaining to be answered is whether the occurrence of non-aggressive males in some insect species can be explained by an absence of defensible oviposition sites and female emergence sites.

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