18 • Function and evolution of antlers and eye stalks in flies

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ABSTRACT

Flies with structures protruding from the head, termed eye stalks or antlers, have long fascinated biologists. In this chapter we consider the possibility that such flies either share developmental predispositions to head modification or face similar selective pressures to augment head width. By randomizing the occurrence of eye stalks and antlers among families of acalyptrate flies over a phylogeny, we demonstrate that eye stalks and antlers have evolved especially often within one superfamily and that eye stalks and antlers exhibit correlated evolution. Because extreme sexual dimorphism of antlers and eye stalks occurs in four families, while correlated evolution of eye stalks in females occurs in others, we suggest that the degree of sexual dimorphism, but not the occurrence of head projections, has been influenced by historical genetic factors. Comparison of the ecology and mating systems of flies from the genus *Phytalmia*, all species of which possess antlers, with flies from the family Diopsidae, all species of which possess eye stalks, indicates selective similarities. All head-projection flies studied to date exhibit some form of resource-defense mating system. *Phytalmia* spp. defend rare oviposition sites, whereas dimorphic diopsids defend protected sites where females aggregate at night. In both groups, males assess the body size of competitors from the head projection, and males of similar size engage in extended physical contests for control of a resource. Females of at least two diopsid species also use eye-stalk length to select mates and can influence sperm precedence by ejecting male spermatophores. Head-structure span exhibits positive allometry with body size in *Phytalmia* and dimorphic diopsids. Because of the high correlation between head-projection span and body size, comparison of head projections provides a quick and accurate method for assessing body size. We postulate that head projections have evolved in tropical flies with resource-defense mating systems because these animals experience many mating opportunities owing to long lifespans and because competing males benefit from reduced average contest duration.

INTRODUCTION

Some of the most unusual flies in the world are those with secondary paired processes of the head capsule, often referred to as antlers or eye stalks. The term 'antler' refers to the shape of some structures, such as the cheek processes of *Phytalmia* species (Fig. 18-1), rather than to any deciduous capability; 'eye stalks' indicate that the eye bulb has been displaced laterally away from the body on peduncles. No fly yet described has both eye stalks and antlers although in a few cases, such as several species in the genus *Zygothrica* (Drosophilidae), the eye bulb is elongated into a cone, which may curl at the tip like the horns of a ram (Grimaldi 1987).

Many workers have speculated on the function of cephalic projections since the first descriptions of flies with eye stalks (Linnaeus 1775) and antlers (Gaerstecker 1860; Saunders 1860). However, until recently few observational studies on these flies had been conducted. In this chapter we summarize what is currently known regarding the mating systems of flies with antlers and eye stalks and, in conjunction with phylogenetic and allometric analyses, use this information to make inferences regarding the function and evolution of these bizarre structures.

PHYLOGENETIC RELATIONSHIP AMONG FLIES WITH HEAD PROJECTIONS

Within the order Diptera, eye stalks occur in eight families and antlers in five families (Table 18-1). The distributions of eye stalks among dipteran families (Hennig 1966; Sanderson 1991) and hypercephaly among species of drosophilids (DeSalle and Grimaldi 1993) have both been interpreted as examples of recurrent evolution. To evaluate these claims further and to determine whether eye stalks and antlers have evolved independently, we performed randomization tests using putative phylogenetic relationships among 64 acalyptrate families (Fig. 18-2) (McAlpine 1989). We restrict our analyses to acalyptrate flies because they may
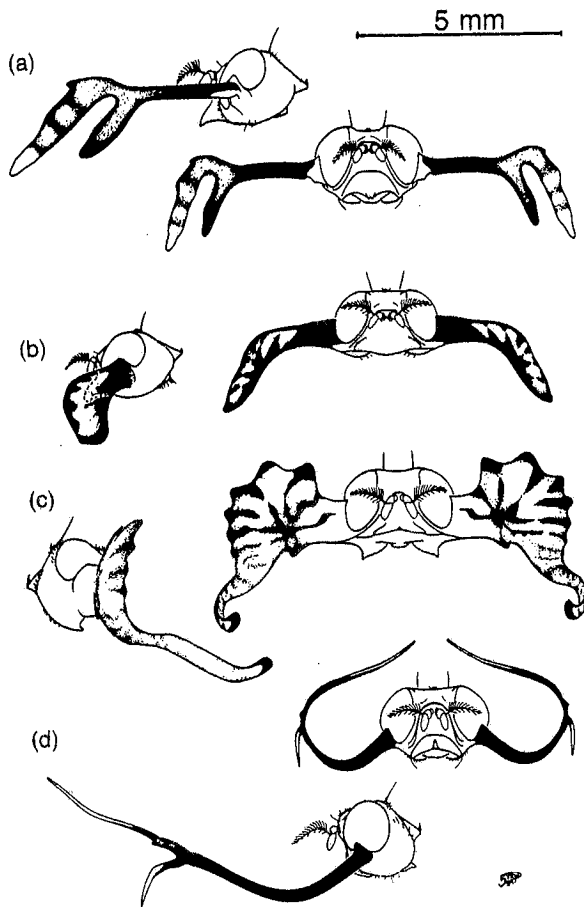
Fig. 18-1. Head projections or 'antlers' of males from (a) *Phytalmia antilocapra*, (b) *P. cervicornis*, (c) *P. mouldsi*, and (d) *P. alcicornis*.

represent the smallest monophyletic group that includes all cases of head projections (McAlpine 1989).

The first question we ask is whether head projections have evolved independently among flies or exhibit clustered evolution on a family-level phylogeny (Fig. 18-2). Because not all members of each family have head projections (Table 18-1), one or more independent evolutionary events has occurred within each family. Consequently, comparing the number of evolutionary steps required to explain head projection evolution to some null expectation (see, for example, Sanderson 1991) is inappropriate at the family level. Instead, we estimated the probability that four families in the Tephritoidea have evolved eye stalks by assuming that eye-stalk acquisition is equiprobable among families. After shuffling the occurrence of eye stalks over 100 replicate phylogenies, only one case of four

families, and none with more families, emerged in this superfamily. The probability of such clustered evolution occurring by chance is therefore 0.01. Similarly, three families with antlers arising within the Tephritoidea is unexpected, as the probability associated with this result is also 0.01. Thus, both eye stalks and antlers are clustered non-randomly on the phylogeny.

The second question we ask is whether eye stalks and antlers have arisen independently of each other. Although antlers are known from only five families of flies, four of these families also contain species with eye stalks (Table 18-1). Using the concentrated changes test (Maddison 1990) with the occurrence of eye stalks in an acalyptrate family as the independent variable and the presence of antlers as the dependent variable, the probability of at least four gains and no more than one loss is less than 0.001.

These analyses suggest that some characteristics of these families facilitate head-projection evolution. Two non-exclusive possibilities can be envisioned. First, some developmental trait may predispose these taxa to evolve head projections. Second, these families may share an environment that favors head elaboration. To evaluate these alternatives we focus discussion on two groups, the genus *Phytalmia* (Tephritidae), all species of which possess antlers (Fig. 18-1), and the family Diopsidae, all species of which possess eye stalks.

PHYTALMIA (TEPHRITIDAE)

Distribution and morphology

Among the fly genera with cephalic projections resembling antlers, *Phytalmia* is the most speciose and their head projections are the most elaborate. When McAlpine and Schneider (1978) revised the genus they reported six species, with one additional species having been described since (Schneider 1993). All but one species are found on the mainland of New Guinea and adjacent islands (McAlpine and Schneider 1978). The single species found elsewhere is *P. mouldsi*, known only from an area of isolated rainforest in the upper Cape York Peninsula of Australia.

Across the genus, as well as throughout the other 'antlered' flies (Table 18-1), head or cheek projections are restricted to males. *Phytalmia* antlers are extensions of the cuticle arising in the cheek area, their bases forming an indentation into the compound eye (Fig. 18-1). Females have a notch at the lateral margin of the eye, but

Table 18-1. *Diptera with Head Projections*

Taxa	Projection	Reference
Clusiidae		
Labomyia mirabilis	cheek process	Frey 1960
Hendelia extensicornis	broad head	Frey 1960
Parahendelia latifrons	broad head	McAlpine 1975
Clusiodes gladiator	broad head	McAlpine 1975
Diopsidae (13 genera, >150 species)	eye stalks	Feijen 1989
Drosophilidae		
Chymomyza (5 species)	eye stalks	Grimaldi 1986a
Diathoneura sp.	cheek process	D. Grimaldi, personal communication
Drosophila heteroneura	eye stalks	Spieth 1981
D. (Hirtodrosophila) caputudis	eye stalks	Grimaldi 1986b
D. (Hirtodrosophila) chandleri	eye stalks	Grimaldi 1988
Mulgravea asiatica	eye stalks	Grimaldi and Fenster 1989
Zygothrica (14 species)	eye stalks or broad heads	Grimaldi 1987 Bristowe 1925
Micropezidae		
Anaeropsis guttipennis	eye stalks	McAlpine 1974
Otitidae		
Plagiocephalus (2 species)	eye stalks	Steyskal 1963
Paragorgopis (4 species)	eye stalks	G. C. Steyskal, personal communication
Opthalmoptera spp.	eye stalks	Grimaldi and Fenster 1989
Periscelididae		
Sphyroperiscelis spp.	eye stalks	Grimaldi and Fenster 1989
Diopsosoma prima	eye stalks	G. C. Steyskal, personal communication
Platystomatidae		
Achias spp.	eye stalks	McAlpine 1994
Achiosoma (2 species)	eye stalks	McAlpine 1975
Agrochira spp.	eye stalks	McAlpine 1982
Angitula nigra	cheek process	McAlpine 1975
Apiola spp.	cheek process	McAlpine 1982
Asyntona tetyroides	broad head	McAlpine 1982
Atopognathus spp.	eye stalks	McAlpine 1982
Brea spp.	eye stalks	McAlpine 1982
Cleitamia spp.	broad head	Malloch 1939
Clitodoca spp.	cheek process	McAlpine 1982
Giraffomyia spp.	cheek process	Malloch 1940
Laglaizia spp.	eye stalks	McAlpine 1975
Mescoctenia spp.	cheek process	McAlpine 1973
Neohemigaster spp.	cheek process	McAlpine 1975
Pogonortalis doclea	broad head	McAlpine 1975
Pterogenia spp.	cheek process	McAlpine 1975
Trigonosoma spp.	eye stalks	McAlpine 1982
Zygaenula spp.	eye stalks	McAlpine 1982
Richardiidae		
Batrachophthalmum spp.	eye stalks	G. C. Steyskal, personal communication
Richardia (3 species)	eye stalks	Hennig 1937
Richardia (3 species)	cheek process	D. Grimaldi, personal communication

Table 18-1. (cont.)

Taxa	Projection	Reference
Tephritidae *Diplochorda* (2 species)	cheek process	McAlpine 1975
Homiothemara eurycephala	broad head	Hardy 1988
Ortaloptera callistomyia	cheek process	Hardy 1988
Pelmatops ichneumonea	eye stalks	Grimaldi and Fenster 1989
Phytalmia (7 species)	cheek process	McAlpine and Schneider 1978
Pseudopelmatops nigricostalis	eye stalks	G. C. Steyskal, personal communication
Sessilina nigrilinea	cheek process	McAlpine and Schneider 1978
Sophira limbata	cheek process	Hardy 1988
Terastiomyia lobifera	cheek process	Hardy 1986

no projections. The size of the cheek process covaries with body size in *Phytalmia* (McAlpine and Schneider 1978) (Fig. 18-3). The smallest males have nothing more than a raised area on the cheek; the largest have spans of more than 1 cm between the tips of each antler. The shapes of the cheek processes are a defining characteristic of the species and are spatulate, cylindrical, or fan-shaped, and either simple or bifurcated (Fig. 18-1).

Apart from the male head projections (and genitalia), the only conspicuous sexual difference is the relatively larger female abdomen, which terminates in a tapering oviscape. More subtle differences between the sexes include recurved spines on the male fore femora, used to grasp female wings during mating and postcopulatory guarding (Moulds 1977), and a strongly produced epistomal margin of the male face in some species (Fig. 18-1) associated with intraspecific agonistic interactions as described below and by Moulds (1977). Otherwise males and females are similar in morphology and have a wasplike appearance.

Life history

Moulds (1977) reported on the reproductive behavior and associated biology of the Australian species, *P. mouldsi*. Subsequently, one of us (GND) has studied *P. mouldsi* and *P. alcicornis* in more detail and made preliminary observations on *P. cervicornis* and *P. biarmata*. These studies have revealed fundamental similarities in the general ecologies and mating systems of *Phytalmia* species. In particular, the larval food source appears to be limited in its distribution, enabling males to defend oviposition sites at the larval substrate, i.e. decaying wood of particular tree species or the fungus/bacteria associated with this decay. Antlers

function within the context of male agonistic behavior at this resource (Moulds 1977; Dodson 1989; G. N. Dodson, unpublished).

Female *Phytalmia* lay eggs by inserting their ovipositors through openings in the bark of downed tree trunks or limbs. The larvae feed within the rotting sapwood. *Phytalmia* may be long-lived as adults. *P. mouldsi* adults of unknown age brought from the field into the laboratory have survived as long as 65 d following capture. Adults reared from field collected larvae have lived for up to 43 d in the laboratory (G. N. Dodson, unpublished).

Resource distribution and visitation

Evidence for the limited distribution of acceptable larval substrates comes from two sources: host suitability tests and measurements of the abundance and persistence of oviposition sites at larval substrates. In Australia and Papua New Guinea (PNG) host suitability has been assessed for fifteen tree species by systematically sampling downed or felled material for fly visitation (Moulds 1977; G. N. Dodson, unpublished). In all cases the trees were accessible over the same period after downing or felling in an area where adult flies were present. Three species of *Phytalmia* (*P. mouldsi*, *P. alcicornis* and *P. biarmata*) were attracted, each to a single host species. Stringent host specificity was indicated by a lack of fly attraction to either confamilial or congeneric tree species (G. N. Dodson, unpublished). Three species of *Phytalmia* have been reared from a single tree species (*Dysoxylum gaudichaudianum*); inspections of innumerable trees, either naturally downed or in logged areas, have revealed only three other species as hosts (Dodson and Daniels 1988; G. N. Dodson, unpublished; H. Roberts, personal communication).
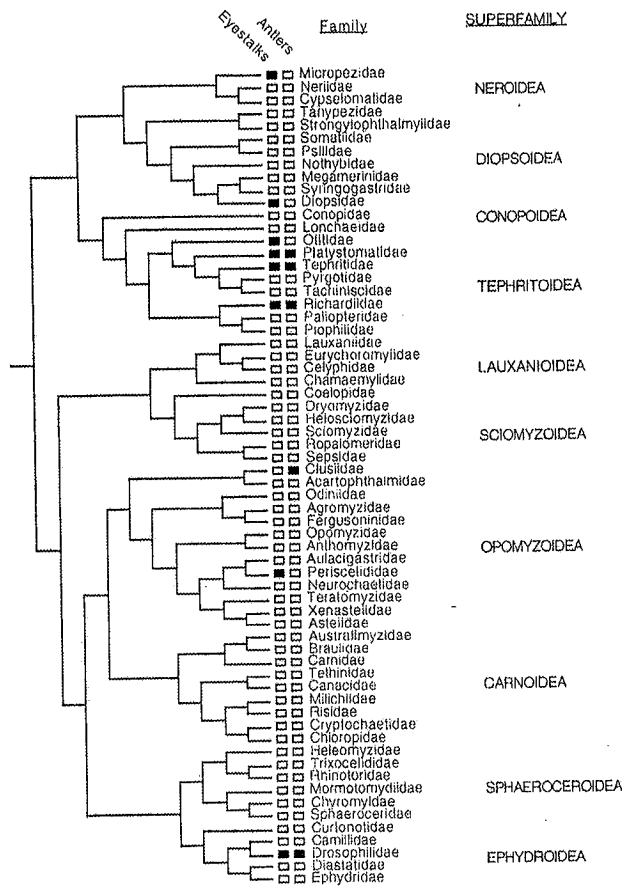
Fig. 18-2. Phylogeny of 64 families of acalyptrate Diptera slightly modified from McAlpine (1989), with the occurrence of eye stalks and antlers indicated by filled boxes adjacent to each family.

Fig. 18-3. Plot of antler span against the sum of thorax and wing length for *P. mouldsi* and *P. alcicornis*. The fitted curves represent least-squares regressions of antler span on the natural log of the sum of thorax and wing length. The dotted line represents the isometric line that passes through the origin.

The window of suitability of the oviposition substrate varied according to the size of the downed material. Tree trunks ranging in size from *ca.* 20 cm DBH to >0.5 m DBH attracted flies for maxima of 40–130 d, respectively (G. N. Dodson, unpublished). Regardless of the overall size of the host substrate, there were generally more males than suitable oviposition sites. For example, a decaying
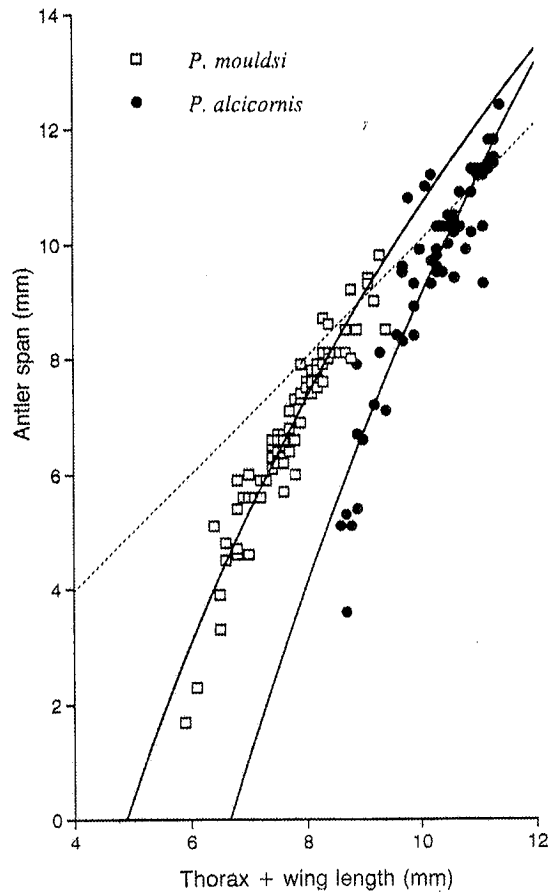
D. gaudichaudianum log monitored for nine consecutive days had at least 13.7 ± 1.1 (mean $\pm$ SE) *P. mouldsi* males visit per day, but only 4.0 ± 0.5 sites were guarded by males and used by ovipositing females each day. Individual oviposition sites ($n = 8$) were attractive to flies for 3.2 ± 0.5 days (G. N. Dodson, unpublished).

Males consistently outnumbered females at the oviposition substrates for all three *Phytalmia* species censused. Males were more numerous in 82% of 154 field censuses, with the proportion of males ranging from 0.62 to 0.85 across the three species (G. N. Dodson, unpublished). The male bias at the resource is apparently not attributable to a skewed sex ratio at eclosion: rearings of *P. mouldsi* (Dodson

and Daniels 1988) and *P. alcicornis* (Roberts and Dodson unpublished) did not differ from unity.

The mean number of days that individual *P. mouldsi* visited the oviposition site during 14 d of censusing was statistically equivalent for males and females, but the pattern of visitation differed between the sexes. Fifty-four percent of 50 marked males visited the resource on consecutive days at least once, whereas only 14% of 34 marked females had consecutive day visits. Coincidentally, 76% of the females returned to the resource after missing at least one day, whereas only 13% of the males did so. Thus, individual males tended to remain for several days and then disappear, whereas females were rarely present for more than one day without absences between visits (G. N. Dodson, unpublished).

Mating

Observations by Moulds (1977) and GND indicate that three species of *Phytalmia* exhibit similar resource-defense mating systems (Emlen and Oring 1977) with minor variation in male contest behavior. Adult flies arrive at the oviposition substrate throughout the daylight hours and depart before sundown. At the resource, males identify specific sites to which females will be attracted and then attempt to exclude other males from them. When another male moves toward a guarded oviposition site, the resident male orients directly toward the intruder with his wings held at roughly a 45° angle from the body axis and above its dorsum. From this point in an interaction, one of three events occurs: (1) the intruder male retreats without contact between them; (2) the two males push their heads against one another momentarily, remaining mainly parallel with the substrate, after which one of the males retreats; (3) the males bring their heads together and engage in a prolonged (escalated) contest until one male retreats. The proportions of non-contact, minor contact, and escalated contact interactions were similar, i.e. 32.3%, 32.6%, 36.6%, respectively, for 420 interactions between marked *P. mouldsi* males in the field (G. N. Dodson, unpublished).

In *P. mouldsi*, escalated interactions occurred between opponents that were the most similar in size and non-contact interactions occurred between those most disparate (Fig. 18-4). The same relationship between relative sizes of opponents and the level of interaction was obvious in *P. biarmata* and *P. alcicornis* as well (G. N. Dodson, unpublished). However, the particular form of escalated interactions differed among species. In *P. mouldsi* and *P. biarmata*,
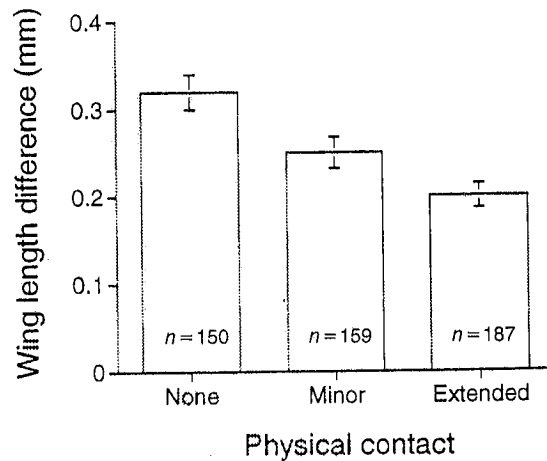

Fig. 18-4. Mean differences in the sizes of *P. mouldsi* male opponents grouped on the basis of the type of interaction (see text for descriptions). Bars indicate standard errors. ANOVA, df = 2,493, F = 16.4, $p < 0.001$.

males rise up on their middle and hind legs until their bodies are perpendicular to the substrate (Moulds 1977; Dodson 1989). The only point of sustained contact between opponents is the strongly produced epistomal margin on the face (McAlpine and Schneider 1978), although the antlers and forelegs make intermittent contact as well. Individual contests can last several seconds, but eventually one of the males falls backwards. This male either retreats, terminating the bout, or rarely, the same two males engage in a series of these 'stilting' contests. In contrast, the escalated contests of *P. alcicornis* (Fig. 18-5a) involve rapid bursts of pushing with less sustained contact and rarely involve the elevation of the anterior of their bodies high above the substrate. Evenly matched opponents exhibit series of bouts lasting up to 3 min, which, at their greatest intensity, include quick, jerking motions while in contact. Details of these rapid thrusts are difficult to distinguish, but it appears that little contact occurs between any facial surfaces other than the antlers.

By defending an oviposition site a male gains access to potential mates. Sexual conflict as described by Alexander *et al.* (this volume) is apparent at several points within the male–female interactions in all three species studied. The oviposition site itself is a minute point above an area of decaying sapwood, which a guarding male regularly dabs with his mouthparts and anus (Moulds 1977; G. N. Dodson, unpublished). Females attempt to move around
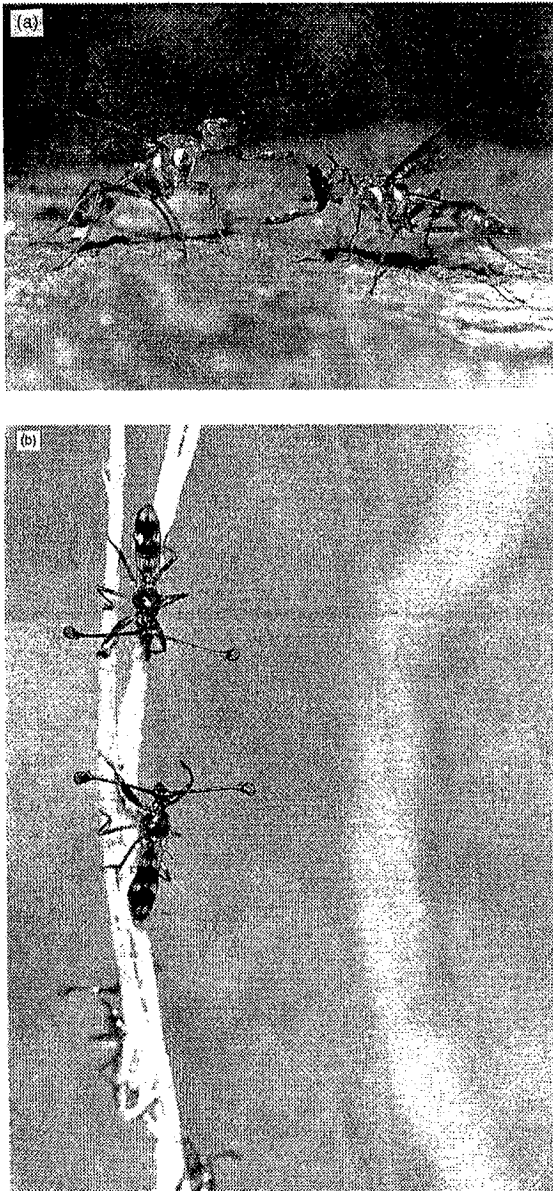
Fig. 18-5. (a) Two *P. alcicornis* males engaged in a contest over an oviposition site in Papua New Guinea. (b) Two large *Cyrtodiopsis whitei* males on a rootlet approaching to compare eye spans at dusk in peninsular Malaysia.

males to the oviposition site but are blocked by the male, who continually positions himself between the female and the site. To gain access to this site for egg-laying, a female must first allow the defending male to copulate. If a female chooses to mate she demonstrates her receptivity by lowering her head to the substrate, at which point the male mounts her from above and secures the bases of her wings with his forelegs (Moulds 1977). Copulations are relatively brief (1–2 min) (Moulds 1977; G. N. Dodson, unpublished), after which the male remains astride the female as she inserts her ovipositor and begins depositing eggs. From this postcopulatory position males sometimes interact with other males who attempt to displace them from the female. Females terminate their association with a male by vigorously shaking until he dismounts (G. N. Dodson, unpublished).

On a spectrum of copulatory acts from luring or enticing to manipulative and coercive (Alexander *et al.*, this volume), *Phytalmia* appear to fall closer to a luring act. Males entice females to mate by controlling access to a required resource. Although females can choose whether or not to mate with a particular male, expediency to oviposit may dictate that they sometimes practice 'convenience polyandry' (Thornhill and Alcock 1983). Even so, the ability of females to exercise mate choice by storing sperm and multiply mating is expected to lead to selection on males to regain some control over fertilization (Alexander *et al.*, this volume). For *Phytalmia* this could account for the evolution of the femoral holding devices, postcopulatory guarding behavior, and the requirement that a female copulate before each oviposition bout, even when she has been only temporarily separated from a guarding male with whom she has already mated (G. N. Dodson, unpublished).

It should also be considered, however, that postcopulatory guarding by males might not be solely an advantage for males. Suitable, unguarded oviposition sites are rare, because there are generally excess males patrolling the substrate. Females will attempt to deposit eggs at a guarded site if a resident male is temporarily absent, but are displaced as soon as a male returns. Oviposition bouts by solitary *P. mouldsi* females were significantly shorter than bouts by guarded females (G. N. Dodson, unpublished). Thus, postcopulatory guarding may represent a confluence of interests to the sexes in these species.

Because copulations occur at oviposition sites monopolized by males, successful defense of a site should translate into mating success. Given that larger males win contests over oviposition sites (84% of 420 *P. mouldsi* male–male field interactions, based on wing length), mating males are expected to be larger than the overall male average. This difference was found in both *P. mouldsi* and *P. alcicornis*. Males collected while paired with a female were larger than males collected as singletons (with size estimated as

the first principal component derived from four metric characters; Mann–Whitney tests: $U = 419$, $p = 0.04$, $n = 19$ paired males, $n = 33$ singletons for *P. mouldsi*; $U = 496$, $p = 0.01$, $n = 17$ paired males, $n = 41$ singletons for *P. alcicornis*).

Antler size is highly correlated with each of four metric body characters (wing, thorax, fore femur and mid femur lengths) in both *P. mouldsi* and *P. alcicornis* (Pearson $r = 0.88$ or higher for each correlation). A plot of antler size on body size reveals positive allometry for antler size in both species (Fig. 18–3). Thus, antler size is an honest indicator of overall size, which itself is a predictor of fighting success. Antler size could be used by males to assess an opponent's fighting ability, thereby avoiding unnecessary contests. At the largest body sizes, antler size appears to level off. Huxley (1932, pp. 60–61) suggested that such a diminishing relationship would be expected in a 'closed' system in which development of adult structures is dependent upon finite food reserves acquired during a larval stage. The theoretically largest heterogonic organs would fall below the sizes expected as the 'limited reserve supply would come to an end, used up by competing organs' (Huxley 1932). Whatever its cause, we suggest that this relationship would have little effect on the value of antler size as a predictor of body size for the majority of opponents because only a small proportion fall at the upper end of the distribution. Furthermore, when two of the largest males interact, an escalated fight is expected *a priori*.

Unlike the eye stalks discussed in detail below, the antlers of *Phytalmia*, and perhaps all cheek projections, are amenable to experimental investigations of function. Antlers can be excised without debilitating effects; one of us (GND) has performed preliminary experiments on the role of these structures in male–male contests in *P. mouldsi* and *P. alcicornis*. Interactions were staged between control males and treatment males whose antler size was either increased or decreased. In *P. mouldsi*, when opponents were equal in body size (as indicated by wing length), lengthening the antlers resulted in a significant increase in fighting success and shortening the antlers significantly lowered fighting success. In experiments in which body sizes differed, lengthening the antlers of small males did not increase their low success rate. Shortening the antlers of large males significantly lowered their success, but these de-antlered males still won a high percentage of fights (75–78%). In *P. alcicornis*, experiments involved differently sized males only. As in *P. mouldsi*, large males won a high percentage of their fights (80%) before the manipu-

lation and this remained unchanged after antler removal. In this species the fighting success of small males increased significantly when their antlers were lengthened. Across all experiments the proportion of interactions involving contact rose significantly for males whose antlers were shortened and did not change for males whose antlers were lengthened.

Thus, it appears that antlers are not required in order to win contests: the outcome is determined primarily by size. However, males without antlers expended more effort in escalated contests before the outcome was determined.

Sensory hairs are located on the antlers of all *Phytalmia* species and on the cheek projections of several other species, sometimes only at the apex of the projection (G. N. Dodson, personal observation). Therefore, although these manipulations may partly test for a role for antlers in visual assessment, any tactile function is probably eliminated.

DIOPSIDS

Classification and distribution

The classification of diopsids is under revision, and new species await description. In 1972, 150 species in 13 genera, including normal-headed flies in the genus *Centrioncus*, were recognized in the family (Steyskal 1972). Feijen (1983, 1989) subsequently created a new family, Centrioncidae, synonymized two genera, and created two new genera. The number of species in the Diopsidae may eventually reach 300 with 50 or more in each of three genera: *Diopsis*, *Diasemopsis* and *Teleopsis* (Feijen 1989; H. R. Feijen, personal communication).

Although most diopsids are found in the old world tropics, the genus *Sphyracephala* (Feijen 1989) is an exception, with species in eastern North America, Russia, India, Africa, and southeast Asia. Several genera – *Diopsis*, *Diasemopsis*, *Diopsina*, *Trichodiopsis*, *Chaetodiopsis*, *Cladodiopsis*, and *Cobiopsis* – are restricted to Africa with the exception of one *Diopsis* species in southeast Asia and three in the Arabian peninsula (Feijen 1989). *Cyrtodiopsis* and *Teleopsis* are limited to southeast Asia; *Eurydiopsis* is found from India to New Guinea and *Sinodiopsis* occurs in China (Feijen 1989). Fossil diopsids 38–50 million years old have been found in Baltic amber or in shale in Montana and France and placed in the genus *Prosphyracephala* (Feijen 1989) because they resemble extant species of *Sphyracephala*.

MORPHOLOGY AND
SEXUAL DIMORPHISM

Diopsids are unique in having antennae at the end of eye stalks, instead of in the facial region. Most species are 5–10 mm in body length, and often resemble ants because of their terrestrial habits (Feijen 1989; Peterson 1987). Although noted for their hypercephaly since Linnaeus' description (Linnaeus 1775), sexual dimorphism in eye span apparently was not detected until Frey (1928)

described differences in eye stalk length between the sexes of three *Teleopsis* species. Subsequently, Descamps (1957), Shillito (1971) and Burkhardt and de la Motte (1983, 1985) pointed out that males of some *Diopsis*, *Cyrtodiopsis* and *Teleopsis* species have longer eye stalks than females. Feijen (1989), however, noted that females have longer eye stalks than males in some *Sphyracephala* species.

Comparison of linear allometric relationships between eye span and body length (Fig. 18-6) reveals that the apparent reversed sexual dimorphism for eye span in
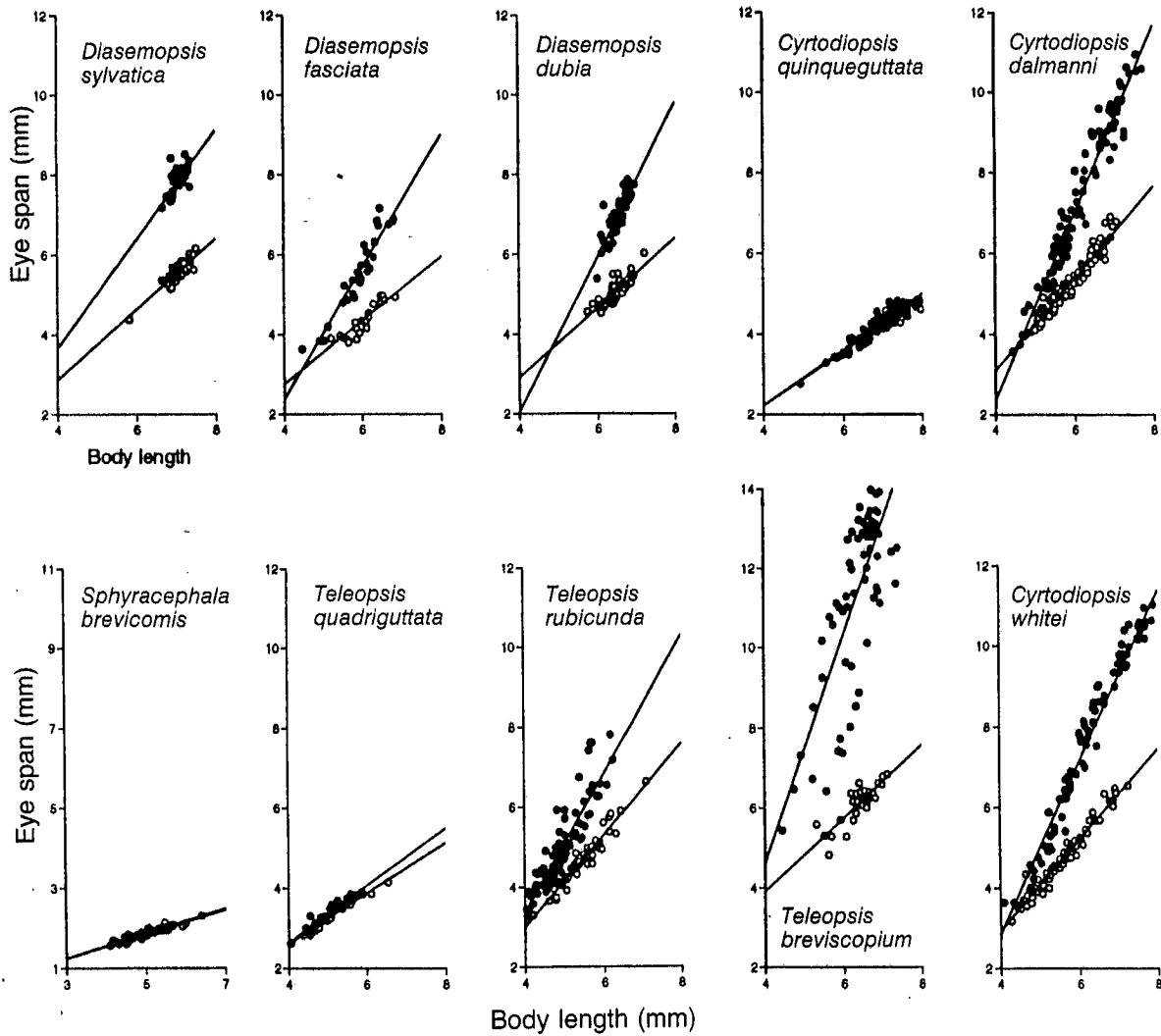

Fig. 18-6. Plots of eye span against body length with least-square regression lines for males (filled circles) and females (open circles) from 10 species of diopsids. All *Cyrtodiopsis* and *Teleopsis* species were collected in peninsular Malaysia, *Diasemopsis* in Africa, and *Sphyracephala* in Maryland.

S. brevicornis is due to females having larger bodies than males. In *S. brevicornis* both eye span ($t = 2.8$, $p = 0.007$) and body length ($t = 3.9$, $p = 0.0002$) are greater for females (Table 18-2). However neither the slopes nor the elevations of the eye span on body length regressions differ between the sexes.

Sexual dimorphism in the eye span of diopsids is not positively correlated with body size, in contrast to enlarged mandibles among lucanid beetles (Otte and Stayman 1979). The eye span on body length regression slopes (Table 18-2) among males for each of three *Cyrtodiopsis*, *Teleopsis* and *Diasemopsis* species differ by ANCOVA (*Cyrtodiopsis*: $F = 137.9$, df $= 2,248$, $p < 0.0001$; *Teleopsis*: $F = 18.0$, df $= 2,168$, $p < 0.0001$; *Diasemopsis*: $F = 3.38$, df $= 2,111$, $p = 0.037$). In contrast, body length of males from the sexually dimorphic species does not consistently exceed that of males from sexually monomorphic species within genera, indicating that evolutionary change has occurred in male allometric relationships. This conclusion is supported by breeding studies on *C. whitei* (G. S. Wilkinson and P. R. Reillo, unpublished) and artificial selection

on the ratio of eye span to body length in *C. dalmanni* (Wilkinson 1993) demonstrating heritable variation for eye span on body length regression slope.

Sexual dimorphism in eye span to body length allometry must have evolved multiple times in the Diopsidae: at least once in *Cyrtodiopsis*, *Teleopsis* and *Diasemopsis* (Fig. 18-6) and probably in other genera. To reach this conclusion, we assume that eye-span monomorphism, as in *S. brevicornis*, *T. quadriguttata* and *C. quinqueguttata*, is plesiomorphic in the family. This assumption is supported by phylogenies derived from morphological characters (Feijen 1989; Steyskal 1972) and mitochondrial DNA sequences (R. Baker and G. S. Wilkinson, unpublished) both of which place the genus *Sphyracephala* basal to the remaining diopsids. Thus, some selective force must have favored a steeper allometric relationship between eye span and body length in males of the dimorphic species. Dimorphism could then arise if the genetic correlation between the sexes for this character was less than one, or if stabilizing selection opposed a correlated response in females, or both.

Table 18-2.
Body Measurements for 10 Species of Diopsids

Parentheses enclose one SE. Regression slope indicates the least-squares regression of eye span on body length. Genera as in Fig. 18-6.

Sex	Species	n	Eyespan	Body length	Thorax width	Regression slope
Male	*C. dalmanni*	93	749 (0.18)	623 (0.08)	167 (0.02)	231 (0.07)
	C. whitei	86	797 (0.23)	637 (0.11)	147 (0.03)	213 (0.05)
	C. quinqueguttata	102	425 (0.04)	697 (0.05)	190 (0.02)	069 (0.03)
	T. breviscopium	60	10.98 (0.28)	632 (0.08)	165 (0.03)	273 (0.30)
	T. rubicunda	89	497 (0.11)	492 (0.06)	130 (0.02)	173 (0.08)
	T. quadriguttata	29	333 (0.07)	498 (0.10)	139 (0.03)	071 (0.04)
	D. obstans	52	700 (0.07)	656 (0.03)	185 (0.01)	193 (0.16)
	D. fasciata	28	566 (0.17)	599 (0.10)	149 (0.03)	166 (0.11)
	D. sylvatica	37	790 (0.05)	709 (0.03)	199 (0.01)	116 (0.22)
	S. brevicornis	32	183 (0.03)	487 (0.08)	142 (0.03)	030 (0.02)
Female	*C. dalmanni*	91	521 (0.08)	585 (0.06)	160 (0.02)	114 (0.03)
	C. whitei	86	467 (0.08)	555 (0.07)	134 (0.02)	112 (0.02)
	C. quinqueguttata	66	428 (0.05)	715 (0.06)	199 (0.02)	067 (0.03)
	T. breviscopium	30	609 (0.09)	638 (0.08)	174 (0.04)	095 (0.11)
	T. rubicunda	52	465 (0.09)	544 (0.07)	148 (0.02)	115 (0.05)
	T. quadriguttata	18	337 (0.09)	521 (0.13)	143 (0.05)	063 (0.04)
	D. obstans	59	509 (0.04)	650 (0.04)	186 (0.01)	087 (0.07)
	D. fasciata	25	437 (0.08)	602 (0.09)	153 (0.03)	080 (0.09)
	D. sylvatica	62	555 (0.03)	705 (0.03)	198 (0.01)	088 (0.07)
	S. brevicornis	33	193 (0.02)	528 (0.07)	157 (0.03)	031 (0.02)

Female *C. dalmanni* exhibit a correlated response to artificial selection on male relative eye span (Wilkinson 1993). Furthermore, female *C. dalmanni* and *C. whitei* have steeper allometric relationships than female *C. quinqueguttata* (ANCOVA, $F = 37.6$, df $= 2,227$, $p < 0.0001$) and female *T. breviscopium* and *T. rubicunda* have steeper allometric relationships than female *T. quadriguttata* (ANCOVA, $F = 15.2$, df $= 2,93$, $p < 0.0001$) (Table 18-2). The differences among females in these two genera are consistent with correlated evolution of female allometric relationships in response to selection on males. By contrast, females from all three *Diasemopsis* species exhibit allometric relationships with the same slope (ANCOVA, $F = 0.38$, df $= 2,140$, $p = 0.69$, Table 18-2). Allometric data for additional *Diasemopsis* species, and a species-level phylogeny for these genera, are needed to determine whether correlated eye-span evolution is absent among females in this genus.

Life history

Despite quantitative differences in life-history traits, such as fecundity, age of sexual maturity and longevity, among species (Descamps 1957; G. S. Wilkinson, unpublished), general life-history patterns are similar among diopsids. Females lay eggs singly on either a plant stem or decaying vegetation. *C. dalmanni* females lay, on average, between 0.1 and 4 eggs per day and may continue laying eggs for many months (G. S. Wilkinson, unpublished). Eggs hatch after 1–3 d (Descamps 1957) and the larvae take from 10 d to several weeks (depending on species, temperature and food quality) to grow and pupate (Descamps 1957). Late-instar larvae typically pupate on emergent vegetation and eclose one to two weeks later. As larval food deteriorates, pupation occurs at smaller larval sizes. In dimorphic species small males exhibit eye span indistinguishable from that of small females (Fig. 18-6). Eye span is, therefore, an honest indicator of body size although at small body sizes it does not reliably signal sex.

Adult diopsids are capable of long lifespans. North American *Sphyracephala* overwinter as adults (Flint 1956; Lavigne 1962) and live 12 months or more in the laboratory (Hochberg Stasny 1985). Individual *C. dalmanni*, *C. whitei*, *C. quinqueguttata*, *T. quadriguttata*, *Diasemopsis dubia*, *D. sylvatica*, *Diopsis fumipennis*, *D. apicalis*, *E. subnotata* and *S. brevicornis* require at least two weeks after eclosion before attaining reproductive maturity (de la Motte and Burkhardt 1983; G. S. Wilkinson, unpublished) and have been kept alive for 6 months or more (G. S. Wilkinson, unpublished).

This longevity is not just due to laboratory rearing. The average adult ages of field-caught *C. dalmanni* (Wilkinson and Reillo 1994) and *C. whitei* (G. S. Wilkinson and P. R. Reillo, unpublished), estimated from pteridine eye pigments, are over 30 days with some large individuals of both sexes surviving for over 200 days.

Resource distribution and visitation

Although the larvae of some *Diopsis* species bore into monocotyledonous stems, most diopsid larvae are saprophagous and feed on decaying vegetation (de la Motte and Burkhardt 1983; Deeming 1982; Descamps 1957; Feijen 1979; 1989; Hochberg Stasny 1985; Tan 1967). Available evidence indicates that oviposition sites for most, if not all, diopsid species are widespread.

Adult diopsids ingest fungi, mold and yeast from decaying leaf litter or dead animals (de la Motte and Burkhardt 1983; Descamps 1957; Feijen 1989; Tan 1967; Wickler and Seibt 1972). During the day, individuals of most species walk on the ground or on low vegetation near streams in secondary or primary forest, although the stem-boring diopsids can be found in cultivated areas (Feijen 1989). Observations of *C. whitei*, *C. dalmanni* and *T. breviscopium* in Malaysia and of *Diasemopsis fasciata* in Kenya indicate that flies from these species typically act aggressively toward conspecifics of both sexes during the day (Lorch et al. 1993; G. S. Wilkinson, unpublished).

At night, adults of most dimorphic species form groups in protected sites. In Malaysia, Burkhardt and de la Motte (1985) found four out of five dimorphic species but none of four monomorphic species in nocturnal clusters. These aggregations occur on rootlets that hang underneath banks along small streams (Fig. 18-7a). In Malaysia, female *C. whitei* (Burkhardt and de la Motte 1987) and *C. dalmanni* (Wilkinson and Reillo 1994) exhibit clumped distributions on rootlets whereas males are overdispersed. In Kenya, *Diasemopsis fasciata* gather on the surface of leaves at night (Fig. 18-7b). Distributions of each sex were scored for 373 flies on 177 leaves from photographs taken at night (G. S. Wilkinson, unpublished). The number of males was not independent of the number of females ($\chi^2 = 26.5$, df $= 8$, $p = 0.001$). The ratio of variance to mean number of flies per leaf was 1.20 for females (Poisson goodness-of-fit $\chi^2 = 4.5$, df $= 4$, $p > 0.5$) and 0.79 for males ($\chi^2 = 53.7$, df $= 4$, $p < 0.001$) indicating that *D. fasciata* males were overdispersed whereas females were distributed randomly among leaves.

Monomorphic *C. quinqueguttata* do not occur along streams but are dispersed during the day on low vegetation in lowland forest (G. S. Wilkinson, unpublished). These flies do not aggregate at night in the laboratory; mating typically occurs during the day (Kotrba 1996). Nocturnal behavior has not been described for any *Diopsis* species although mating of *D. longicornis* has been observed on rice plants (Alghali 1984). More quantitative data on spatial dispersion patterns are needed for additional species to determine whether female aggregation tendency correlates with degree of sexual dimorphism.

Nocturnal aggregation sites persist for many months. Wilkinson and Reillo (1994 and unpublished) found significant positive autocorrelations in the number of *C. dalmanni* and *C. whitei* flies roosting on individually marked rootlets over a 10 month period. Only a small fraction of available rootlets were occupied, with the same ones often attracting the largest aggregations every night. Similar stable roosting preferences have been observed for *D. fasciata* in Kenya (G. S. Wilkinson, unpublished). As Fig. 18-7 indicates, flies on rootlets or leaves orient toward the end of the substrate attached to the ground. Because terrestrial predators must approach from that direction, aggregations may serve an antipredator function in addition to protecting the flies from rain.

The female bias observed in nocturnal aggregations of *C. whitei* and *C. dalmanni* is partly a consequence of a biassed adult sex ratio (de la Motte and Burkhardt 1983). This bias is caused by a sex-linked, sex-ratio-distorting gene, *sr* (G. S. Wilkinson, E. Severance and D. Presgraves, unpublished), that behaves much like sex-distorting genes in *Drosophila* (James and Jaenike 1990). Some *sr* males father only daughters. *Sr* appears to be maintained in natural populations at relatively high frequencies owing to the presence of autosomal modifiers (G. S. Wilkinson, E. Severance and D. Presgraves, unpublished).
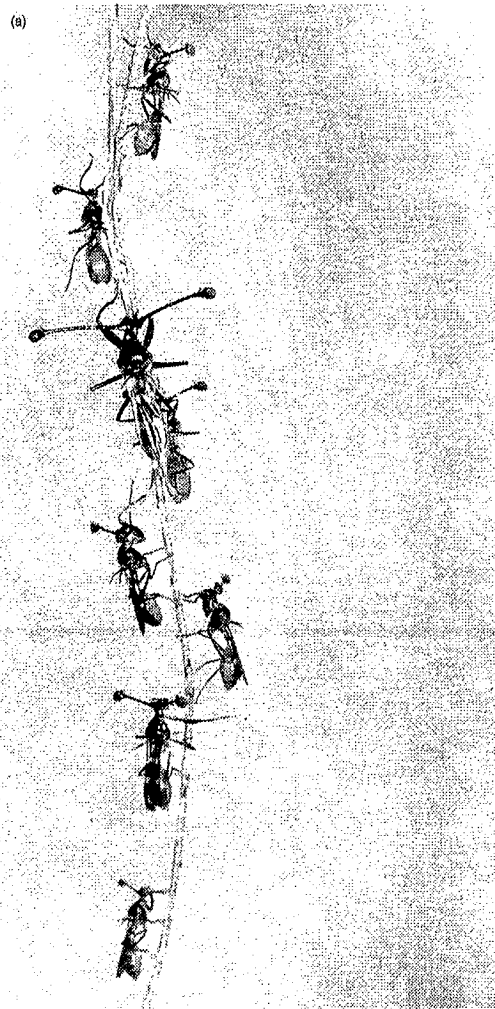

Fig. 18-7. (a) Nocturnal aggregation of *C. whitei* on a rootlet from peninsular Malaysia. Large male has an eye span of 10 mm. (b) Nocturnal aggregation of *Diasemopsis fasciata* from the Taga National Forest, Kenya.

Mating

Obvious courtship signals do not occur in diopsids. In most species, a male approaches a female, leaps onto her back, and attempts to copulate. Species recognition is probably effected by diagnostic wing patterns, as in *Cyrtodiopsis* and *Teleopsis* species (Shillito 1971) or abdomen patterns, as in *Diasemopsis* species (Descamps 1957). Although diopsid mating resembles a coercive act as described by Alexander, Marshall *et al.* (this volume), females from at least some dimorphic species can control fertilization by

resisting male mating attempts (Kotrba 1996), selecting aggregation sites for mating, or influencing which sperm are stored.

In highly-dimorphic species, such as *C. whitei* and *C. dalmanni*, males fight for control of aggregation sites (Burkhardt and de la Motte 1983, 1987; Lorch *et al.* 1993). Males with similar eye span approach head-to-head (Fig. 18-4b), and if similar in size, they rise upon their mid and hind legs, spread their forelegs alongside their eye stalks, and in a series of very rapid lunging moves attempt

Fig. 18-7. (cont.)

to displace each other from the rootlet. In C. whitei 91% of all fights are won by the male with the longest eye span (Burkhardt and de la Motte 1987). In the lab, the duration of a contest between two male C. whitei, as measured by the amount of time spent orienting toward each other, was inversely proportional to the difference in their eye spans (G. S. Wilkinson, unpublished), as expected if these animals use sequential assessment to decide contests (Enquist and Leimar 1983).

Large male C. whitei can mate with over 20 females in an aggregation within 30 min after dawn; most females mate at least once a day (Burkhardt et al. 1994; Lorch et al. 1993). Small males that resemble females sometimes successfully mate in aggregations after avoiding detection by large males (Burkhardt and de la Motte 1988; Lorch et al. 1993). However, the average lifetime reproductive success of female

mimics is less than that of large males because small males rarely live longer than 30 d in the field (G. S. Wilkinson and P. R. Reillo, unpublished). Thus, mate selection approximates a best-of-n process in at least C. whitei and C. dalmanni and results in extreme polygyny (Alexander et al., this volume).

Experiments with dummy male C. whitei and artificially selected male C. dalmanni have demonstrated that females can choose mates on the basis of eye-span comparison. By extending the eye span of dead males and then glueing those males on strings, Burkhardt and de la Motte (1988) found that female C. whitei prefer to alight in the evening on strings containing males with the longest eyespan. Moreover, Wilkinson and Reillo (1994) showed that female C. dalmanni, given a choice between two males separated by a perforated partition, preferred to roost with males from

lines selected for increased eye span. Females from lines in which males had been selected for decreased eye span preferred males with a shorter eye span whereas females from lines selected for increased male eye span preferred males with a long eye span. Because artificial selection was exerted only on males, these results indicate that female preference is genetically correlated with male eye span: a result consistent with both arbitrary cue (Lande 1981) and good genes (Iwasa *et al.* 1991) models of sexual selection.

Female *C. whitei*, and possibly other female diopsids, can control fertilization after copulation because most diopsid males transfer sperm in a spermatophore (Kotrba 1996). Each male *C. whitei* transfers 90 sperm, on average; females hold up to 400 sperm in three spermathecae (Lorch *et al.* 1993). Sperm precedence depends on when females remate and eject spermatophores. Spermatophore ejection occurs between 5 and 60 min after mating (Kotrba 1990, 1993), sometimes before sperm is emptied from the spermatophore. First-male sperm precedence occurs when a female remates before ejecting the first male's spermatophore, whereas sperm-mixing occurs when the second male mates after the first male's spermatophore is ejected (Lorch *et al.* 1993). Paternity analysis of offspring from *C. whitei* females each paired with two males of differing eye span provides evidence consistent with postcopulatory mate choice. Males with twice the eye span of an opponent sired an average of 88% of the young even though both males mated equally often (Burkhardt *et al.* 1994). Whether this result is due to differences in sperm transfer, number, motility or utilization deserves further study.

Although females may be able to influence which sperm are stored, males control copulation duration. In *C. whitei*, sexual conflict over fertilization control is indicated by the presence of short copulations, which do not transfer sperm, shortly after a female has mated (Lorch *et al.* 1993). Males presumably abort copulations after detecting a previous male's spermatophore to reduce copulation time and avoid sperm loss. Copulation duration also varies widely across diopsid species, from 50–60 s in *C. whitei* and *C. dalmanni* (Lorch *et al.* 1993; Wilkinson and Reillo 1994) to over 40 min in *T. quadriguttata*, and correlates positively with spermatophore area (Kotrba 1996). Although some dimorphic species, such as *T. breviscopium*, have long copulation durations, within a genus dimorphic species have smaller spermatophores than monomorphic species, suggesting that selection for rapid male remating in aggregations has led to reduced spermatophore size and

copulation duration (Kotrba 1996). An exception to this pattern occurs in the genus *Sphyracephala*, where postcopulatory mate guarding occurs for up to 1 h (Kotrba 1996). These flies have short eye spans and mate when overwintering aggregations emerge in the spring (Hochberg Stasny 1985).

The consequences of these mating and sperm-precedence patterns for *C. whitei*, *C. dalmanni*, and probably for other dimorphic diopsids, are that strong sexual selection is exerted on males with long eye span. Because body length correlates highly with eye span in all diopsids (Fig. 18-6), selection on eye span is difficult to separate from selection on body length (Mitchell-Olds and Shaw 1987). Nevertheless, the selection intensity on the ratio of eyespan to body length among *C. dalmanni* males, as estimated from collections of nocturnal aggregations, exceeds half of a standard deviation (Wilkinson and Reillo 1994), and as noted above, dimorphic species do not have larger body sizes than related monomorphic species (Fig. 18-6). By contrast, no sexual selection for eye span or body length was found for two monomorphic species, *T. quadriguttata* or *C. quinqueguttata*, during mate-choice experiments conducted in the lab (G. S. Wilkinson and H. Kahler, unpublished).

DISCUSSION

Sex limitation

Comparisons of morphology and mating systems between species of *Phytalmia* and Diopsidae reveal interesting differences and similarities that shed light on the evolution of head projections. In the *Phytalmia* and all other known species with cheek processes, the structures occur only in males. By contrast, not only do both sexes of all species of diopsids exhibit eye stalks, but females of some sexually dimorphic species, e.g. *Cyrtodiopsis* and *Teleopsis*, have significantly higher eye span on body length regression slopes than monomorphic species, presumably owing to a correlated response to selection on male eye span. These differences in sex limitation of sexually selected traits may reflect a difference in the degree to which antlers and eye stalks are developmentally coupled, i.e. genetically correlated, between the sexes.

One interpretation of sex-limited head projections is that the genes that influence the growth of cells that give rise to antlers or eye stalks are located on the male-determining sex chromosome. Crosses between *Drosophila*

sylvestris and *D. heteroneura* indicate, for example, that hypercephaly in *D. heteroneura* is influenced by a major sex-linked gene (Templeton 1977). The often extreme sexual dimorphism in eye stalks found in tephritid, richardiid (Grimaldi and Fenster 1989) and platystomatid (McAlpine 1979, 1994) flies might be the result, therefore, of a genetic organization shared with antler-bearing species for developmental modification of the head capsule. In contrast, crosses between selected lines of *C. dalmanni* demonstrate that genes influencing eye span exhibit no detectable sex linkage and that eye span is developmentally coupled between the sexes (Wilkinson 1993). Autosomal influences on eye-stalk expression apparently occur in other species of *Drosophila* with broad heads or eye stalks as well because females often exhibit noticeably wider heads and steeper head width to thorax length allometric regressions than monomorphic relatives from the same species group (Grimaldi and Fenster 1989). Thus, genetic constraints appear to influence the degree to which head projections are sex-limited, but cannot explain the occurrence of eye stalks or antlers because related species lack these structures.

Allometry and assessment

Antler expression in *Phytalmia* and eye-stalk development in sexually dimorphic diopsids are similar in that both traits exhibit positive allometry with body size in males (Figs. 18-3, 18-6). When the benefit to developing a trait for male–male competion or mate assessment is relatively greater for a large than for a small animal, positive allometry should be favored by sexual selection (Green 1992; Otte and Stayman 1979; Petrie 1988, 1992). We propose an additional explanation for positive allometry in flies with head projections. When projection span and body size are measured with the same degree of error and the allometric slope exceeds one, it follows that a unit change in projection span will be less than a unit change in body size, i.e. the projection-span scale will be finer than the body-length scale. Thus, the high correlation between head projection and body size, together with positive allometry, enables flies to use either antler or eye span to assess body size with greater accuracy than would be possible if body size was measured directly. Furthermore, because both antlers and eye stalks are located on the fly's head, two flies facing each other can see the extent of their opponent's process without inspecting from the side, as would be necessary to obtain a comparable perspective on body

length. By placing their eyes in close proximity during face-to-face frontal displays, stalk-eyed flies directly compare eye span (Burkhardt and de la Motte 1983; McAlpine 1979).

Frontal displays between males have been reported for all stalk-eyed flies (Bristowe 1925; Burkhardt and de la Motte 1983; Grimaldi 1987; McAlpine 1979; Spieth 1981) and antler-bearing flies (Dodson 1989; McAlpine 1975; Moulds 1977) that have been studied, strongly implicating the association of head projections with selection to assess rival body size. An alternative, but not mutually exclusive, hypothesis, that head projections function as weapons or for transmitting force in pushing contests, can be ruled out by observation in stalk-eyed flies and is inconsistent with antler-manipulation experiments in *Phytalmia*. Alexander *et al.* (this volume) suggested that extreme traits such as massive jaws and horns in insects 'are not 'ornaments' in the sense of many sexually selected traits in birds' and probably function as intraspecific weapons. Although we agree that these traits differ from bird ornaments that can vary within a lifetime, we argue that eye stalks and antlers function as ornaments to the extent that they serve as costly signals of competitive ability.

The use of head projections in male–male contests does not preclude the possibility that females may also use eye or antler span to assess males as potential mates. Female choice of head projections could be favored by direct selection (Kirkpatrick and Ryan 1991) if projection length correlated with a trait that influenced female fecundity, such as spermatophore size, or by indirect selection if head-projection length indicated either viability or sexual attractiveness of male progeny. Female choice based on eye-stalk length has been demonstrated for *C. whitei* (Burkhardt and de la Motte 1988) and for *C. dalmanni* (Wilkinson and Reillo 1994). Whether female choice in these stalk-eyed flies provides direct fitness benefits to females or genetic benefits to their progeny has not yet been determined. In order to exert choice, females must be able to visit and compare more than one male. The opportunity for female choice in any species, therefore, depends on the mating system.

Mating system

The evidence summarized above suggests that *Phytalmia* and sexually dimorphic diopsid flies have resource-defense mating systems (Emlen and Oring 1977). *Phytalmia* males defend detectable oviposition sites that are temporally and spatially clumped in the environment. Females visit fallen

logs of a few tree species containing one or more potential oviposition sites and a number of males. Although females may have little choice of mates once they select an oviposition site, they clearly have an opportunity to inspect males at more than one oviposition site. In contrast, diopsids appear to have much less specific larval food preferences. Consequently, oviposition sites are dispersed and indefensible. Sexually dimorphic diopsids, however, form nocturnal aggregations in predictable locations where mating frequently occurs. Although an aggregation may be controlled by a single male, other males often roost within sight, allowing females to assess the eye span of more than one male prior to roosting. Female choice, therefore, is possible in *Phytalmia* and dimorphic diopsids.

The mating systems of other flies with head projections also appear to involve male defense of a resource or a mating site. The clumped distribution of male *D. heteroneura* display sites has been described as a lek (Spieth 1981) because males do not defend a resource and females are presumably free to choose mates (Bradbury 1985; Shelly and Whittier, this volume). However, whether or not male head width influences female mate choice in *D. heteroneura* has not been investigated. Male Australian stalk-eyed flies, *Achias australis* and *A. kurandanus*, form aggregations on trunks of trees (McAlpine 1979), but whether males are defending oviposition sites or courtship territories remains to be determined. Grimaldi (1987) found that up to 21 species of *Zygothrica*, many of which have broad-headed males, feed and mate on fungi (Polyporaceae). Male *Z. dispar* have been reported to butt heads with one another on fungi (Bristowe 1925; Burla 1990). Oviposition and larval development of many *Zygothrica* species occurs in flowers away from aggregations on fungi (Grimaldi 1987). Because suitable fungi are also clumped in the environment, males of these broad-headed drosophilids appear to defend feeding sites to gain access to mates.

Suggestions for future research

This review illustrates that flies with head projections exhibit resource-defense mating systems in which males attempt to mate with females at sites where feeding, ovipositing, or nocturnal resting occurs. In all cases, males compete with each other for control of these sites. Grimaldi and Fenster (1989) cited territoriality as a precondition for male hypercephaly in drosophilids. Of course, some related species compete for control of sites attractive to females,

yet have no head projections (for example, males of a temperate tephritid (*Rhagoletis completa*) defend oviposition sites on walnuts (Boyce 1934)). Another conspicuous attribute of all flies with sexually dimorphic head projections noted by McAlpine (1982) is that they live in the tropics. Perhaps all species with head projections are tropical simply because of the greater number of species in the tropics.

We suggest, however, that tropical fly species may live longer, on average, and thereby have more mating opportunities during their lifetimes than flies in temperate regions. An increase in the average number of mating opportunities in flies with resource-defense mating systems can have two consequences on male fitness. With each successive contest the degree to which each male contest improves male relative fecundity will diminish and the cost to male survival (owing to energy expenditure or injury risk) will increase. Long-lived male flies should, therefore, benefit from the evolution of traits, such as head projections, that improve assessment of competitive ability and decrease costs associated with contest settlement. In contrast, short-lived male flies should continue to fight with rivals independent of size assessment because few alternative mating possibilities exist.

Our hypothesis leads to at least four predictions that could be tested in other flies with head projections. (1) Head projection expression should exhibit positive allometry with body size. (2) Head projections should be displayed, directly compared, and used to determine the outcome of male contests over a site where mating occurs. (3) In comparison with close relatives or experimentally manipulated animals, flies without head projections should take longer to settle territorial disputes than flies with head projections that differ to the same degree in body size. (4) Flies with head projections should engage in more contests over their lifetimes than temperate relatives without head projections. Although it would be difficult to estimate the number of contests a fly has in a lifetime, it is possible to estimate age and the rate at which contests occur. Our observations on diopsids indicate that large males can participate in multiple contests each night for several hundred consecutive nights. As described above, *Phytalmia* males are known to defend territories for multiple hours over consecutive days, interacting with intruders at rates that periodically exceed $1\,min^{-1}$. Any honest signal that minimized the time spent in each contest should be favored by selection.

Rather than list alternative explanations for eye-stalk function, we recommend previous reviews (de la Motte

and Burkhardt 1983; Feijen 1989; Grimaldi and Fenster 1989; Wickler and Seibt 1972) and acknowledge that our hypothesis does not explain cases of monomorphic expression of head projections. However, none of the alternative explanations does any better. Any general advantage to having eye stalks, such as improving the visual field to detect predators, fails to explain why eye stalks are not as long in monomorphic species as in males of dimorphic species. The evidence in support of sexual selection through assessment of male size as perceived by either rival males or receptive females seems sufficiently strong, in our opinion, to predict that all cases of head projections in flies will involve male size assessment. Whether our more specific predictions relating to the number of mating contests are supported awaits further study of these fascinating animals.

ACKNOWLEDGEMENTS

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