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Density- and Food-Resource-Dependent Courtship Behaviour in the Fly *Poecilobothrus nobilitatus* L. (Diptera, Dolichopodidae)

Dichte- und ressourcenabhängiges Balzverhalten bei der Langbeinfliege *Poecilobothrus nobilitatus* L. (Diptera, Dolichopodidae)

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Summary: Males of the dolichopodid fly species *Poecilobothrus nobilitatus* display conspicuous wings with apical white and subapical dark areas when courting a female. In this study, we analyse how the presence of prey objects influences the aggregation of males and females, and how the performance of courtship is correlated with the density of males and females. Within few minutes, the exposure of prey led to an increased number of both males and females in experimental areas. Males were more likely to detect the prey items before the females did; females were more likely to start feeding on the prey items before the males did. When large numbers of males and females have aggregated in suitable areas, courting males are frequently interrupted by male competitors. Males courted females longer if the females were feeding on prey. The length of male courtship display decreased with increasing density of conspecifics, caused by shorter individual courtship phases, less repetitions of courtship phases, and more frequent interruptions of courtship by male competitors.

Keywords: *Poecilobothrus nobilitatus*, Dolichopodidae, courtship, mating

Zusammenfassung: Männchen der Dolichopodidenart *Poecilobothrus nobilitatus* präsentieren ihre auffälligen Flügel mit apikalen weißen und subapikalen, schwarzen Bereichen während der Balz dem Weibchen. In dieser Studie analysieren wir, wie das Vorkommen von Beuteobjekten die Aggregation von Männchen und Weibchen beeinflusst und wie sich das Balzverhalten mit der Dichte von Männchen und Weibchen ändert. Innerhalb von wenigen Minuten nach der Exposition von Beuteobjekten stieg die Anzahl von Männchen und Weibchen in den Versuchsarealen. Männchen fanden die Beuteobjekte häufiger als Weibchen, während Weibchen häufiger als Männchen mit dem Fressen begannen. Wenn Männchen und Weibchen in geeigneten Habitaten in großer Anzahl aggregieren, unterbrechen Störungen von Männchen häufiger die Balz. Männchen balzten Weibchen länger an, wenn diese an Beutetieren fraßen. Die Dauer des Balzverhaltens der Männchen sank mit steigender Dichte von Artgenossen, verursacht durch kürzere Balzphasen, weniger Wiederholungen einzelner Balzphasen und häufigere Unterbrechungen der Balz durch männliche Konkurrenten.

Schlüsselwörter: *Poecilobothrus nobilitatus*, Dolichopodidae, Balz, Paarung

1. Introduction

The courtship behaviour of male dolichopodid flies (Diptera, Dolichopodidae) is outstanding, because of the males' display of signalling structures (Lunau 1992; Zimmer et al. 2003) and spectacular action on the wing (Land 1993a,b). Various aspects of the courtship behaviour of the common species *Poecilobothrus nobilitatus* L. have been extensively studied, namely male-male-interactions (Land 1993b), aerial male display (Land 1993a), and

body size-dependent mating success (LUNAU 1992). Males and females of *P. nobilitatus* are frequently found ashore of lakes, ponds, puddles and rivers. However, areas of low and high density are found. In these areas, males and females can be seen feeding on prey and courting. In this study, we tested whether males and females aggregate in areas with available food and the dependence of male courtship behaviour on the density of conspecifics.

1.1. Ecological background

The two most species-rich families of the Empidoidea, Empididae and Dolichopodidae, show marked peculiarities in their courtship behaviour. The Empididae are outstanding, because the males' courtship is associated with the transfer of a nuptial gift to the female. Several authors have stated an evolutionary shift from the transfer of a prey object as a nuptial gift, which females feed on during copulation, to the display of an empty gift without any nutritional value (CUMMING 1994; SADOWSKI et al. 1999). In some species the great male investment in reproduction is associated with the procurement of the nuptial gift and has led to male choice and sex role reversal (FUNK & TALLAMY 2000). Like the Empididae, dolichopodid flies are predators preying on small crustaceans, insects, and enchytraeid worms (SMITH & EMPSON 1955; ULRICH 2004). It has never been tested, whether the availability of prey plays a role in mating of Dolichopodidae.

Many species of the Dolichopodidae show sexual dimorphism. The males display ornamental structures during courtship. Among the Dolichopodidae there is an enormous diversity of organs bearing the male signalling structures and a surprisingly high homogeneity of signal structures. The diversity of organs bearing the male signalling structures includes signalling structures on the antennae, forelegs, middle legs, hind legs, wings, cerci, and those with special protuberances of the abdomen. Closely related species often possess analogous signalling structures on homologous organs, e.g. middle legs in *Dolichopus plumipes* with a modified tarsal segment 1, in *D. pennatus* with ornamented tarsal segments 2-5, and in *D. popularis* with modified tarsal segments 3-5. Some species even have a double set of male signalling structures, as for example *Nodicornis nodicornis* possessing black and white signalling structures on the elongated antennae and on the middle legs. The signalling structures are very uniform with the apical ends of elongated organs bearing black and/or white signalling areas (LUNAU 1996). A rare exception is the genus *Eucoryphus*, in which the males display an orange crown-like signalling structure on the head. It has been hypothesised that in dolichopodid flies there is a shift from courtship on the wing to courtship on the ground associated with a shift from wings as signalling structures towards other organs bearing signalling devices mimicking the wings' signal (LUNAU 1996, 2002; ZIMMER et al. 2003). It is still unknown whether specific adaptations in the dolichopodid eyes are related to courtship. Many Dolichopodidae exhibit metallic green reflections of the ommatidial cornea caused by the wavelength-selective spectral reflectance of the cornea which is built like a multilayer mirror (BERNARD & MILLER 1968; LAND 1993a) and reduces the transmission of green light to the photoreceptors by that amount of light that is reflected from the coloured cornea (KNÜTTEL & LUNAU 1997). The reduction of light transmission caused by reflection from the cornea can amount up to 50 % in distinct wavelength ranges (LUNAU & KNÜTTEL 1995).

1.2. Previous studies of the courtship of *Poecilobothrus nobilitatus*

The spectacular courtship dances of the common dolichopodid fly *P. nobilitatus* have been studied in some detail (SMITH & EMPSON 1955; LUNAU 1992; LAND 1993a,b). Only males have

conspicuous wings comprising an apical white tip and a subapical dark area. The wing length of males is about 5.7±0.4 mm and that of females 5.2±0.3 mm. The wing spread of males is about 1 mm larger that that of equally-sized females (sized determined by thorax width). Females preferably mate with large males: Copulating males have a larger wing length of 6.0±0.3 mm as compared to randomly caught males with 5.7±0.4 mm long wings. Do features of the courtship display allow for an assessment of a male's size by a female? The courtship of males consists of several parts: (1) the courting male positions himself exactly in front of the courted female at a distance of about 3 cm; (2) the wing-fanning display consists of several wing-fanning actions in the head-to-head position with the female; (3) the flight display is a series of rapid flights from one side of the female to the other. The male turns 180° when flying over the female and always lands in a face-to-body position to the courted female. The aerial turn on the wing is the fastest known rotation around the yaw axis known in the animal kingdom (LAND 1993a). The courting male can repeat one or several phases, before he flies behind the courted female and attempts to copulate. However, successful copulation requires co-operation by the courted female as she has to spread her wings slightly. As in other dolichopodid flies, the hypopygium of the males is very prominent and movable by an intraabdominal joint associated with a complete 180° inversion and forward-bending of the abdomen (ULRICH 1974).

2. Material and methods

The study areas were the natural habitats of *P. nobilitatus* in the surroundings of Düsseldorf in the summer of 2002. The boundaries of the specific study sites were marked for identification in the video material. All experiments were filmed with a video camera (Digital Handycam Sony). Studying the video tapes was possible in a frame-by-frame analysis with 0.04 s intervals between frames.
Experiment 1: Two flat dishes (24 cm in diameter) completely filled with sterilised soil were exposed close to each other. The surface of one of the two dishes was supplied with 3 g of chironomid larvae. In the video analysis it was registered how many males and females of *P. nobilitatus* were present on the dishes for 1 min beginning 5 min after exposure. At this time interval, usually some flies had detected the prey, but none had left the dish. The experiment was repeated ten times by the exposure of fresh dishes in the same area.
Experiment 2: To study the courtship in areas with and without food in more detail, single dishes (24 cm in diameter) either filled with sterilised soil without food or filled with sterilised soil with food (3 g chironomid larvae and half a teaspoon of honey) were filmed. In the video

Table 1: Categories of density of conspecifics (DOC) and density of male competitors (DOM) in experiment 3.
Tab. 1: Kategorien der Dichte von Artgenossen (DOC) und der Dichte von Männchen (DOM) in Versuch 3.

Registrated density	Category
1-2 individuals in a 225 cm² area	low density of conspecifics
2.5-3.5 individuals in a 225 cm² area	middle density of conspecifics
4-7 individuals in a 225 cm² area	high density of conspecifics
0-1 male conspecifics in a 225 cm² area	low density of male competitors
1.5-2.5 male conspecifics in a 225 cm² area	middle density of male competitors
3.0-4.5 male conspecifics in a 225 cm² area	high density of male competitors

analysis the courtship behaviour in dishes with food was compared to the control.

Experiment 3: In the natural habitat of *P. nobilitatus,* plots of 225 cm² were marked and filmed for 10 min. If possible, three courtships from each film, selected by chronological order, were analysed in detail. The number of males and females was registered at the beginning and at the end of each courtship sequence in order to calculate the density of conspecifics (DOC) and the density of male competitors (DOM) (tab. 1).

3. Results

Experiment 1: In the dishes without food 0.4±0.7 females and 0.8±1.2 males were registered 5 min after the exposure of the dishes in the natural habitat for one minute. In the dishes with food 1.4±0.8 females and 2.9±1.7 males were observed. For both sexes the number of conspecifics in dishes with food significantly surpassed the number of conspecifics without food (fig. 1).

Experiment 2: Following exposure of experimental dishes with food, in 7 of 10 cases a male fly settled on the dish before a female, but in 8 of 10 cases a female started feeding before a male did. Altogether 363 males including 85 territorial males, and 96 females were observed. Males that patrolled within the dish area were considered as territorial males. Territorial males frequently left dishes for fighting against intruders; during male-male-interactions the territorial male was likely to leave the area which was registered by the video, and possibly was registered as a new male if coming back to his territory. That is probably one of the reasons why the number of registered males surpasses that of females.

To test the influence of food on the courtship behaviour only courtships that were not disturbed by conspecifics were analysed, including 12 courtships in dishes without and 40 courtships in dishes with food. The total duration of courtships was significantly longer in dishes with food than in dishes without food (fig. 2). The total courtship had several components: Males in dishes with food took more time to position themselves opposite to the females, exhibited longer

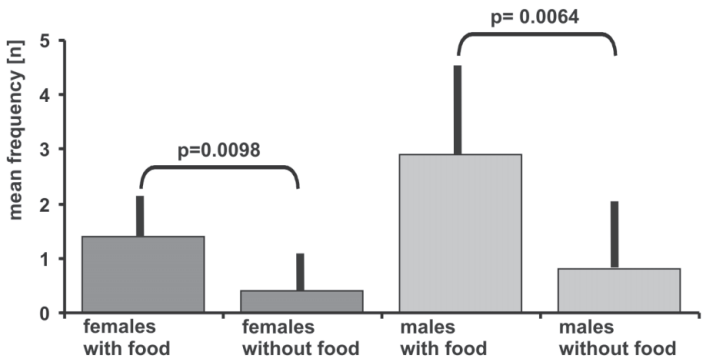

Fig. 1: Mean frequency of male and female *Poecilobothrus nobilitatus* in dishes with and without food in the 6th minute after exposition of dishes. The columns give the mean frequency of males and females out of ten trials; the bars indicate the positive standard deviation. Unpaired p-values are given according to the t-test with comparison of the indicated means.

Abb. 1: Mittlere Häufigkeit von Männchen und Weibchen von *Poecilobothrus nobilitatus* in Schalen mit und ohne Futter in der 6. Minute nach Exposition der Schalen. Die Säulen geben die mittlere Häufigkeit von Männchen und Weibchen aus zehn Versuchen an; die Balken geben die positive Standardabweichung an. Die angegebenen p-Werte wurden mit einem ungepaarten t-Test zum Vergleich der angegebenen Mittelwerte berechnet.

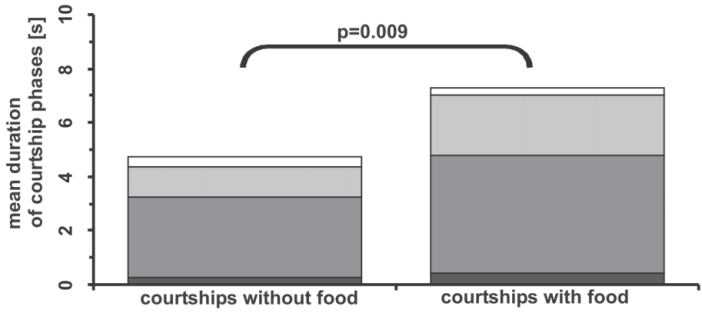

Fig. 2: Mean duration of courtship phases of *Poecilobothrus nobilitatus* males in areas with (n = 40) and without food (n = 12): positioning in front of female (black), wing-fanning display (dark grey), flight display (light grey), and copulation attempt (white). The duration of the four courtship phases are not significantly different in areas with and without food, the total courtship duration is (unpaired t-test).

Abb. 2: Mittlere Dauer der Balzphasen von *Poecilobothrus nobilitatus*-Männchen in Bereichen mit (n = 40) und ohne (n = 12) Futter: Positionierung gegenüber dem Weibchen (schwarz), Flügelpräsentation (dunkelgrau), Sprungflug (hellgrau) und Kopulationsversuch (weiß). Die Dauer der einzelnen Balzphasen unterscheidet sich nicht signifikant voneinander in Bereichen mit und ohne Nahrung, jedoch die Gesamtdauer der Balz (ungepaarter t-Test).

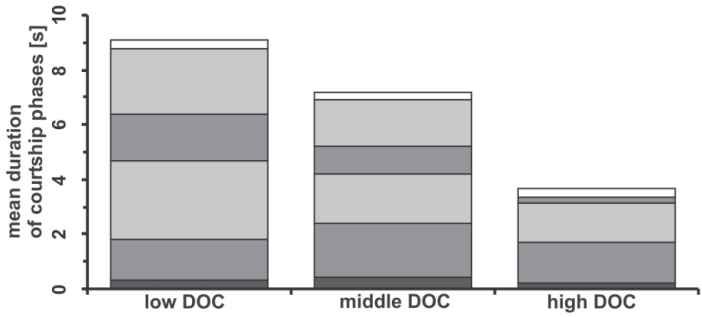

Fig. 3: Mean duration of courtship phases of *Poecilobothrus nobilitatus* males with low density of conspecifics (DOC) (n = 59), middle DOC (n = 51), and high DOC (n = 25); positioning in front of female (black), wing-fanning display (dark grey), flight display (light grey), and copulation attempt (white). Repetitions of courtship phases were not combined.

Abb. 3: Mittlere Dauer der Balzphasen von *Poecilobothrus nobilitatus*-Männchen in Bereichen geringer Dichte von Artgenossen (DOC) (n = 59), mittlerer DOC (n = 51) und hoher DOC (n = 25); Positionierung gegenüber dem Weibchen (schwarz), Flügelpräsentation (dunkelgrau), Sprungflug (hellgrau) und Kopulationsversuch (weiß). Wiederholungen von Balzphasen wurden nicht zusammengefasst.

wing-fanning display and longer flight display; however, the duration of these courtship phases dependent to the presence or absence of food differed not significantly.

Experiment 3: The total duration of courtships (n = 135) was longer when density, DOC or DOM (see tab. 1), was low (figs. 3 and 4). Particularly, the males exhibited a second flight display only rarely when density was high. Statistical analysis by linear regression was done with the raw data; we found a negative correlation between the total duration of courtship

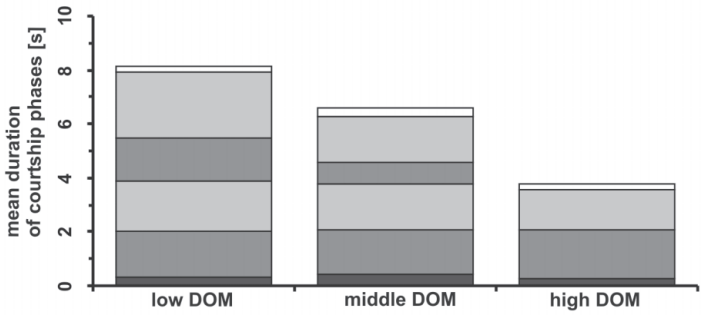

Fig. 4: Mean duration of courtship phases of *Poecilobothrus nobilitatus* males with low density of male competirors (DOM) (n = 59), middle DOM (n = 51), and high DOM (n = 25); positioning in front of female (black), wing-fanning display (dark grey), flight display (light grey), and copulation attempt (white). Repetitions of courtship phases were not combined.
Abb. 4: Mittlere Dauer der Balzphasen von *Poecilobothrus nobilitatus*-Männchen in Bereichen geringer Dichte von Männchen (DOM) (n = 59), mittlerer DOM (n = 51) und hoher DOM (n = 25); Positionierung gegenüber dem Weibchen (schwarz), Flügelschlagen (dunkelgrau), Flugbalz (hellgrau) und Kopulationsversuch (weiß). Wiederholungen von Balzphasen werden nicht zusammengefasst.

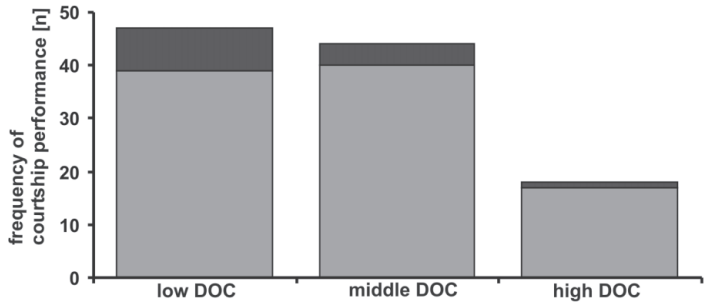

Fig. 5: Number of *Poecilobothrus nobilitatus* males that exhibited one courtship sequence including wing-fanning display and flight display (grey), or two courtship sequences (black) plotted against the density of conspecifics (DOC). Chi-square-test: df = 2, χ^2 = 2.194, p = 0.334, n = 109.
Abb. 5: Anzahl von *Poecilobothrus nobilitatus*-Männchen, die eine Balzsequenz (Flügelpräsentation und Sprungflug) zeigten (grau) oder zwei Balzsequenzen (schwarz) in Abhängigkeit von der Dichte der Artgenossen (DOC). Chiquadrattest: df = 2, χ^2 = 2,194, p = 0,334, n = 109.

and both DOC (R^2 = 0.042, p = 0.018) and DOM (R^2 = 0.061, p = 0.004).

Among 135 courtships analysed, 109 included at least one wing-fanning display or one flight display. Among these, more males exhibited only one wing-fanning display or flight display than two such displays (fig. 5), which was, however, not significantly dependent of DOC.

Altogether 135 courtship sequences of *P. nobilitatus* have been analysed from video data. Only a single copulation was observed. The remaining 134 courtship sequences were interrupted, either by the courted female (51 %), by a male competitor (43 %) or by the courting male (6 %). The interruption of courtship was dependent of DOC. Generally, the frequency of interruption of courtship increased with DOC. In areas with low density, females were more likely to interrupt the courtship, whereas in areas with middle and high density, male competitors were more likely to interrupt the courtship (fig. 6).

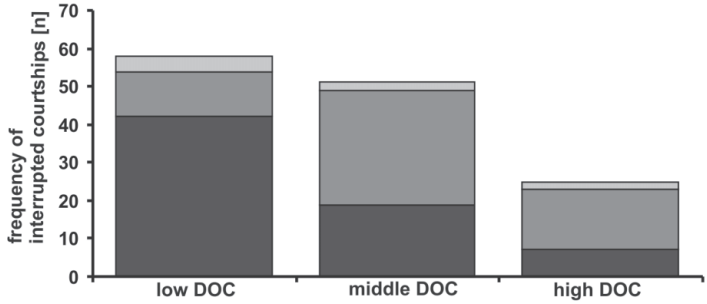

Fig. 6: Frequency of interrupted courtships by females (black), male competitors (dark grey), and courting males (light grey) plotted against the density of conspecifics (DOC), with n = 58 for low DOC, n = 51 for middle DOC, and n = 25 for high DOC. Chi-square-test: df = 4, χ^2 = 22.523, p = 0.0002, n = 134.

Abb. 6: Häufigkeit des Balzabbruchs durch Weibchen (schwarz), konkurrierende Männchen (dunkelgrau) und balzende Männchen (hellgrau) in Abhängigkeit von der Dichte der Artgenossen (DOC), mit n = 58 für geringe DOC, n = 51 für mittlere DOC und n = 25 für hohe DOC. Chiquadrattest: df = 4, χ^2 = 22,523, p = 0,0002, n = 134.

4. Discussion

The courtship of male *P. nobilitatus* is focussed on a single female. However, the presence of other males can strongly determine female choice enabling simultaneous choice instead of successive choice behaviour, and the presence of many females and males may stimulate mating activities as well as hamper courtship and mating due to time consuming male-male interactions. When the probability of meeting conspecifics of the opposite sex is low, the aggregation of both sexes at rendezvous sites facilitates encounters between males and females, e.g. many dipteran and hymenopteran males swarm above species-specific landmarks such as hilltops or single trees (Alcock 1998). Many insects combine feeding and mating activities, e.g. many oligolectic bees mate on the flowers of their pollen food-plants (Westrich 1990), tephritid gall-flies mate close to the oviposition sites of the females which are the larval food habitats (Zwölfer 1974). The dolichopodid fly *P. nobilitatus* is very common and frequently found in the direct vicinity of water in various numbers, i.e. single individuals, small or large groups. Feeding as well as mating behaviour can easily be observed. The relationship between food density, feeding and mating behaviour has not yet been studied, although it is obvious that many students of the courtship and mating behaviour of *P. nobilitatus* took advantage of the fact that sexes aggregate in large numbers at feeding sites (Lunau 1992; Land 1993a,b).

The trade-off between time for feeding and time for courtship seems to differ between males and females: most of the time males are engaged in male-male interactions and courtship, whereas females are feeding most of the time even if they are courted by males. Males defend small territories of about 100 cm^2 in size against male intruders and court females entering the territory (Lunau 1992). In a dense aggregation of *P. nobilitatus*, territorial males have 13 antagonistic interactions with other males per minute, initiate courtship displays 6 times per minute, and start feeding only less than once per minute on average, which is a new action every 4 seconds.

Both experiments in which the flies' behaviour in experimental areas with and without prey items was compared provide evidence that the flies aggregate in areas with food. In

areas with food, females were feeding on prey most of the time, which obviously had impact on the courtship duration of the males. This is probably related to females staying longer; thus, a male with a territory that is rich in prey has a prolonged chance to court a female. Courting males displayed longer when the courted female was feeding, and shorter when the courted female was not feeding. However, we were not able to show any relationship to mating success, because among hundreds of observed courtships only a single courtship ended up with a copulation. The analysis of the video data showed that there are three different causes for a premature end of courtship: (1) the courting male stops courting; (2) the courted female flies off; and (3) the courting male interacts with another male. Obviously, courtships are more frequently interrupted by male-male interactions when the density of individuals is increasing. In addition, females fly off rarely when feeding. No indication was found that females actively search in areas of high density of males for mating opportunities, and prefer low or high density of males for mating, mostly because the great majority of courtships do not end up with a copulation, and only a single copulation was observed. It is unknown whether females of *P. nobilitatus* mate several times or only once.

It remains thus an unanswered question why males of *P. nobilitatus* engage in such complex courtship behaviour. There is good evidence that male size plays a role in female choice, and in the outcome of male-male interactions (LUNAU 1992). Most likely males demonstrate size by wingspread during the wing-fanning display. The way how males carefully position themselves in a distinct distance exactly in a head-to-head position in front of the female before starting courtship indicates the male's position during the wing-fanning display is decisive for how optimal the wingspread is presented. It is not known whether the male's flight display also determines female choice. Body size including wingspread in holometabolous insects is fixed when the imagines harden following hatching from the pupa. Size is an index of larval growth and does not change during imaginal life, i.e. size is not an index of bad or good condition. Distinct features of a flight display are likely dependent of actual condition and indices of nutrition and parasitism.

In many species of the Dolichopodidae the males display very similar apical black-and-white signalling structures which in some cases are born on different organs such as wings, antennae, forelegs, middle legs, hind legs, cerci, and specific protuberances (LUNAU 1996). The key feature explaining both homogeneity of signals and convergence of signalling organs likely is an original innate female preference. From a female's perspective, the male's wing size is not easy to determine due to the rapid movement of the wings during flight courtship (ZIMMER et al. 2003). The amount of wing movement is largest on the tip of the wings which will appear bright as opposed to the base of the wings which will appear dark. White wing tips and subapial dark areas thus amplify the wing signal. Additional similar signals from other organs spread like the wings may further amplify the signal. In this interpretation the black-and-white signalling structures on the wings are amplifications of natural signals, the black-and-white signalling structures on other organs are automimetical signal copies (LUNAU 2002), and the females' use of these black-and-white signals for the estimation of male size is caused by an ancestral preferential behaviour.

DARWIN (1871) first recognised that many conspicuous signalling traits that males use in courtship display probably confer a survival disadvantage to those males that bear them. Therefore, explaining the existence of these traits poses a difficult problem. DARWIN proposed a solution with the theory of sexual selection. If males that exhibit these conspicuous traits are more successful in obtaining a mate, then these traits might evolve

through what he termed sexual selection in spite of the fact that they result in a survival disadvantage. DARWIN claimed an aesthetic sense of females as an explanation for the existence of many conspicuous male traits.

It may be interesting to interpret the conspicuous traits of so many male dolichopodid flies such as the black and/or white coloured, exaggerated morphological characters, and complex display behaviours in the light of modern theories of sexual selection and female choice (DAY 2000; SMITH & HARPER 2003): FISHER's runaway process (FISHER 1958) postulates that a positive genetic correlation between the females' preference and the males' traits. The runaway process requires an initial female preference for a male's trait. As a consequence, females choosing conspicuous males are incidentally also choosing males that carry genes for the female preference. The handicap theory of ZAHAVI (1975) assumes that certain exaggerated male structures and conspicuous forms of male behaviour have evolved because they apparently act to reduce the chances of individual survival of the animal exhibiting the behaviour. He argued that females which select males with the strongest handicaps can be sure that they have selected from among those males which have successfully passed a survival test largely dependent on good genes for survival. The indicator hypothesis (SMITH & HARPER 2003) claims that female preferences evolve to exploit the condition-dependence or 'indicator value' of male traits, which in turn may cause these traits to evolve to elaborate extremes. Condition of males is determined by resistance against parasites, uptake and utilisation of food, and many other parameters.

These theories of female choice are not mutually exclusive. Nothing is known about how these theories can explain the courtship and mating behaviour in Dolichopodidae. The genetic linkage between genes determining male traits and female preference for these traits postulated by FISHER's model is unknown. The handicap associated with the possession of male traits for male survival or courtship could be related to the predation risk caused by the conspicuousness of male traits, and to the flight performance caused by larger wing load of large-winged individuals. The indication hypothesis is plausible, because wingspread is a good indicator of larval growth and flight display is a good indicator of actual condition both of which are parameters known to play a role in female choice.

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