Developmental stability and predation success in an insect predator–prey system

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I investigated the relationships among developmental stability (as measured by individual bilateral asymmetry values), two measures of locomotory performance and predation success in an insect predator–prey system. In this system yellow dungflies *Scathophaga stercoraria* preyed upon houseflies *Musca domestica* in laboratory-controlled conditions. There was no relationship between locomotion and absolute asymmetry or mean size of two morphological traits (fourth longitudinal wing vein, foreleg tibia) in either species. Analysis of single predation trials indicated that locomotion performance and trait size are not associated with the probability of predation. However, *Musca* that were captured had tibia that were more asymmetric than *Musca* that survived. Similarly, *Scathophaga* that were successful predators had more symmetric forelegs than unsuccessful predators. There was no relationship between predation and wing vein asymmetry, which may indicate the importance of terrestrial-based predatory avoidance tactics in this system. There were no relationships between morphology or locomotion with predation latency, prey handling times, or the number of times a prey "escaped" from a predator. The mechanisms behind the relationship between tibia asymmetry and predation success are discussed. This is the first experiment to reveal direct evidence for selection for symmetric, developmentally stable individuals through differential predation. *Key words:* developmental stability, dungfly, fluctuating asymmetry, housefly, *Musca*, predation, *Scatophaga*. *[Behav Ecol 8:433–436 (1997)]*

Minor deviations from left–right symmetry in bilateral traits (fluctuating asymmetry; Ludwig, 1932) are a reliable indicator of developmental instability (e.g., Beardmore, 1960; Van Valen, 1962; Waddington, 1960). Low levels of asymmetry have been associated with some indicators of high individual fitness (reviews in Møller and Pomiankowski, 1993; Møller and Swaddle, 1997; Watson and Thornhill, 1994), and low asymmetry can be directly selected for through mate-choice processes (Bennett et al., 1996; Møller, 1992, 1993; Swaddle, 1996; Swaddle and Cuthill, 1994a, 1994b). Investigations into direct selection for low asymmetry (i.e., developmental stability) through other selection processes have been limited (review in Møller and Swaddle, 1997). One such mechanism could be differential rates of predation and predatory success in symmetric and asymmetric individuals. Møller (1996) has demonstrated that houseflies *Musca domestica* captured by an aerial predator, barn swallows *Hirundo rustica*, have wings and tibia that are more asymmetric than a random sample of flies from the same location. Similarly, barn swallows captured by European sparrowhawks *Accipiter nisus* were found to be more asymmetric in their tail length than a live field sample (Møller AP, Nielsen JT, unpublished data). It is possible that in both of these examples, trait asymmetry could directly impair locomotory performance and hence increase the probability of predation (cf. Swaddle et al., 1996). It is therefore interesting that Moodie and Reimchen (1976) reported greater lateral plate asymmetry, which will have no direct effect on locomotor performance, in a population of three-spined sticklebacks *Gasterosteus aculeatus* from lakes without predators than in those with predatory fish (although it is possible that there may be other differences between the two classes of lakes in this study).

The experiment reported here investigated the relationship between developmental stability and predation success in an insect predator–prey system. Yellow dungflies *Scathophaga ster-*

coraria are obligate blood-sucking carnivores that are known to prey on many insect species in the wild, including houseflies *Musca domestica* (Hammer, 1942). In laboratory predation trials, male *Scathophaga* are particularly active and appear to preferentially prey on larger insect species (*M. domestica*, *Delia antiqua*) than on smaller flies (*Drosophila* spp.) (Failes et al., 1992). Therefore, *M. domestica*, and in particular the larger female houseflies, are suitable and ecologically relevant prey items for such a predator. Both species are readily maintained in laboratory colonies and hence are ideal for studying predation under controlled experimental conditions (e.g., Failes et al., 1992). This system also has advantages in that *Scathophaga* prey upon *Musca* by seizing the prey in their forelegs, and, following a struggle during which the prey attempts to escape, the *Scathophaga* inserts its proboscis into the thorax of the *Musca* through the skin between the head and thorax without damaging the leg and wing morphology (Hammer, 1942, and references therein). Therefore, it is possible to accurately quantify most of the external morphology of the prey after predation has occurred. Additionally, the developmental stability of both predator and prey can be assessed within a single experimental design. This is the first study to investigate the importance of asymmetry in both predator and prey in any system.

Because high asymmetry indicates developmental instability, I hypothesized that asymmetric prey (*Musca*) are more likely to be preyed upon than their symmetric counterparts. Similarly, *Scathophaga* that are relatively more symmetric may be more successful predators than asymmetric *Scathophaga*.

METHODS

Housing conditions

Outcrossed populations of *Musca domestica* and *Scathophaga stercoraria* were maintained in laboratory cages (approximately 0.4 × 0.3 × 0.3 m) on a constant 10 h:14 h light:dark photoperiod at 22°C with ad libitum food (mixture of skimmed milk powder, powdered egg, and icing sugar) and water. The *Scathophaga* were provided with fresh cow dung

(as this is known to increase predatory behavior in captive populations; Failes et al., 1992) and also fed live *Musca* prey items. All the *Scathophaga* were observed to prey upon *Musca* before the experiment began. From these housing colonies, I randomly selected 26 female *Musca* and 26 male *Scathophaga* for the experiment. All flies used in the experiment were approximately 8–11 days old.

Locomotion trials

Two measures of locomotion were quantified for all flies (N = 26 for both species). (1) Tube time: the time taken (to 0.01 s accuracy) for a fly to climb the inside of a glass measuring cylinder (diam = 17 mm, height = 152 mm). (2) Catch time: the time taken (to 0.01 s accuracy) for the experimenter to catch, by hand, a single fly released into a cage (0.25 × 0.25 × 0.25 m) in a small glass vile. Two different-sized vials were used to catch *Musca* and *Scathophaga* (*Musca* vial diam = 8 mm; *Scathophaga* vial diam = 18 mm). The experimenter practiced the catching procedure before quantifying this measure in the experimental flies so that experimenter's performance had reached an asymptote. All measures were taken blind of asymmetry and size values. Both tube and catch times were repeated five times for each fly and were shown to be repeatable (intraclass correlation coefficient, r_I > .717, p < .046, in all cases). I used the two measures of locomotion because they may reflect different modes of locomotion. The tube time involved terrestrial locomotion, whereas catch time relied mainly on aerial locomotion. The two measures were not correlated (*Musca*, Pearson r = .101, p = .609; *Scathophaga*, r = −.199, p = .310).

Predation trials

Before predation trials, all *Scathophaga* were deprived of live prey for 24 h. I randomly allocated the experimental flies to mixed-species pairs (N = 26 pairs of one *Musca* and one *Scathophaga*). These pairs were put, in turn, under an inverted, transparent beaker (diam = 103 mm, height = 123 mm), and their behavior was recorded on Hi-8 videotape with a video camera (Sony CCD-FX700E) at a shutter speed of 1/4000 s and at a distance of 0.3 m. Hence there were 26 separate predation trials. Each trial lasted for 1 h or until the *Scathophaga* had successfully captured the *Musca*. I analyzed videotapes using frame-by-frame playback on a Sony EV-2000E video player to derive measures (to 0.04 s accuracy) of predation latency (time in trial to successful predation event) and prey handling time (time from when *Scathophaga* first made contact with *Musca* until the *Musca* stopped struggling to escape). These videotapes also revealed occurrences where the *Musca* successfully escaped from an attempted *Scathophaga* predation event; these were termed "escapes."

Size and asymmetry measurements

After each trial, both flies were sacrificed by freezing and were measured using a binocular microscope with a drawing tube attachment. The distance along the fourth longitudinal wing vein from the anterior cross vein to the posterior cross vein and foreleg tibia size were measured on both left and right sides of all flies (N = 26 for both species) to 0.01 mm accuracy. All measurements were repeated, in pairs of left and right measures, five times over a period of 2 days. Absolute asymmetry (L − R) and trait size [(L + R)/2] were derived from the averages of the five asymmetry and five size measures for each individual to minimize measurement error (Palmer, 1994; Swaddle et al., 1994). All asymmetry measures were highly repeatable ($F_{25, 200}$ > 22.91, p < .00001, in all cases; see

Swaddle et al., 1994). Signed asymmetry values exhibited a normal distribution (Anderson-Darling normality test, a^2 < 0.63, p > .07, in all cases) around a mean of zero (one-sample t test, t < 1.52, p > .14, in all cases) and hence exhibited the statistical properties of fluctuating asymmetry (Palmer, 1994; Swaddle et al., 1994). Unsigned asymmetry values are given as means (±SE): *Musca*, tibia = 0.0337 ± 0.0043 mm, wing vein = 0.0182 ± 0.0029 mm; *Scathophaga*, tibia = 0.0347 ± 0.0046 mm; wing vein = 0.0301 ± 0.0048 mm. Trait size and asymmetry were not correlated (*Musca* tibia, Spearman rank r_s = −.074, wing vein r_s = −.177; *Scathophaga* tibia r_s = .327, wing vein r_s = .369); neither were levels of asymmetry between traits on the same individuals (*Musca* r_s = .203; *Scathophaga* r_s = .178).

All analyses were performed on Minitab for Windows (Minitab Inc., 1994) using two-tailed tests of probability. All asymmetry values were Box-Cox transformed to leave residuals of all analyses normally distributed (Swaddle et al., 1994).

RESULTS

### Predation, locomotion, and morphology

There were no significant relationships between the locomotion variables and either trait size or asymmetry in both species (locomotion and trait size, N = 26, Pearson −.463 < r < .385, p > .05, in all cases; locomotion and trait asymmetry, N = 26, Spearman rank r_s −.273 < r < .359, p > .05 in all cases).

Successful predation occurred in 17 of the 26 1-h trials. The morphology measures and locomotory performance variables of flies from trials in which predation occurred (predate) were compared with flies from trials in which predation did not occur (survive). The two locomotion variables did not appear to differ among flies from successful and unsuccessful trials in either species (*Musca*: tube time, $F_{1,24}$ = 0.24, p = .630; catch time, $F_{1,24}$ = 0.16, p = .689; *Scathophaga*: tube time, $F_{1,24}$ = 0.02, p = .899; catch time, $F_{1,24}$ = 1.21, p = .282). Similarly, wing vein and foreleg tibia size did not differ between flies from trials in which predation occurred or when predation did not occur in either species (*Musca*: wing vein size, $F_{1,24}$ = 0.45, p = .507; tibia size, $F_{1,24}$ = 0.84, p = .368; *Scathophaga*: wing vein size, $F_{1,24}$ = 0.32, p = .579; tibia size, $F_{1,24}$ = 2.83, p = .105). Wing asymmetry was also not related to whether predation occurred in either species (Figure 1a). However, *Musca* that were captured had tibia that were more asymmetric than those that survived; additionally, *Scathophaga* that were successful predators possessed tibia that were more symmetric (Figure 1B).

Within successful predation trials, there were no associations among locomotion variables, trait size, and trait asymmetry with latency to predation, prey handling time, or number of escapes performed by prey (locomotion variables, −.274 < r < .116, p > .251; trait size, −.313 < r < .166, p > .192; trait asymmetry, −.432 < r_s < .130, p > .0647; N = 17 in all cases).

DISCUSSION

It is clear from the results that there are no associations between the locomotion variables and trait size with predatory success. However, there is a relationship between tibia asymmetry and predation. *Musca* that were captured were more asymmetric than those that survived; similarly, *Scathophaga* that were successful predators were more symmetric than unsuccessful individuals. From both the predator's and prey's perspective, increased asymmetry was related to poor predatory performance. Although developmental stability was associated with the occurrence of predation within trials, the

a

b
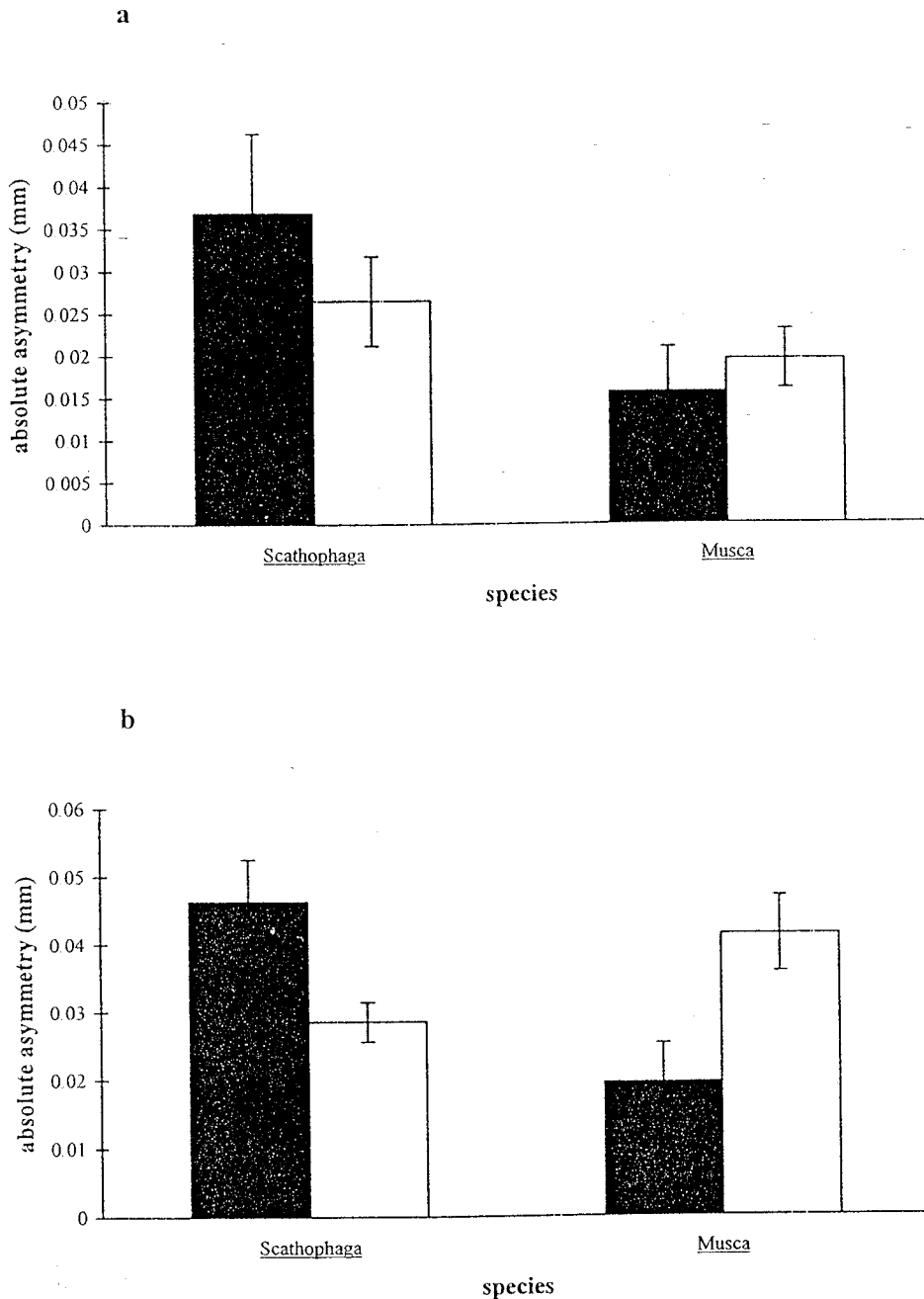
Figure 1
Means (±SEs) of (a) wing vein absolute asymmetry (mm) and (b) foreleg tibia absolute asymmetry (mm) for flies from trials in which predation occurred (predated, open bars) or did not occur (survived, filled bars). There was no difference in wing asymmetry between predated flies or flies that survived (Musca: $F_{1,24}$ = 0.79, p = .382; Scathophaga: $F_{1,24}$ = 1.23, p = .278). Musca that were captured had tibia that were more asymmetric than those that survived ($F_{1,24}$ = 6.58, p = .017). Similarly, Scathophaga that were successful predators had tibia that were more symmetric ($F_{1,24}$ = 5.22, p = .031).

latency to predation, prey handling time, and the number of times prey escaped from the predator were not related to morphology or locomotion. This may have been related to the smaller sample size for this subgroup (N = 17). Nevertheless, this study reveals that asymmetric prey are more likely to be preyed upon and symmetric predators have a greater probability of capturing a prey item successfully (Figure 1B). Noticeably, this relationship only occurs for tibia and not for wing veins (Figure 1A). This may be because the predatory tactics of the Scathophaga (i.e., grasping the prey in its forelegs) result in the developmental stability of foreleg elements being more important in determining predation success than stability of wing elements. Likewise, the ability of Musca to avoid predation may also be more dependent on the stability of leg elements, as both species spent a large proportion of time within predation trials crawling on the surface of the beaker. In the wild, Scathophaga show similar predatory tactics by

preying upon flies crawling on the surface of dung pats and the surrounding vegetation (Hammer, 1942). It is possible that the ability of Musca to take off quickly and in a direction away from the predator may be more related to leg structures than to wing structures.

The relationships between asymmetry and predation could occur through direct effects of asymmetric morphology influencing performance or, alternatively, developmental instability may reflect an individual with low phenotypic (and perhaps genotypic) quality. Morphological asymmetry has been shown to directly impair locomotion parameters related to predatory avoidance in European starlings, Sturnus vulgaris (Swaddle et al., 1996). Although asymmetry was not correlated with the two forms of locomotory ability measured here, this does not necessarily exclude the possibility that asymmetry could still directly affect locomotor performance (cf. Thomas, 1993).

It is also possible that individual asymmetry reliably reveals

an individual of poor genetic constitution, as a number of genetic factors are known to increase asymmetry (reviews in Møller and Pomiankowski, 1993; Møller and Swaddle, 1997; Parsons, 1992; Watson and Thornhill, 1994). Additionally, asymmetry may indicate that an individual has been exposed to suboptimal environmental conditions during development (reviews in Møller and Swaddle, 1997; Parsons, 1992). Therefore, asymmetric individuals may be more likely to suffer from predation. In this experiment, all the flies were maintained in homogenous housing conditions; therefore any differences in expression of asymmetry are more explainable by intrinsic genetic differences among individuals than by different environmental experiences during development.

It has previously been reported that predation risk could impose physiological stress on an organism, which may result in greater levels of asymmetry. Witter and Lee (1995) demonstrated that starlings molting in aviaries without access to protective cover and whose food was placed a greater distance from this cover grew primary feathers that were more asymmetric than birds who did not have to compromise predation risk in order to obtain food. It would appear that an increase in predation risk, associated with leaving protective cover for longer, can impose some form of stress on an individual that leads to developmental instability and hence an asymmetric phenotype. This situation could not have occurred in the context of this particular experiment, but it is important to consider the possible mechanisms by which a relationship between predation and developmental stability could arise in other biological systems.

To explore the mechanisms by which the relationship between asymmetry and predation success have occurred in the fly, it will be necessary to perform experiments in which the morphology of the flies are manipulated independent of their "true" developmental stability (cf. Swaddle et al., 1996). This will reveal whether phenotypic asymmetry can directly influence both the success of the predator and the susceptibility of the prey to predation. These experiments are currently in progress. It will also be interesting to manipulate asymmetry and developmental stability in a factorial design to indicate the relative indirect influences of intrinsic processes related to developmental stability and the mechanical performance differences of levels of asymmetry.

This study provides the first experimental evidence that low levels of individual asymmetry can be selected for through differential rates of predation and differential predatory success. On both accounts, asymmetric individuals are at a disadvantage, and hence there will be selection pressures in favor of individuals with stable developmental pathways. This further indicates the importance of developmental stability and fluctuating asymmetry in biological systems.

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