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Flight initiation distance in dragonflies is species-specific, positively related to starting distance and sometimes body length

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Predator escape behaviour is a critical component of dragonfly life history. Flight initiation distance is the distance at which escape commences, and is well studied in vertebrates, barely studied in invertebrates, and entirely unstudied in dragonflies. Here we test four principles regarding flight initiation distance as derived from studies of vertebrates to examine if they apply to dragonflies in Sri Lanka: (1) flight initiation distance is a species-specific trait; (2) flight initiation distance increases with starting distance (the distance at which the experimenter begins an approach); (3) larger individuals have longer flight initiation distances; and (4) flight initiation distance varies between the sexes in some species. We collected 105 flight initiation distances from 11 species (known sex and size). Flight initiation distances varied between species and positively with starting distance. In one of three data-rich species ($n \geq 10$), flight initiation distance was positively associated with body length. Flight initiation distance did not vary with sex in our sample. Escape responses evoked by standardised human approaches represent a fruitful methodology to study dragonfly escape behaviour in the wild.

Keywords: escape; FID; optimal escape theory; predators; Odonata; dragonfly

Introduction

Animals monitor and assess predator risk, balancing the cost of leaving a particular patch with the costs of staying (Cooper & Blumstein, 2015). A commonly used index of escape propensity is flight initiation distance (FID), the distance at which an animal initiates escape during a standardised human approach (Cooper & Blumstein, 2015). However, few FIDs have been published on invertebrates (exceptions include one crab and 17 butterfly species; Blumstein, 2010; Harbour et al., 2019), and to the best of our knowledge, none have been published on dragonflies (Bateman & Fleming, 2015).

The widespread collection and analysis of vertebrate FIDs has led to a series of 'principles' of escape ecology which are thought to apply broadly. Four prominent principles are:

(1) That FID is a species-specific trait, i.e. FIDs vary between species because of species-specific predator risk profiles and antipredator adaptations and capacities;

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(2) With a few exceptions, that starting distance (StaDist; the distance at which an approach commences), is positively related to FID. The causes and implications of this effect remain unclear, but this widespread effect appears to be a methodological artefact;

(3) That larger species/individuals have longer FIDs, either because of their antipredator capacity (sensory and escape abilities) or because they are preferentially targeted by predators; and

(4) That sometimes the sexes may differ in FID, because of sexual dimorphism or dichromatism, or different lifetime reproductive fitness which influences risk-taking (Blumstein, 2003, 2006; Cooper & Blumstein, 2015; Guay et al., 2018; Tätte, Møller & Mänd, 2018; Weston, McLeod, Blumstein & Guay, 2012).

There is a need to expand the taxonomic breadth of FID studies, to understand whether these principles are universal, or widespread, among major life forms (Blumstein, 2010; Harbour et al., 2019). We collected FIDs on dragonflies in Sri Lanka and analyse this dataset to test whether the general principles elucidated above apply to dragonflies. Thus, this is an exploratory effort, aimed at examining variation in FIDs among and within dragonfly species. We use a staged analysis approach:

- Firstly, we examine whether FID differs between species, sex and size, once StaDist is controlled via its inclusion as a covariate. We do this for all species for which we achieved replication, and for a data-rich subset of species which enabled more statistically powerful analysis.
- Secondly, given that sex and size vary within species, we analyse data-rich species in separate single-species models to examine the influence of sex and size on FID, again controlling for StaDist.

While we aim to examine whether any of the four prominent principles of FID apply to dragonflies, we note that one principle we examine is predominately related to a methodological artefact (StaDist; conceptually under the control of the experimenter not the dragonfly). So, we include this as a covariate in all our models, but not in interaction terms which include those factors which represent attributes of the responder (species, sex and size).

Materials and methods

We sampled dragonflies across an extensive area of Central Province, Sri Lanka, including roadside verges, traditional agricultural areas, lake shores and grasslands (see Harbour et al., 2019). We often observed predators of dragonflies, e.g. Bee-eaters (Meropidae) and Drongos (Dicruridae), active in the study area and consuming dragonflies. Sampling occurred during daylight hours between November and December 2018. We selected dragonflies that were resting near foraging areas, and on or near the ground, and avoided dragonflies which were mate-carrying (see Almbro & Kullberg, 2008). Air temperatures were an almost constant 29–31°C (temperature could influence capacity to escape; Bateman & Fleming, 2015) and we avoided data collection in rain or wind. We also avoided shadowing focal animals as we approached. Flight was readily discernible, and distances were measured with a tape measure (in cm). A marker was used to indicate the start of the approach, and StaDist was measured after flight using a tape measure. StaDist was defined by an observer standing still for at least 30 seconds, in an area where dragonflies were active, and selecting a focal animal (the closest, settled dragonfly), then commencing the approach. Approaches involved a single person wearing dull clothing, with no other people nearby. Multiple observers were carefully trained in consistency of measurements, an approach shown to be reliable in other animals (Guay et al., 2013; van Dongen, McLeod,

Mulder, Weston, & Guay, 2015). We avoided resampling individuals (at the same location we tracked individuals such that we sampled them only if we could be assured they were not already sampled), and visited numerous sites, not resampling the same species at the same locality if we revisited. Sites were > 200 m apart. These procedures are used for more mobile taxa to minimise the risk of pseudoreplication (Weston et al., 2012).

Species and sex were identified (using Sumanapala, 2017), aided by images which were taken from a distance using a digital SLR. After flight occurred, the individual was tracked, captured, and measured when possible before release. When we could not recapture the individual (49.2% of occasions), we estimated body length from these images. Size was estimated from images by measuring aspects of its perch to scale the image. In 51 cases, we inferred size and compared this with actual size. Estimations were highly accurate ($r_{Pearson} = 1.0$, $p < 0.001$).

Data were analysed using general linear models (GLMs) using standard techniques, and were analysed on SPSS Ver. 25. All standard assumption testing was performed; data were normally distributed, as were residuals. We first analyse between species, to examine if species differ in FID and with respect to the influence of sex and size, while controlling for StaDist. We run GLMs on FIDs, with predictors of species and sex and covariates of size and StaDist (firstly for the full dataset where n > 1 and secondly for species where n ≥ 10). Two two-way interactions involving species were of particular interest, between: (1) species and sex (sexes may respond differently among species), and (2) species and size (any size effects may occur differently among species). We omitted interactions involving StaDist as StaDist is largely a human artefact; instead StaDist is included as a covariate in these analyses as it usually is in FID analyses (e.g. Weston et al., 2012). We acknowledge a degree of unbalance in this analysis, unavoidable due to differential sampling between species likely reflecting different abundances, and this is why we run these analyses for data-rich species separately. The effects of sex and size may be evident within as well as between species, so we selected species where n ≥ 10 (relatively data rich, enabling more powerful analyses), and for each ran a GLM as above but without sex as a factor because it was not significant in any model. For these species, we also tested for sexual size dimorphism (see Johansson & Stoks, 2005) which could have confounded our comparisons of sex and size. Summary statistics are presented as means ± SE.

Results

We collected 105 FIDs from 11 species (four of these species were sampled only once and are excluded from further analyses; see Figure 1), for which we could identify species, sex and measure or estimate size. For 10 approaches (9.5%), individuals flew when the investigator brushed against them (FID = 0 cm; 9 species); they otherwise took flight earlier. Overall, StaDist was 201.3 ± 7.2 cm and FID was 71.6 ± 5.1 cm. A GLM was run with FID as the response variable, StaDist and body size as covariates, and species and sex as fixed factors, plus two-way interactions between species, size and sex ($R^2 = 0.65$). This revealed significant effects of species ($F_{6,80} = 3.3$, $p = 0.006$) and StaDist ($F_{1,80} = 41.5$, $p < 0.001$) and an interaction between species and body size ($F_{5,80} = 4.4$, $p = 0.001$); all other terms were not significant. A GLM ($R^2 = 0.42$) with three data-rich species (n ≥ 10) revealed significant effects of StaDist ($F_{1,77} = 26.8$, $p < 0.001$) and size ($F_{1,77} = 7.2$, $p < 0.009$) and an interaction between species and body size ($F_{2,77} = 4.1$, $p < 0.020$).

Given that species featured as a significant effect in interaction terms, separate GLMs therefore explored within-species variation (for three species where n ≥ 10) of FID against StaDist and size. These revealed that StaDist was always positively related to FID, and also that for one species, body length was positively associated with FID (Table 1; Figure 2).
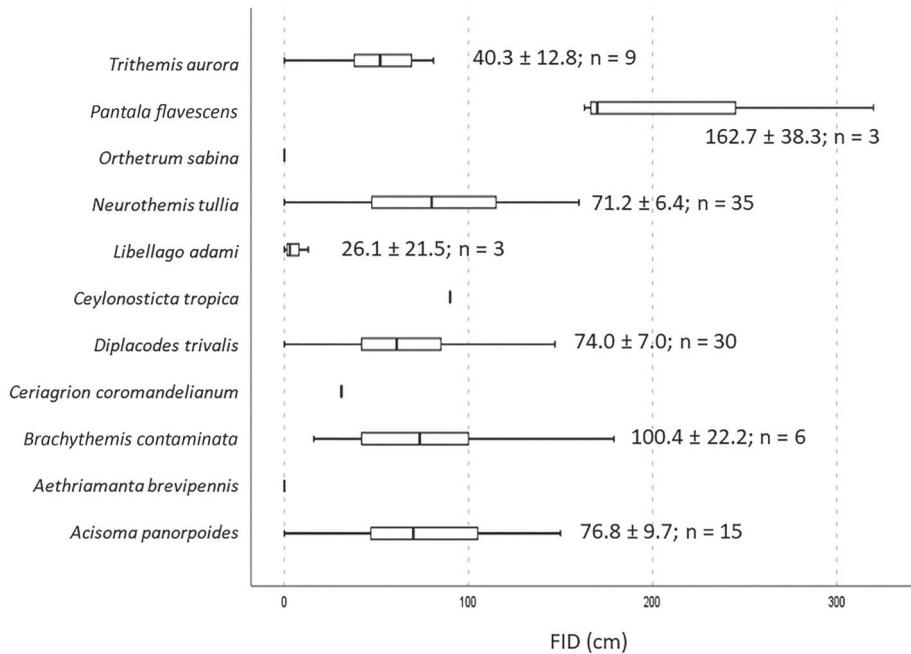
Figure 1. Flight initiation distance (FID; cm) of dragonfly species in Sri Lanka. For species with replication, model-predicted mean and standard errors and sample sizes are also provided. Predicted values are from a GLM with StaDist and size as covariates (at 203.80 cm and 1.74 cm, respectively). Species where n = 1 are depicted with lines.

Table 1. Separate single-species General Linear Models exploring: 1) flight-initiation distance within dragonfly species, in relation to starting distance, sex and body length and 2) tests demonstrating sexual size monomorphism and 3) niche. Parameter estimates are provided (mean ± SE) for significant effects (emboldened).

Analysis	Variable	*Acisoma panorpoides* ($R^2 = 0.29$)	*Diplacodes trivalis* ($R^2 = 0.57$)	*Neurothemis tullia* ($R^2 = 0.34$)
FID	StaDist (cm)	$F_{1,16} = 6.3$, ***p = 0.023***, ß = 0.558 ± 0.222	$F_{1,27} = 15.6$, ***p = 0.001***, ß = 0.326 ± 0.083	$F_{1,37} = 17.3$, ***p < 0.001***, ß = 0.289 ± 0.069
	Body length (cm)	$F_{1,16} = 0.1$, $p = 0.770$	$F_{1,27} = 14.0$, ***p = 0.001***, ß = 91.178 ± 24.343	$F_{1,37} = 2.5$, $p = 0.119$
Sexual size dimorphism	Body length (cm)	T = 0.8, df = 7.2, $p = 0.425$	T = 0.1, df = 27.4, $p = 0.951$	T = -0.2, df = 31.9, $p = 0.835$
Niche		Marshy, swampy habitats (Mens, Schuette, Stokvis, & Dijkstra, 2016)	Generalist, including human-dominated environments (Fraser, 1924)	Modified and natural wetlands (Fraser, 1924)

Discussion

Bateman and Fleming (2015) caution against over-interpreting results of FID studies from invertebrates, pointing out physiological and/or sensory capabilities may drive observed patterns. For dragonflies, FID appears to be a species-specific trait (in the model including seven species), as has been shown for vertebrates (Cooper & Blumstein, 2015) and butterflies (Harbour et al., 2018). This may reflect species differences in predator risk profiles, escape capabilities, visual acuity, life histories, and functional traits (Bateman & Fleming, 2015). Some unbalance was
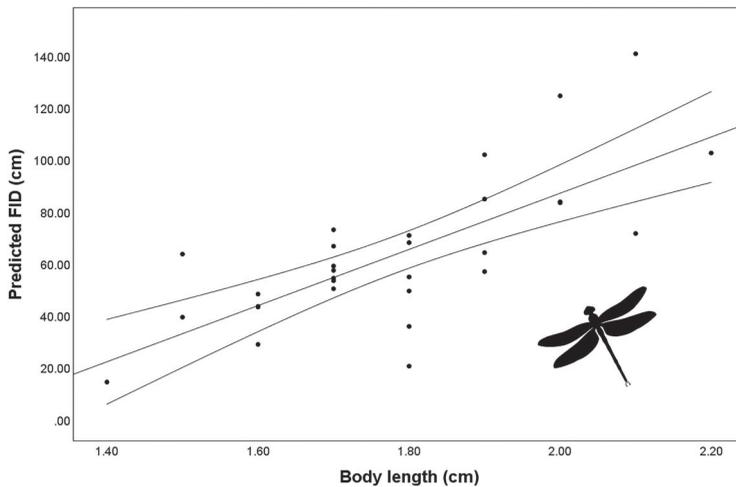
Figure 2.   The relationship between model-predicted flight initiation distance and body length in *Diplacodes trivialis*. Line of best fit and 95% confidence intervals (linear regression) also shown. Predicted values are from a GLM (Table 1) with StaDist and size as covariates (at 170.07 cm and 1.78 cm, respectively).

evident in the dataset used, so additional analyses on a broader array of well-sampled species would be a useful future endeavour.

StaDist was positively related to FID both across and within species. While the mechanisms underlying this relationship are unclear, it may result from perceptive capacities, costs of vigilance, or the inability to judge distance and the use of persistence of approach to judge risk. Alternatively, it could be a result of methods, such as a mathematical artefact (StaDist must exceed FID) or an association of longer StaDists with the heightened probability of non-escape flight, which is nevertheless interpreted as escape (see Harbour et al., 2019). For invertebrates, this relationship has been documented for one species of crab (Blumstein, 2010) and for butterflies (Harbour et al., 2019). The finding that it also occurs in dragonflies strengthens the idea that the effect might be a general rule of animal escape (Blumstein, 2010), which may need to be considered (standardised experimentally or statistically) in studies of dragonfly escape behaviour that rely on an approaching stimulus to elicit a response (Harbour et al., 2019). A deeper understanding of specific escape-ecology and physiological and sensory capacity of dragonflies is required to understand the mechanisms underpinning this relationship (Bateman & Fleming, 2015).

Larger animals (usually vertebrates indexed by body mass) are generally associated with longer FIDs (Cooper & Blumstein, 2015). This study reported no such relationship between species (though body length varied modestly between species) but we describe one (of three) species within which longer individuals exhibited longer FIDs. Several possibilities may explain this. Larger individuals may have larger eyes, and so able to detect threats at longer distances (Bateman & Fleming, 2015). Physiological constraints may manifest themselves differently for different-sized individuals (Bateman & Fleming, 2015). They may be preferentially preyed upon, slower to take off and manoeuvre, or more easily tracked by predators (Bateman & Fleming, 2015). Larger individuals may have accumulated oxidative stress associated with chronic predator stress, or wing damage, and thus experience reduced escape capacity (Combes, Crall, & Mukherjee, 2010; Janssens & Stoks, 2014), and so might tend to initiate escape earlier. Further study of a broader range of taxa is required to establish how widespread this relationship is, and to explore any correlations with life history and functional traits. The result we describe indicates that variation in FID can, at least sometimes, occur within (as well as between) populations

of invertebrate species (most variation is expected between populations; Bateman & Fleming, 2015).

Sexual colour dimorphism is common among dragonflies, and the sexes likely experience different lifetime fitness throughout their lives, which is expected to influence escape decisions (Cooper & Blumstein, 2015). We found no effect of sex on FID, either between or within species (our within-species comparisons involved sexually size monomorphic species). Studies of vertebrate FIDs report that linkages between colour and FID are not universal (Guay et al., 2018). Again, a broader taxonomic study is required, as is an understanding of the sensory ecology of predators in the associated ecosystems.

Dragonfly predator escape behaviour is complex, nuanced, and flexible between, and evidently also sometimes within, populations/species (Hopper, 2001; Mikolajewski et al., 2010; this study). We have demonstrated that standard FID protocols are likely to be useful in the study of dragonfly escape behaviour, and could underpin broad taxonomic comparative analyses exploring the evolution of escape among invertebrates.

Acknowledgements

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