

PROXIMATE BEHAVIORAL AND MORPHOLOGICAL MECHANISMS
THAT MAY MEDIATE INTRAGUILD PREDATION
STABILITY IN THE ANISOPTERA

By

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Abstract

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Intraguild Predation (IGP) is a form of interference competition characterized by an intraguild predator consuming interspecific competitors, the intraguild prey. This interaction is extremely common in nature, but mechanistic and descriptive models usually predict that it is unstable with either the IG prey or IG predator becoming locally extinct, dependent on initial conditions. Only intermediate shared prey availability leads to IGP stability in these models, and this condition is not common. In this work, I used dragonfly nymphs to examine behavioral and morphological aspects of consumptive competition and predator avoidance that may act to stabilize IGP, particularly in systems with more than two predators. There are two primary hypotheses in this treatment. The first is that prey capture is morphologically mediated and that this leads to differences in diet composition that can promote IGP stability by allowing prey specialization. The second is that there is a behavioral tradeoff that leads to disproportionate feeding on competitively superior IG prey by an IG predator that may lead to IGP stability. This tradeoff was hypothesized to exist in terms of direct prey capture as well as movement and space use patterns. Both of these mechanisms were found to exist, with variation in mortality being explained by behavior, in spite of morphological defenses compensating for the lack of behavioral defenses in some species. While the effect of this possible mechanism on IGP stability was not directly examined, further long-term study should elucidate it.

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Chapter 1

Overall Question and Introduction to Dissertation

Intraguild Predation

Intraguild predation (IGP) involves both competition and predation and occurs when organisms kill and eat potential competitors, often taking place between species of relatively high trophic position (Polis et al. 1989). There are three basic models of IGP (Fig. 1-1) (Hammen et al. 2010):

Type 1. Linear intraguild predation in which an intraguild predator (P2) consumes both an intraguild prey species (P1) and a shared prey (SP) species (i.e., 'non-reciprocal');

Type 2. 'Reciprocal' intraguild predation in which two predator species feed on each other as well as shared prey;

Type 3. Reciprocal size-structured IGP in which two predator species (L) feed on smaller (s) individuals of the other species, as well as shared prey (Figure 1-1. Modified from Hammen et al. 2010).

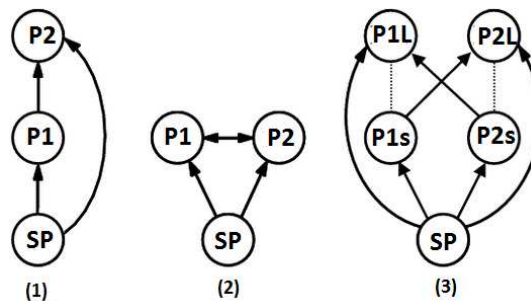


Figure 1-1. Predicted forms of intraguild predation.

1. Non-reciprocal IGP, 2. Reciprocal IGP, 3.

Size-structured reciprocal IGP

Models of IGP generally predict that it should be stable at intermediate productivity where equilibrium is maintained (Holt and Polis 1997, Holt and Huxel 2007, Hammen et al. 2010). Under these conditions, the expected parameter space for the stability of IGP is narrow, which initially leads to the prediction that IGP should be uncommon. Yet, much research has shown that IGP is ubiquitous in nature (Wissinger and McGrady 1993, Arim and Marquet 2004). The mechanisms that allow for the persistence of IGP have thus been a focal point of ecological research (Table 1-1). Below, I describe the progress that has been made in elucidating the mechanisms that favor the persistence of IGP.

Size-structured interactions have been shown to be key factors in the stability of IGP (Crumrine 2005, Crumrine 2010). Research has shown that size-structured interactions can provide stability when the top IG predator is gape-limited and the size of the IG prey exceeds this limited gape thereby attaining a size-refuge from intraguild predation (Urban 2007b). Individuals can then transition from IG prey to IG predator during development as they prey upon the small size classes of the original IG predator. This size-structured interaction has implications for the stability of IGP because: First, the IG prey can regulate the IG predator species via consumption of small-size classes (Montserrat et al. 2012). Second, the IG prey species can grow large enough to attain a size refuge from the IG predator (Crumrine 2005, Henkanaththegedara and Stockwell 2013), which can expand conditions that should theoretically permit stability.

The intensity of competition can strongly influence the stability of IGP. Theory predicts that IGP is unlikely to be stable when competitive interactions (among IG predators) are intense (Polis et al. 1989). Conversely, if competition for shared prey is relatively weak, IGP is predicted to be more stable (Hin et al. 2011, Schellekens and van Kooten 2012a). As a result, the extent to which two competitors consume similar (or different) diet items is likely to be an important characteristic (Hin et al. 2011). In gape-limited predators, larger individuals often have broader diets than smaller individuals (Woodward and Hildrew 2002a). Such a trend implies that the strength of competition may be reduced as IG predators increase in size. This also means that it

is important to consider, both theoretically and empirically, multiple shared prey items when evaluating the conditions that allow for the persistence of IGP (Holt et al. 1994).

Similar to frameworks that consider competition, the incorporation of density dependence can also modify the conditions that favor IGP (McPeck 2014). McPeck (2014) predicted that density dependent mortality (independent of the resource considered in the model) in IG prey species keeps multiple species from excluding each other, thus increasing the number of species that any given system can support above what is predicted by mechanistic models of competition and predation (Holt et al. 1994). Differential predation by IG predators preferentially on the IG prey species with the weakest density dependent mortality response increases the likelihood that multiple predator species can coexist. McPeck's (2014) model also indicates that IG prey species richness increases when a predator disproportionately consumes species with strong interspecific competitive ability, and weak density dependent population growth. A trade-off is implied between consumptive competition and predator vulnerability that can operate via several different proximate mechanisms. However, our understanding of the roles of IG predator avoidance, prey preferences, IG predator capture success, size refuges from IGP and the stability of IGP is limited.

Habitat heterogeneity and refuge use can also increase species richness, and increase the stability of intraguild predation by weakening the effect of intraguild predation on the IG prey (Janssen et al. 2007). This hypothesis assumes that habitat heterogeneity provides cover and thus reduces prey mortality rates (Gilliam and Fraser 1987, Sih et al. 1988, Hixon and Beets 1993, Tarr and Babbitt 2002). The use of refuges can also lower rates of energy acquisition in prey due to less time spent actively foraging (Wellborn and Robinson 1987, Hossie and Murray 2010). The extent to which species utilize refuges may depend on several key characteristics such as foraging strategy, capture success, and morphological traits. For instance, sit-and-wait predators can utilize a refuge against their own predators while also foraging as prey seek the same habitats (Burks et al. 2001, Shine and Sun 2002, Tsairi and Bouskila 2004, Meutter et al. 2005, Sagrario et al. 2009, Schultz et al. 2009). On the other hand, active predators can have

their movement impeded (Gotceitas and Colgan 1989), their prey detection systems disrupted (Michel and Adams 2009), and their foraging efficiency decreased, which may affect their preference for those habitats when under predation risk (Stoks 1999).

It is also clear that predator species can vary in their preferred prey species, handling time and capture success (Bergelson 1985, Blois and Cloarec 1985, Husseman et al. 2003, Hill et al. 2004, Alvarez and Nicieza 2009). Such differences are often driven by differences in morphological features (Luczkovich et al. 1995, Hill et al. 2004, Hampton 2011). In species with high diet overlap, there is the possibility that dietary niche shift will reduce the impact of competition (Bonesi et al. 2004), which can stabilize IGP on its own (Schellekens and van Kooten 2012b).

Thus, morphological features of predators as well as morphological defenses and escape mechanisms in prey are likely to be very important in determining the net result of competitive and predator-prey interactions. (Mikolajewski et al. 2006, Touchon and Warkentin 2008, Strobbe et al. 2010). This interplay between morphological characteristics of predator and prey leads to a great complexity of interactions. Some IG prey species co-specialize with respect to morphological and behavioral defenses and these two trait sets are positively correlated (Bourdeau 2012). Other species compensate for a deficiency in one form of defense by utilizing the other, and they are negatively correlated (Cotton et al. 2004). This needs to be determined empirically for each species in an assemblage under consideration when evaluating the mechanisms that may favor the stability of IGP.

To better understand the mechanisms that allow for the persistence of IGP, a size-structured food chain with a diversity of IG predators and IG prey is needed. Differences in morphology, both defensive and in the prey-capture apparatus are also required, as are differences in foraging mode, and cover use. Dragonfly (Insecta: Odonata, Anisoptera) nymphs meet the criteria. They are large predatory insects with an aquatic larval stage (Merrit et al. 2008). The juveniles have varying periods of reliance on the aquatic environment, remaining aquatic prior to a final molt anywhere between three months and three years; depending on species

(Corbet 1962, Corbet 1999), prey availability (Baker 1982, Pickup and Thompson 1990), and water temperature (Pickup and Thompson 1990, Pritchard et al. 2000). Differences in the timing of development and reproduction create asynchronicity in occupation times that facilitate size-structured IGP, with the nymphs of late breeders being exposed to competition and IGP by the nymphs of early breeders and those that over-winter (Harabis et al. 2012). Importantly, this system provides documented variation in competition for prey (Wissinger 1992, Burcher and Smock 2002), gape-limited predation (Wissinger and McGrady 1993, Crumrine 2005, Crumrine 2010), and considerable behavioral and morphology traits that are correlated with prey capture and predation avoidance (Corbet 1999). I will leverage all of these characteristics to answer the following questions:

- 1) How do differences in prey-capture morphology and size affect prey capture success, and in turn, prey preference and diet overlap between species?
- 2) Does increased competition and the threat of predation facilitate prey switching behavior?
- 3) Does prey density affect prey preference and the risk of intraguild predation?
- 4) Does IG predator foraging mode influence the risk of mortality for IG prey?
- 5) Do dragonfly nymphs use defensive trait compensation or cospecialization, and how do defensive morphological traits affect intraguild predation risk from IG predators with different morphology?
- 6) Is there a direct tradeoff between competition for prey and vulnerability to IGP?

These questions will be addressed experimentally, utilizing a sample of species common across numerous habitats in Tarrant County, Texas.

Chapter 2

Mouthparts and Prey Specialization

Introduction

Predation is a sequence (Relyea 2001); encounter, detection, initial capture, handling, and finally consumption. Sensory modalities (Gaino and Reborja 2001), foraging mode (Secor and Nagy 1994), and the morphology of the prey-capture apparatus, in conjunction with prey anti-predator strategies determine the outcome (i.e., success or failure) of a given predatory (Figure 2-1) event (Sih and Christensen 2001, Herberholz et al. 2004, Hoverman et al. 2005, Alvarez and Nicieza 2009). In a system that consists of a single prey species shared between two predator species, the successful predator is the superior competitor. When multiple species of prey are present, the ultimate outcome of the predator-prey dynamics and the overall stability of the system depend upon differences in vulnerability of prey to different predators, as well as variation in prey selection (Dudgeon 1989, Woodward and Hildrew 2002a, Amarasekare 2007b). Here, I examined the connection between variation in predator morphology and prey capture success to determine their influence on competitive and predatory interactions between species.

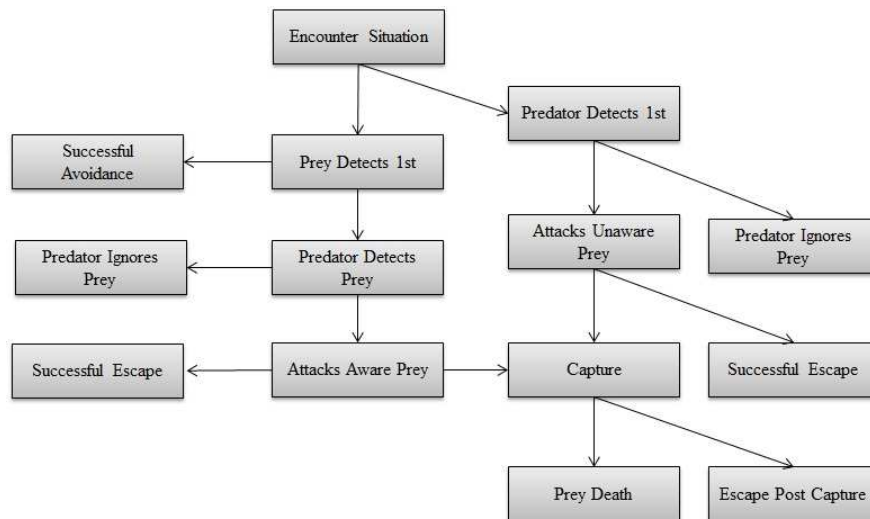


Figure 2-1. Stages of predation and points of predatory failure for generalized predator-prey encounter.

Morphology

A full description of the functional morphology of dragonfly nymph prey-capture is lacking in the literature (but see Sahlen et al 2008), despite other taxa being well represented (Lauder and Shaffer 1986, Taylor 1987, Reilly and Lauder 1992, Wainwright and Richard 1995, Wainwright et al. 2001, Hampton 2011), and despite odonates being important model organisms in studies of predator-prey interactions (Relyea 2003, Van Buskirk et al. 2011, Mogali et al. 2012). If the morphology of mouthparts affects prey capture, then variation in these structures should influence the ability of a species to persist in competitive environments. In intraguild predation systems, the strength of competition affects the stability of trophic interactions and species persistence (Revilla 2002). For instance, in a system with multiple shared prey species, decreased diet overlap—that could be morphologically mediated—can stabilize intraguild predation (Rickers et al. 2006, Flynn and Moon 2011).

Dragonfly nymphs are gape-limited predators (Crumrine 2005, 2010). They possess a projectile labial mask consisting of their postmentum, prementum, and palpal lobes. This structure is projected by means of a hydraulic pump (Tanaka and Hisada 1980). The prementum and palpal lobes often have setae in a pair of lateral to medial ridges along the prementum, and a single row along the dorsal margin of each of the palpal lobes (Merritt et al. 2008). The anterior margins of the palpal lobes in some species also possess crenellations and setae as well. Interspecific variation (Figure 2-2) in these structures is considerable, while intraspecific variation is determined almost entirely by size (Table 2-1).

There are two generalized forms for the labial mask (Figure 2-3): a flat pincer form, and a cup-shaped form with the two palpal lobes forming the walls. In species with a cup shaped labial mask, the palpal lobes vary in size and shape between species (Hirvonen and Ranta 1996, Suhling and Lepkojus 2001). This can have several potential effects. First, palpal lobe size may mediate gape-limitation in a similar fashion to other mouthpart structures and thereby (Luczkovich et al. 1995, Hill et al. 2004, Hampton 2011) be positively correlated with capture success of prey.

Second, the palpal lobes may create a pressure-wake when the labial mask is extended, which may, in turn, alert prey to attack (Holzman and Wainwright 2009, McHenry et al. 2009).

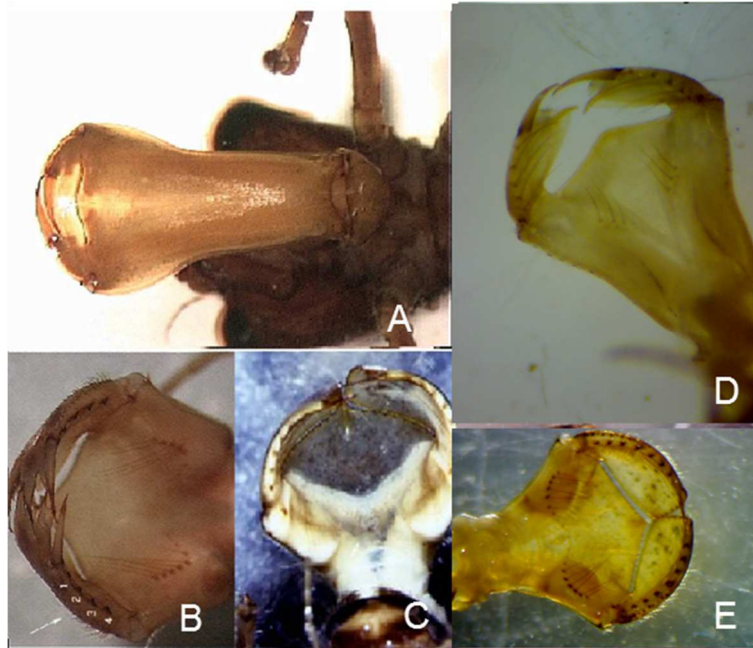


Figure 2-2. Variation in dragonfly nymph labial mask morphologies.

Photos A, B, and C are from the University of Michigan collection (Bright and O'Brien 1999)

If the prey item is sufficiently small, this pressure wake may directly move them out of the way of a predatory strike as observed in ram-feeding fish and aquatic reptiles (Summers et al. 1998, Hibbitts and Fitzgerald 2005, Hampton 2011). If this is indeed the case, a faster strike may reduce initial capture success for small prey. For larger prey, a faster strike may also mean that prey have less time to initiate an escape (Webb 1984, Walker et al. 2005, Meager et al. 2006).

In species with a flat pincer-like labial mask, the palpal lobes are flush with the prementum and should not contribute to a significant pressure wake because the cross sectional area pushing against the water column is smaller. In these species, the palpal lobes do not envelope prey or grab them using the distal margin like those with a cup-shaped mask. Instead, they pin prey against the distal margin of the prementum or impale them on one or both lobes. This should make them less able to capture prey that are very small relative to their body size

because the chance of pinning a small organism against a small surface is low. However, the ability of a species with a pincer-shaped labial mask to capture prey that are relatively large should be higher than those with a cup-shaped labial mask, because they are not restricted by catchment volume or the maximum extension of the palpal lobes (Yurewicz and Relyea 2002, Herberholz et al. 2004).

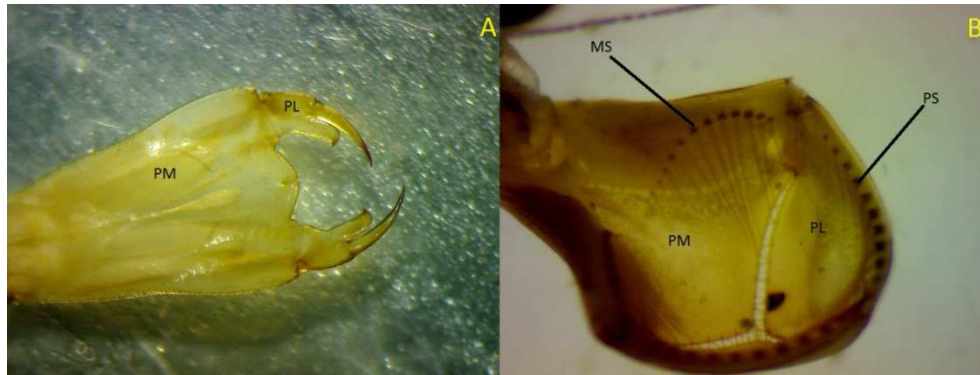


Figure 2-3. Comparison of odonate labial masks and major morphological features.

A. *Anax junius*. B. *Pachydiplax longipennis*. PM=prementum, PL=palpal lobes,
MS=mental setae, PS=palpal setae.

The prementum forms the floor of labial mask, with lateral attachment sites for the palpal lobes. A wide prementum can increase strike accuracy by permitting a higher degree of deviation from centerline on attacks, by forcing prey to travel a larger distance to avoid the strike, or both. The width of the prementum also restricts what prey items can be completely enveloped within the labial mask. Prey larger than this have to be grabbed by the distal margins of the palpal lobes and cannot be restrained by the more solid structure of the prementum.

Table 2-1. Morphological variation in the Odonata by species.

The regressions shown here describe the relationship between the morphology of various dragonfly nymphs and width of their heads

Species	N	Character	Regression Equation (x=Head Width: mm)	R ²
<i>Anax junius</i>	26	Prementum Width	$F(x) = 0.6455x - 0.2670$	0.9850
		Palpal Lobe Length	$F(x) = 0.4244x - 0.1616$	0.9786
		Palpal Lobe Width	$F(x) = 0.000$	1.0000
<i>Erythemis simplicicollis</i>	35	Prementum Width	$F(x) = 0.7824x - 0.0442$	0.9848
		Palpal Lobe Length	$F(x) = 0.5351x - 0.1287$	0.9655
		Palpal Lobe Width	$F(x) = 0.4138x + 0.0333$	0.9630
<i>Libellula lydia</i>	31	Prementum Width	$F(x) = 0.7837x + 0.2998$	0.9813
		Palpal Lobe Length	$F(x) = 0.5609x + 0.0701$	0.9714
		Palpal Lobe Width	$F(x) = 0.3728x + 0.1591$	0.9704
<i>Pachydiplax longipennis</i>	31	Prementum Width	$F(x) = 0.6237x + 0.1158$	0.9601
		Palpal Lobe Length	$F(x) = 0.4858x - 0.1276$	0.9290
		Palpal Lobe Width	$F(x) = 0.4043x - 0.1200$	0.8683
<i>Tramea lacerata</i>	29	Prementum Width	$F(x) = 0.8179x - 0.0103$	0.9865
		Palpal Lobe Length	$F(x) = 0.6143x + 0.0008$	0.9836
		Palpal Lobe Width	$F(x) = 0.5086x + 0.0912$	0.9608
<i>Sympetrum corruptum</i>	22	Prementum Width	$F(x) = 0.7846x - 0.0232$	0.9953
		Palpal Lobe Length	$F(x) = 0.4869x + 0.3011$	0.9600
		Palpal Lobe Width	$F(x) = 0.4068x + 0.2688$	0.9733
<i>Enallagma civile</i>	20	Prementum Width	$F(x) = 0.6051x - 0.1282$	0.8387
		Palpal Lobe Length	$F(x) = 0.3156x - 0.0524$	0.7776
		Palpal Lobe Width	$F(x) = 0.1206x - 0.0303$	0.7451

Palpal and mental setae may also affect prey-capture success by preventing prey held in the cavity formed between the palpal lobes and prementum from escaping (Corbet 1962, Sahlen et al. 2008). The number and density of setae is correlated with instar for each species rather than strictly by size (Figure 2-4, 2-5). As a result, significant within-species and between-species variation in setae density should exist. The setae may also serve a sensory function (Sahlen et al. 2008), and thus may affect the success of initial prey seizure attempts.

The following predictions will be tested:

1. Species with a cup-shaped labial mask will exhibit linear gape-limitation, i.e. their success rate capturing a relatively large prey item will be directly related to their size.
2. Species with a flat labial mask will exhibit an inverse or non-linear relationship between their own size and prey-capture success against small prey. The smaller the prey item is relative to themselves, the less successful they will be in capturing it.
3. As the density of palpal and mental setae increases, predator success rates against small prey items will increase during the capture and handling stages.
4. In species with a cup-shaped labial mask, the size of the palpal lobes (for one or more axes of measurement) will be directly related to prey capture success in the handling stage for larger prey items, and inversely related in the initial capture stage.
5. Strike speed will be inversely related to prey capture success in the initial capture stage for small prey items in species with a cup-shaped labial mask, but *may* be directly related to prey capture success in that stage or the handling stage for larger prey items.

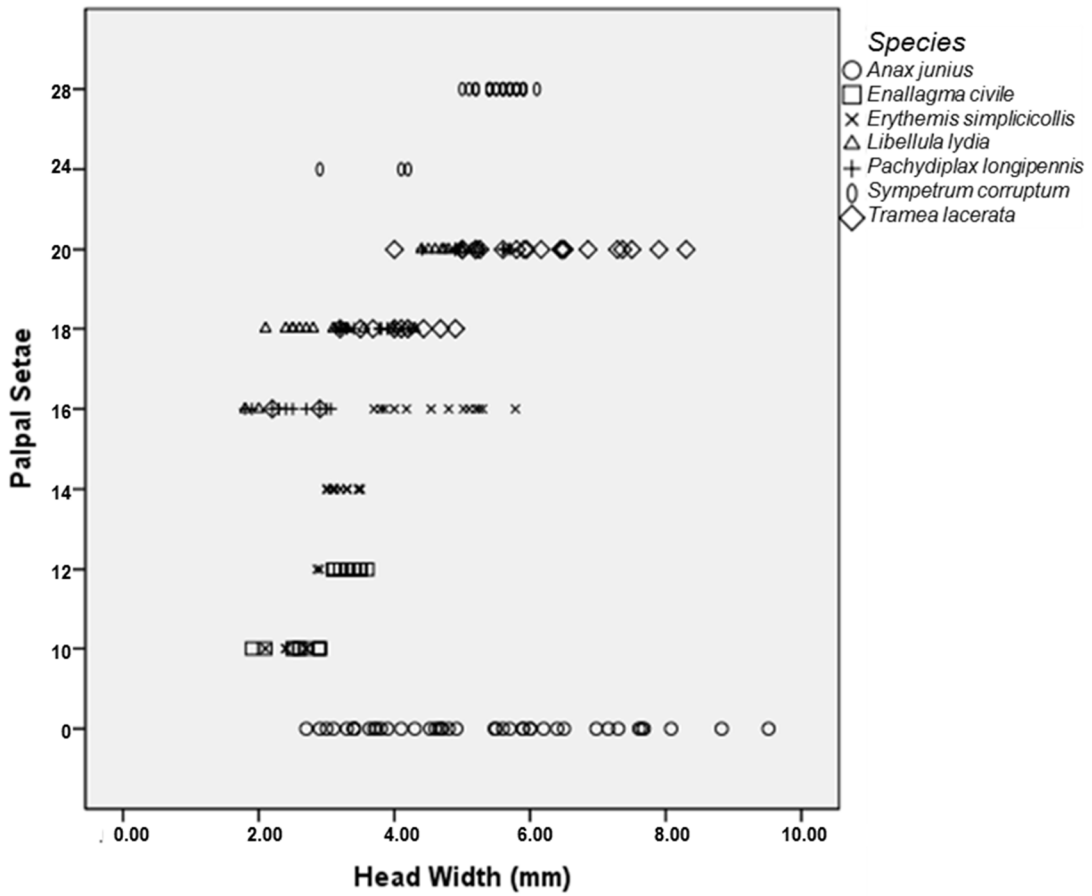


Figure 2-4. Head width and palpal setae by species. Palpal setae in dragonfly nymphs increase in number at transition points in head width that likely indicate molts resulting in additional palpal setae.

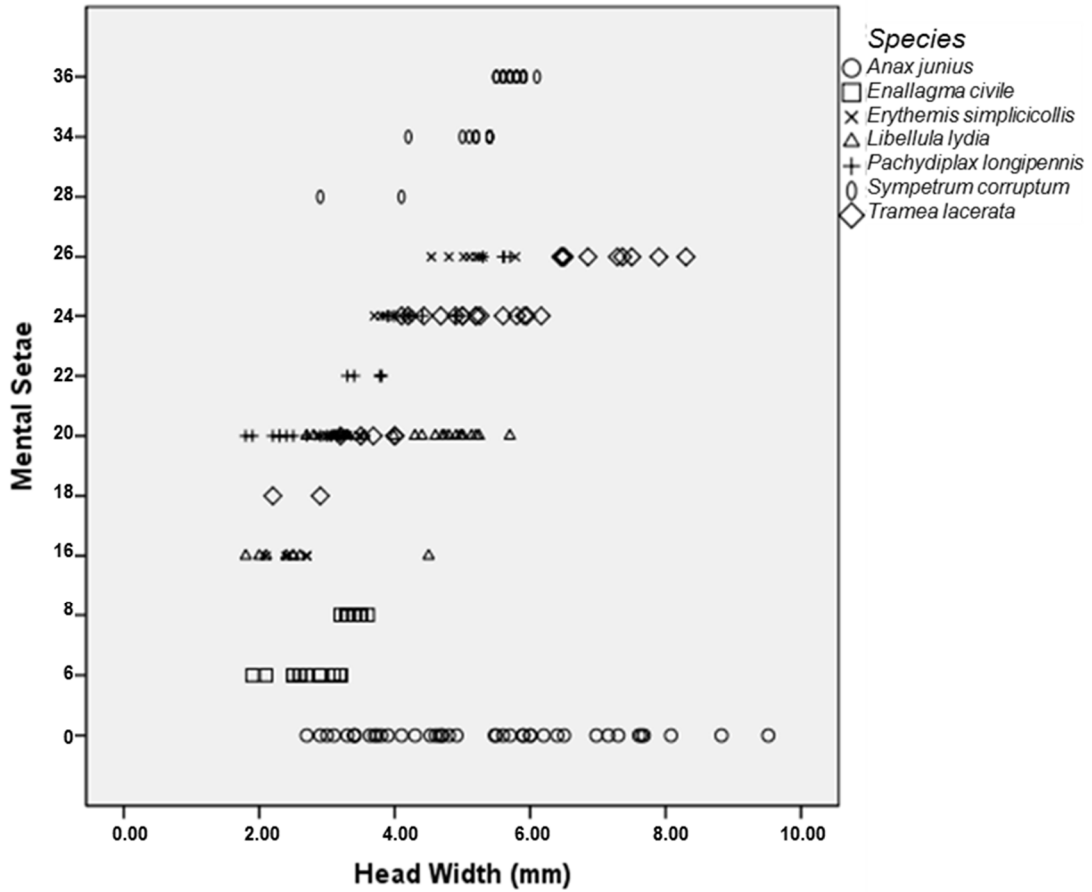


Figure 2-5. Head width and mental setae by species.

Mental setae in dragonfly nymphs increase in number at transition points in head width that likely indicate molts resulting in additional mental setae.

Methods and Results

Components of Prey Capture Success Between-Subjects (Predator Species)

The first experiment used a between-subjects design to determine which prey are easiest for dragonfly nymphs to capture. The predator species used in this experiment included *Anax junius*, *Enallagma civile*, *Erythemis simplicicollis*, *Pachydiplax longipennis*, *Sympetrum corruptum*, and *Tramea lacerata*. *Anax* possess a flat labial mask while the other species have a cup shaped mask. *Enallagma civile* has a labial mask that, while cup-shaped, is more flattened than other species, representing an intermediate state. *Anax* is expected to behave very differently with respect to the characteristics of its strikes and ability to capture prey.

An initial analysis of specimens to assess morphological variation was performed using preserved dragonfly nymphs of all focal species. These data were collected using a stereomicroscope with an attached AmScope MD200 camera. Due to a lack of intraspecific variability in morphology (Table 2-1), morphological data for the analysis of prey capture results were estimated using high-quality measurements obtained from preserved specimens. This allowed for reliable assessment of morphological traits even in the event of subject death and molting, or variation in camera angle. When morphological measurements were regressed with head width as a predictor, the residuals were examined. Deviations from expected values were very small, and similar in magnitude to measurement error. Palpal and mental setae counts were estimated in a similar fashion, though not with regression. Setae are acquired as individuals molt at different developmental instars for each species, and so the relationship was non-linear. However, there were transition points in development where new setae emerged during molting, and these more readily observable transition points were used to estimate setae counts (Figure 2-4, 2-5). If the head of an individual was smaller than the nearest transition point, the lower number was used. If the head was larger than the nearest transition point, the higher number was used.

To test the influence of morphology on prey capture success, all predator species were randomly assigned to treatments that received 10 adult *Daphnia* sp. or 5 *Gammarus* sp. The

different prey densities were used to compensate for the low mobility of *Daphnia*. Success rate was the variable under consideration rather than the actual number consumed. These prey species are commonly observed at high densities in the ponds from which all odonates were collected. *Gammarus* is larger than *Daphnia*, with an average length of 3.99 mm (SD=0.98) compared to 1.17 mm (SD=1.01). The number of replicates varied due to some subjects failing to attempt to feed in the lab, but never fewer than 12. Trials took place in 55 mm petri dishes filled with aged and treated tap water. Attacks were recorded on digital video using a Nikon L610 digital camera at a resolution of 1920 x 1080 and 30 frames per second for ten minutes or until all prey were consumed. These recordings were processed using Kinovea (Version 1.21, 2014). For all trials, the success of initial capture, prey escapes after initial capture and overall success rate were recorded. In addition, strike velocity was measured from the first five attacks that could be reliably measured, and corrected for size using a regression procedure for use as a predictor variable. Data regarding initial capture, prey escape success, and total attack success were analyzed using ANCOVA between species, using head width as a covariate. Strike success data are proportions and were arcsine square root transformed to meet normality assumptions.

How morphology affects components of capture success was analyzed by excluding *Anax* from the other species; then regression was used to examine relationships of morphological features with components of prey capture success. *Anax* was analyzed separately, and the only hypotheses that required testing using *Anax* relate to relative size and size-corrected strike speed, so linear regression was used.

Initial capture success of *Daphnia* prey was significantly higher than the initial capture of *Gammarus* prey (df=1, F=6.577, P=0.011, mean difference=0.098) for all odonate predator species, which did not differ significantly in initial capture success, (Figure 2-6). *Gammarus* were also significantly more likely to escape (Figure 2-7) after initial capture than *Daphnia* (df=1, F=151.5551, P<0.001, mean difference=0.671). There was a significant prey by predator species interaction for escape success wherein dragonfly nymph species mediates the difference between prey type (df=6, F=2.889, P=0.01). Dragonfly head width ($Y=-0.095x+1.013$, df=1,

F=17.075, P<0.001) decreased prey escape success the larger it became. Total prey capture success differed between prey (df=1, F=94.070, P<0.001, mean difference=0.456). There was also a significant effect of dragonfly nymph head width ($Y=0.053x+0.434$, df=1, F=6.997, P=0.009). R² was 0.307 (Figure 2-8).

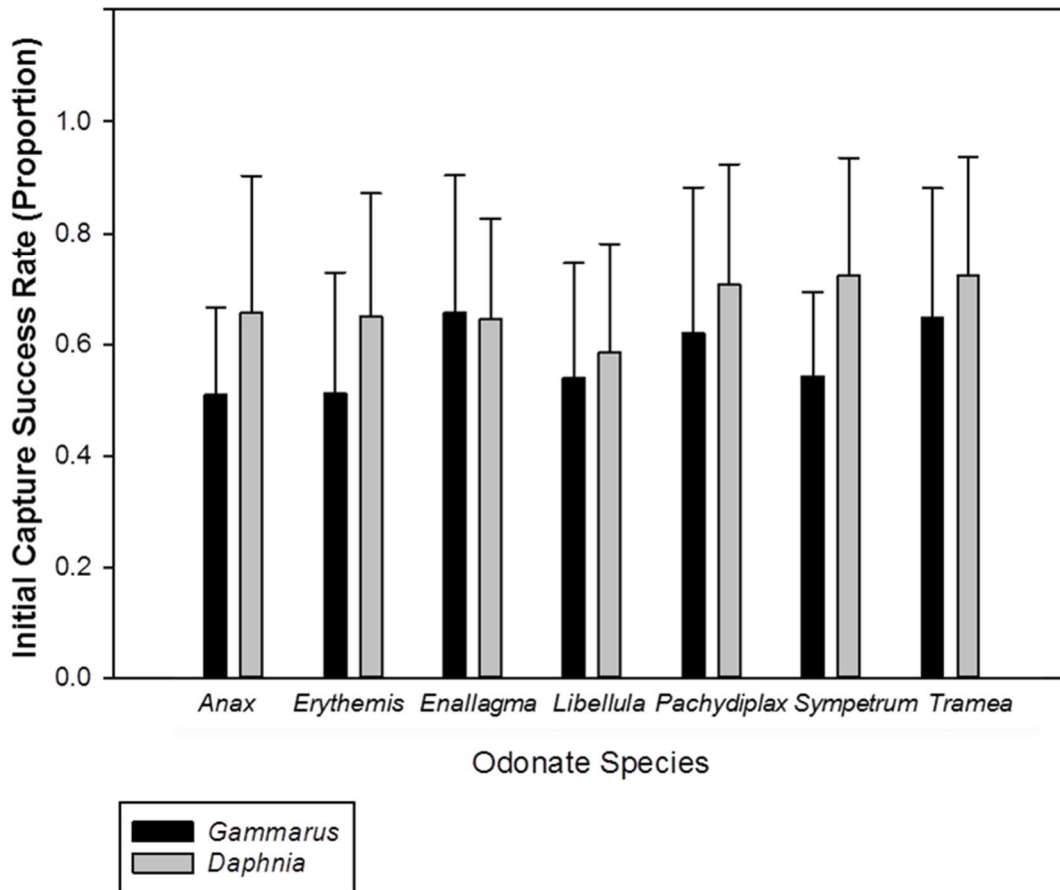


Figure 2-6. Initial capture success varies by prey type.

Initial capture of *Gammarus* by dragonfly nymphs has a lower success rate per attack than attacks on *Daphnia*. These are expressed here as a proportion of attacks that resulted in initial capture. Error bars=1 SD.

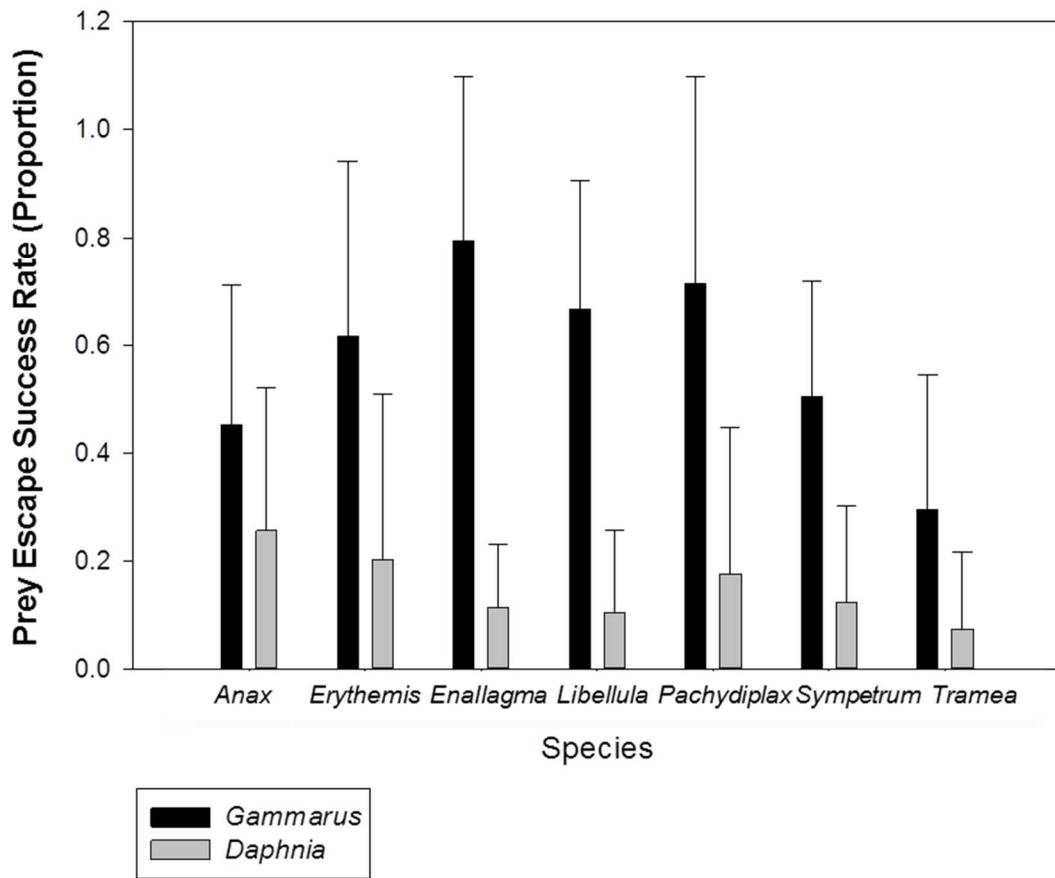


Figure 2-7. Prey escape success varies by prey type and odonate species. Post capture escape by *Daphnia* was less likely than post-capture escape by *Gammarus*. The relationships are expressed here as a proportion of initial captures that resulted in the prey item escaping. Error bars=1 SD.

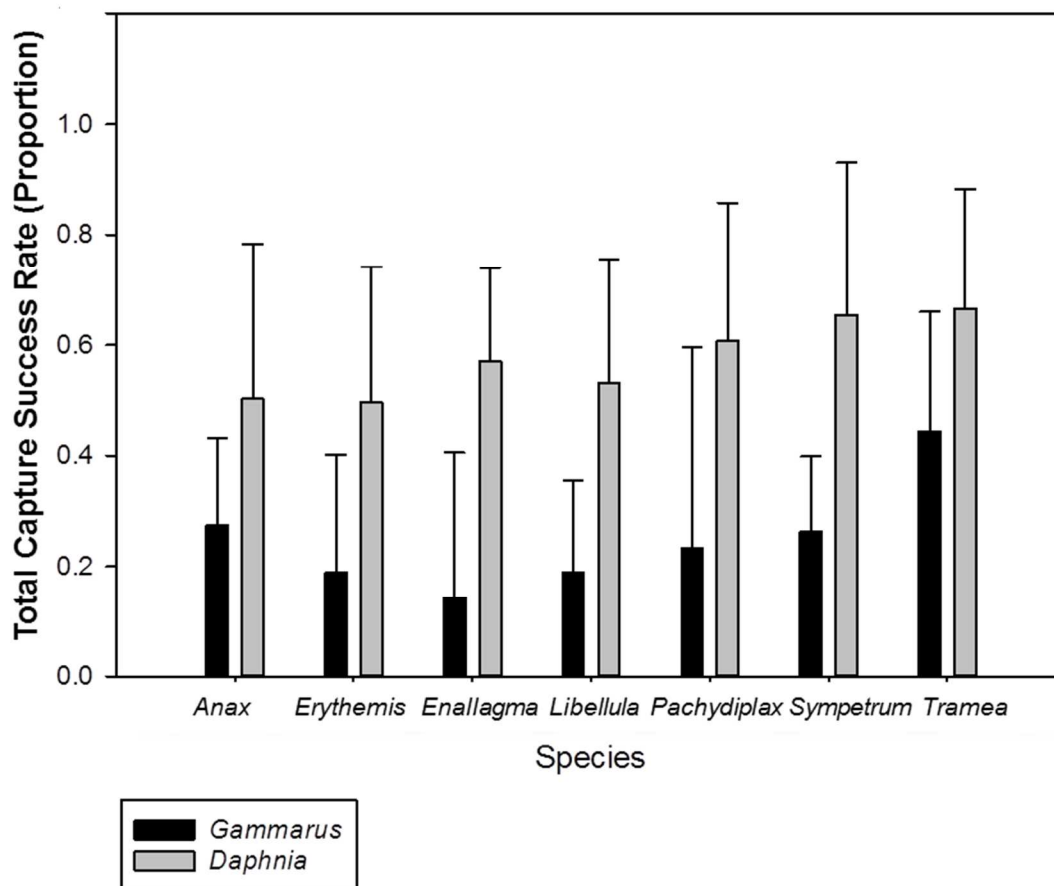


Figure 2-8. Total prey capture success varies little by species and prey type. Data are total capture success, the product of initial capture success and prey escape. Recapture post escape is treated as a separate attack. Generally, *Daphnia* were easier to capture than *Gammarus*, though the magnitude of the difference varied somewhat among dragonfly species. The data expressed here are the proportion of attacks that resulted in prey capture and consumption. Error bars=1 SD.

With *Anax* excluded there is a positive relationship between palpal lobe length and initial capture of *Gammarus* ($Y=0.591x+1.458$, $P=0.015$), and a significant negative relationship with the width of the prementum and initial capture of *Gammarus* ($Y=-0.514x+1.458$, $P=0.01$). There was also a near-significant negative relationship between the density of mental setae and initial capture of *Gammarus* ($Y=-0.026x+1.458$, $P=0.062$).

Gammarus escape post capture was positively related to the density of mental setae with marginal significance ($Y=0.034x+1.241$, $P=0.071$), and significantly negatively related with the width of the palpal lobes ($Y=-0.312x+1.241$, $P<0.001$). This relationship explained 35% of the variance observed. Only the width of the palpal lobe was positively related to successful predation on *Gammarus* ($Y=0.192x+0.123$, $P<0.001$). This relationship explained 20.1% of observed variance (Figure 2-9).

For *Anax*, there was a negative relationship between head width and initial *Gammarus* capture ($Y=-0.049x+1.097$, $P=0.009$) that explained 27.1% of observed variance (Figure 2-10). There were no significant relationships between any variable and *Gammarus* escape. By contrast, the species with cup shaped labial masks (all non-*Anax*) display no relationship between size and initial capture of *Gammarus*, but a negative relationship between *Gammarus* escape and odonate head width ($Y=0.277x+1.904$, $P<0.001$), that extends into a positive (Figure 2-11) size-*Gammarus*-consumption relationship ($Y=0.138x-0.139$, $P<0.001$).

When *Anax* was excluded, initial *Daphnia* capture was positively related to the length of the palpal lobes ($Y=0.069x+0.884$, $P=0.044$). Escape by *Daphnia* was negatively related to strike speed ($Y=-0.005x+0.615$, $P<0.001$). Total predatory success was positively related to the length of the palpal lobes ($Y=0.66x+0.115$, $P=0.037$). There was also a marginally negative relationship between predatory success and the width of the palpal lobes ($Y=0.632x+0.115$, $P=0.055$) and a positive relationship with strike speed ($Y=0.003x+0.115$, $P=0.024$). These relationships explained 13.3% of observed variance in total (Figures 2-12, 2-13).

Size was positively related to initial *Daphnia* capture ($Y=0.05x+0.826$, $P=0.035$) for non-*Anax* species but the relationship only explained 3.9% of observed variance. There was a weak

non-significant negative relationship between head width and *Daphnia* escape ($Y=-0.048x-0.437$, $P=0.09$). There was a significant positive relationship between successful predation and size ($Y=0.075x+0.623$, $P=0.003$) that explained 8.6% of observed variance. *Anax* displayed a negative if marginal relationship between size and initial *Daphnia* capture ($Y=-0.092x+1.411$, $P=0.076$) that explained 11.2% of observed variance.

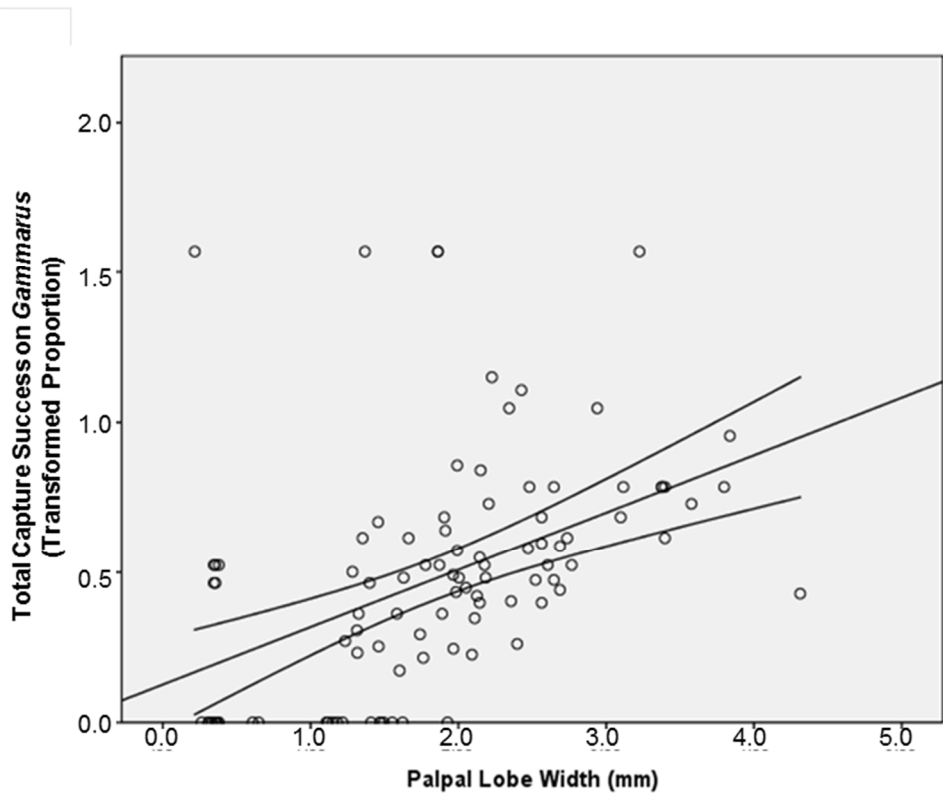


Figure 2-9. Palpal lobe width positively affects *Gammarus* consumption.

The relationship depicted here shows a positive relationship between length of a dragonfly nymph's palpal lobes and net prey-capture success against *Gammarus*.

Curves denote a 95% confidence interval around the best fit line.

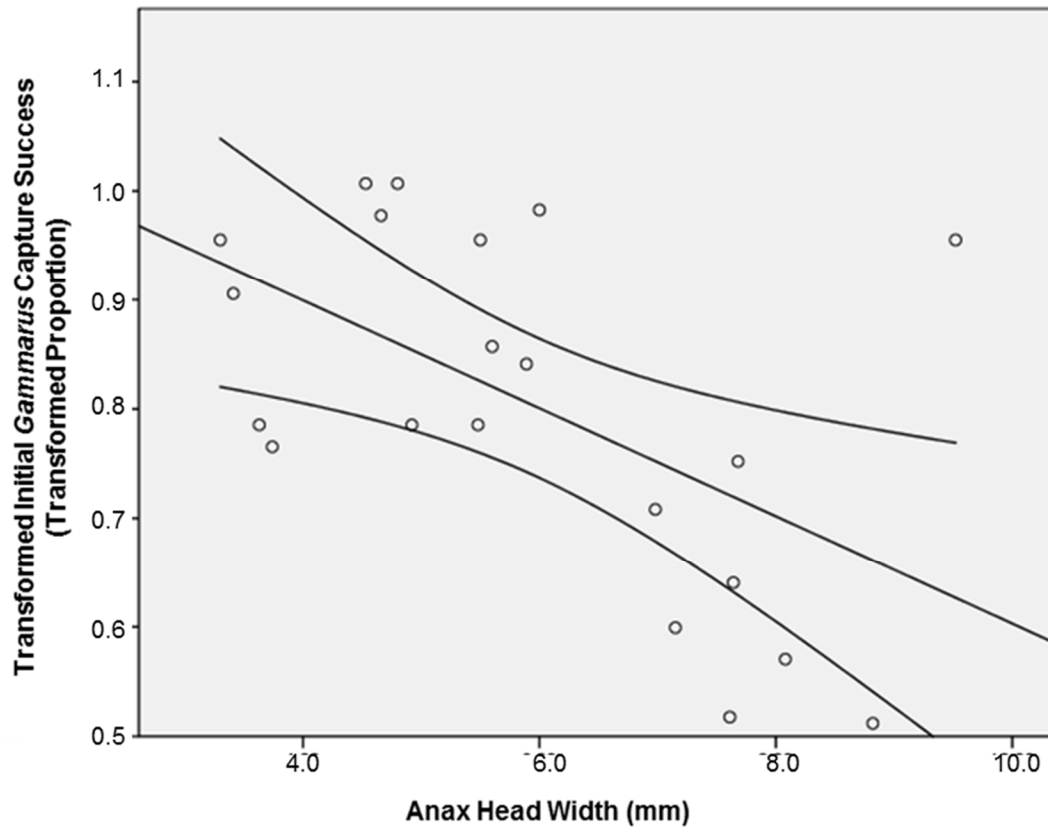


Figure 2-10. *Gammarus* capture by *Anax* varies negatively with *Anax* head width.

This shows that it became more difficult for *Anax* to succeed at initial capture of *Gammarus* the larger *Anax* was. Curves denote a 95% confidence interval around the best fit line.

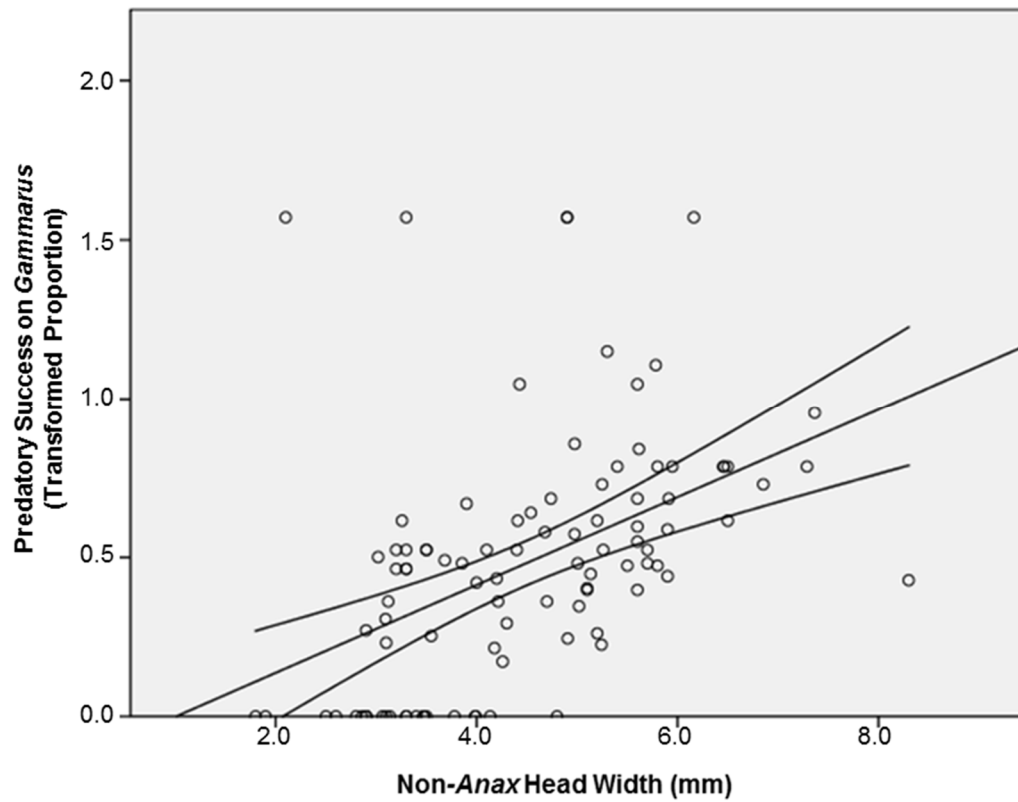


Figure 2-11. Head width is positively related to total *Gammarus* capture success. By contrast to *Anax*, the other species (all of which have cup-shaped labial masks) became more successful capturing *Gammarus* the larger they were. Curves denote a 95% confidence interval around the best fit line.

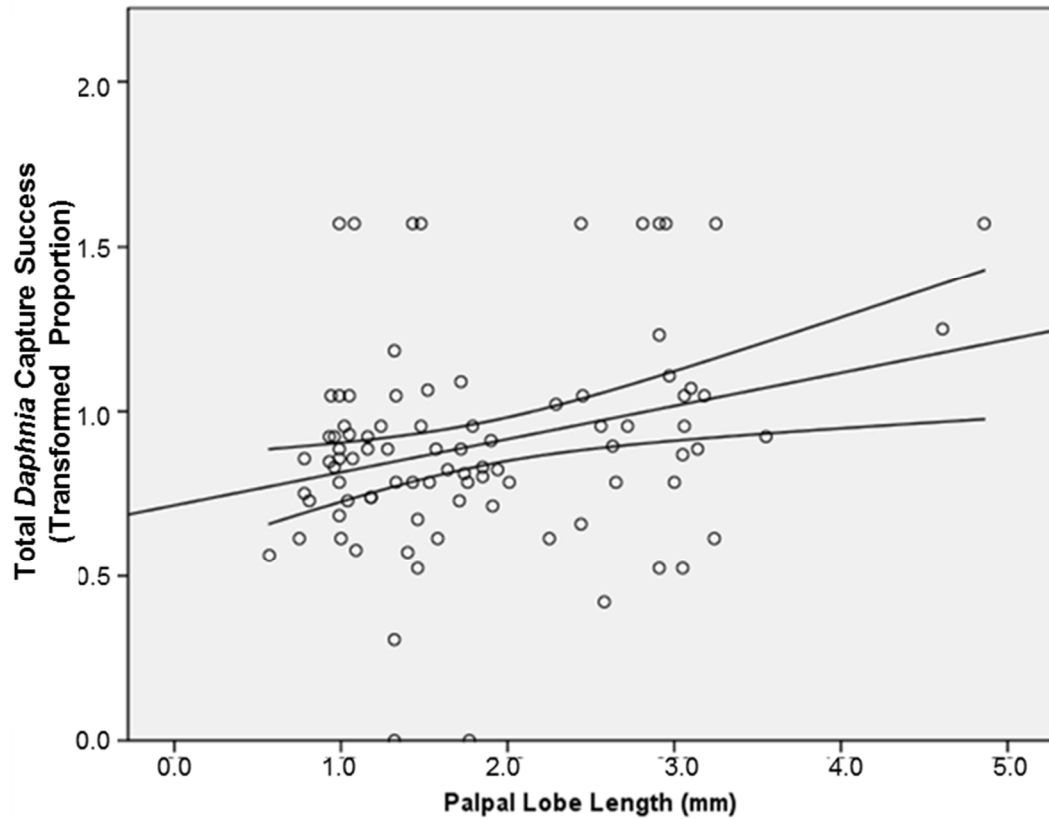


Figure 2-12. Capture of *Daphnia* is positively related to palpal lobe length.

Total prey capture against *Daphnia* became easier as palpal lobe length increased.

Curves denote a 95% confidence interval around the best fit line.

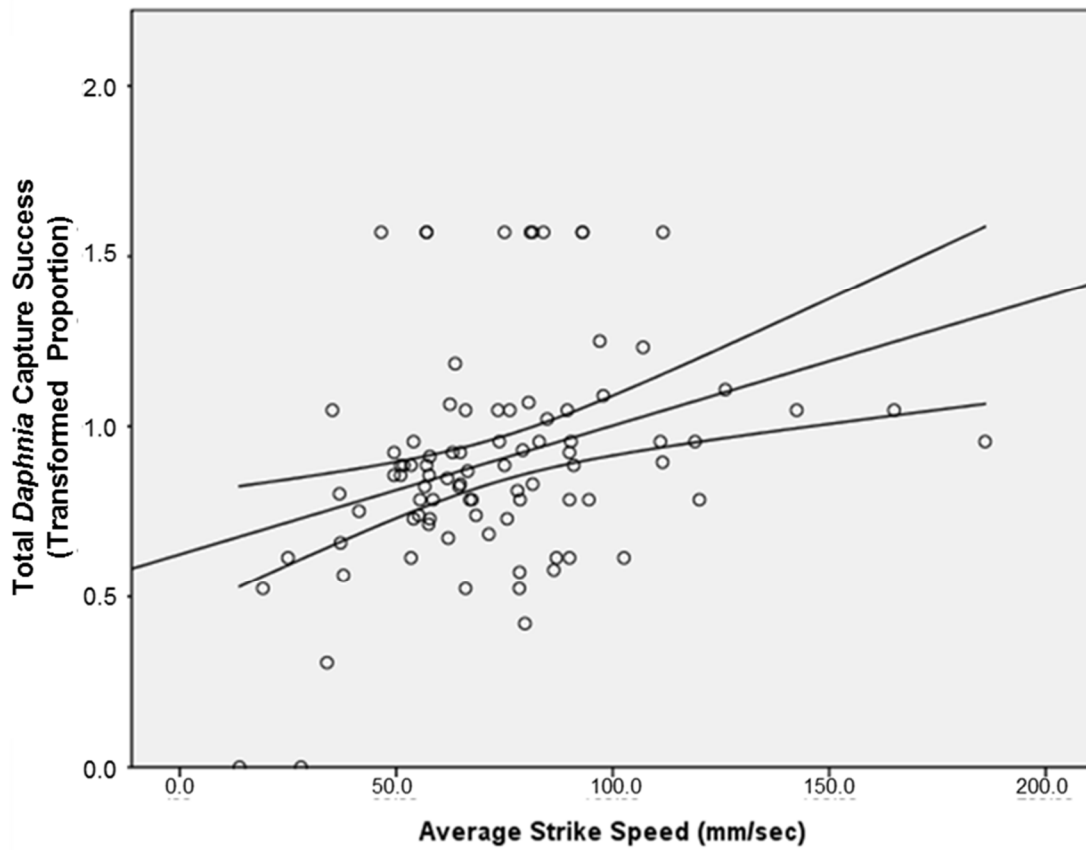


Figure 2-13. Total *Daphnia* capture success is positively related to strike speed. Strike speed by dragonfly nymphs increased total capture success when attacking *Daphnia*. Curves denote a 95% confidence interval around the best fit line.

Components of Prey Capture Success Within-Subjects

In order to test whether individual differences in prey capture success were affected by species and prey type, *Anax junius*, *Erythemis simplicicollis*, *Libellula lydia*, *Pachydiplax longipennis*, and *Tramea lacerata* were used as focal species, and were provided with ten each of *Gammarus* sp. and *Daphnia* sp. in a 90 mm petri dish. Data on components of prey capture were collected as above. Individuals were filmed for ten minutes and all attempts at prey capture were recorded, to test for within-subjects effects a repeated-measures ANCOVA between species was performed using prey type as a within-subjects variable. Morphological variables were estimated as above, and pooled with the first sample from this chapter to obtain a higher sample size. In the repeated-measures ANCOVA, there was a significant effect of the predator species by prey combination on initial capture success (Figure 2-14, Table 2-2) in within-subjects contrasts (df=4, F=3.432, P=0.011), and a significant effect of predator species on initial prey capture between subjects (df=4, F=4.108, P=0.004). It is possible that the within-subjects effect was driven primarily by *Anax*.

Within-subjects contrasts testing for effects on prey escape success showed a statistically significant difference between prey species (df=1, F=22.294, P<0.001), a significant interaction (Table 2-3, Figure 2-15) between species and prey species (df=4, F=13.368, P<0.001) and between dragonfly nymph head width and prey species (df=1, F=6.789, P=0.011, $Y_{\text{Gammarus}} = -0.191x + 1.344$, $P_{\text{Gammarus}} < 0.001$, $Y_{\text{Daphnia}} = -0.062x + 0.364$, $P_{\text{Daphnia}} = 0.119$). Within-subjects tests of total prey capture success between prey species found significant differences between prey types (df=1, F=18.86, P<0.001), and a significant interaction (Table 2-4, Figure 2-16) between odonate species and prey type (df=4, F=10.137, P<0.001). There was also a significant interaction between odonate head width and prey type in total prey capture success (df=1, F=10.038, P<0.001, $Y_{\text{Gammarus}} = 0.14x + 0.129$, $P_{\text{Gammarus}} < 0.001$, $Y_{\text{Daphnia}} = 0.013x + 0.987$, $P_{\text{Daphnia}} = 0.746$).

Table 2-2. Mean initial capture success by prey and odonate species. This displays the means for initial capture success for all dragonfly species against both prey types, along with standard error and the confidence intervals for the mean. All values are for arcsine square root transformed proportions, which have a range between 0.0 and 1.52.

Predator	Prey	Mean Initial Capture Success		
		Mean	Std. Error	95% C.I.
<i>Anax</i>	<i>Gammarus</i>	0.842	0.059	0.726-0.959
	<i>Daphnia</i>	0.549	0.098	0.356-0.743
<i>Erythemis</i>	<i>Gammarus</i>	0.827	0.060	0.708-0.946
	<i>Daphnia</i>	0.990	0.099	0.793-1.187
<i>Libellula</i>	<i>Gammarus</i>	0.784	0.063	0.659-0.909
	<i>Daphnia</i>	0.908	0.105	0.701-1.115
<i>Pachydiplax</i>	<i>Gammarus</i>	0.906	0.044	0.818-0.993
	<i>Daphnia</i>	0.936	0.073	0.791-1.080
<i>Tramea</i>	<i>Gammarus</i>	0.936	0.056	0.825-1.048
	<i>Daphnia</i>	1.075	0.093	0.890-1.259

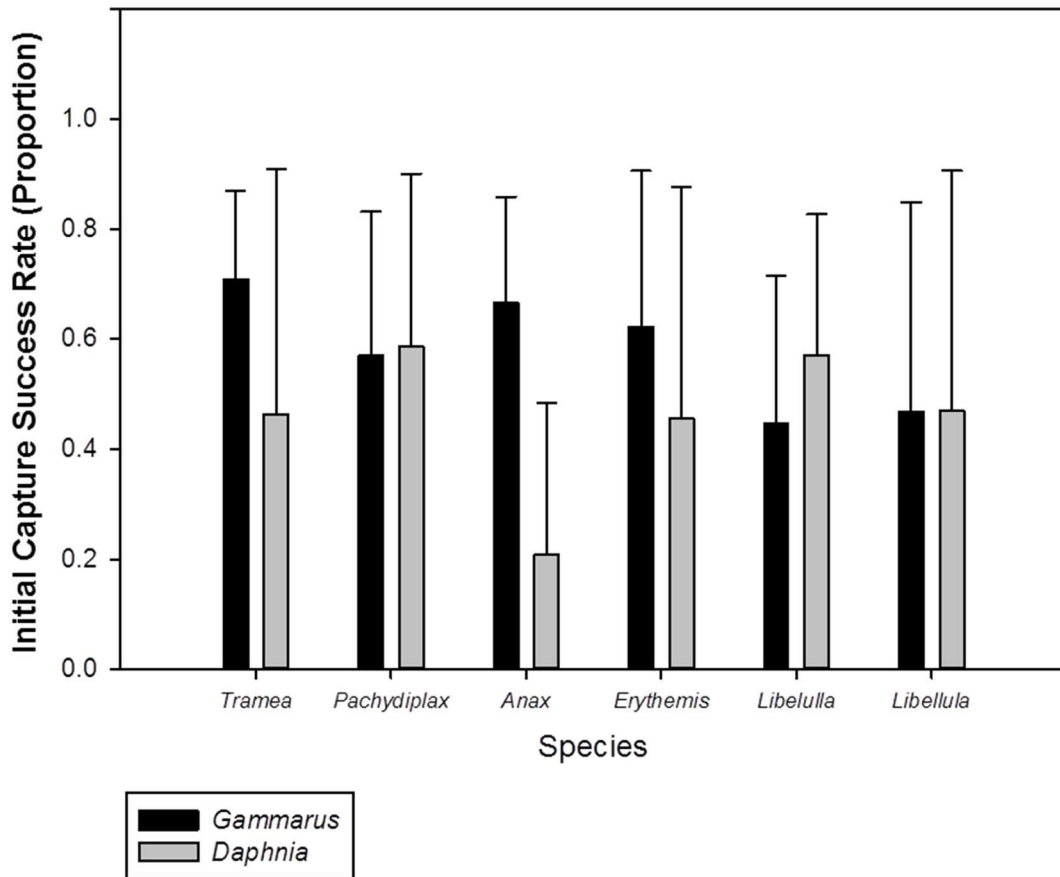


Figure 2-14. Within-subjects initial prey capture was affected by both species and prey type.

This graph shows initial capture success in within-subjects tests by prey and species. Initial capture of *Daphnia* was more difficult than *Gammarus*, but there was a greater degree of variation between dragonfly species in these tests, which control for individual variation more effectively. Here, success rate is expressed as a proportion of attacks that resulted in initial prey capture. Error bars=1 SD.

Table 2-3. Mean prey escape success by prey type and odonate species.

This displays the means for prey escape success for all dragonfly species against both prey types along with standard error and the confidence intervals for the mean. All values are for arcsine square root transformed proportions of initial captures that resulted in escape.

Species	Prey	Mean Prey Escape Success		
		Mean	Std. Error	95% C.I
<i>Anax</i>	<i>Gammarus</i>	0.697	0.084	0.530-0.863
	<i>Daphnia</i>	0.897	0.104	0.691-1.103
<i>Erythemis</i>	<i>Gammarus</i>	0.557	0.076	0.407-0.708
	<i>Daphnia</i>	0.220	0.094	0.034-0.407
<i>Libellula</i>	<i>Gammarus</i>	0.929	0.080	0.770-1.088
	<i>Daphnia</i>	0.028	0.099	-0.169-0.225
<i>Pachydiplax</i>	<i>Gammarus</i>	1.047	0.055	0.939-1.155
	<i>Daphnia</i>	0.225	0.068	0.091-0.359
<i>Tramea</i>	<i>Gammarus</i>	0.580	0.075	0.430-0.729
	<i>Daphnia</i>	0.114	0.093	-0.071-0.298

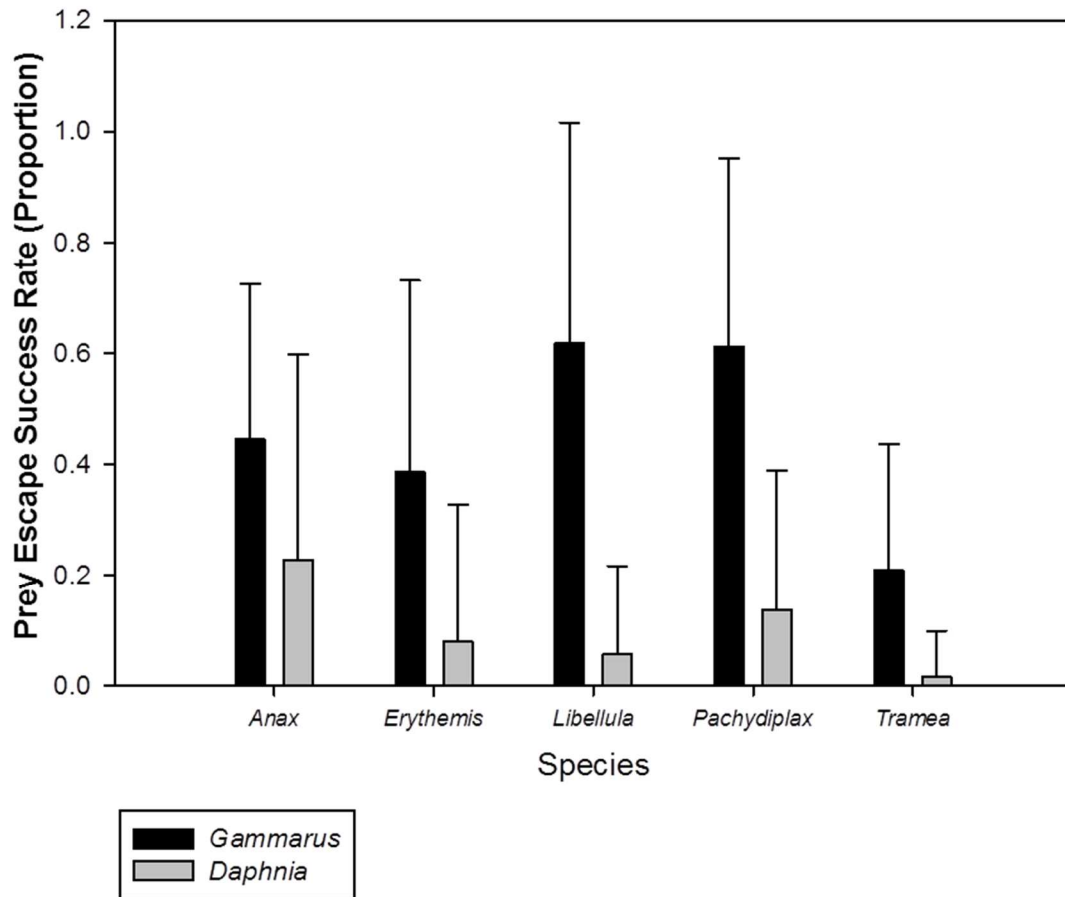


Figure 2-15. Within-subjects prey escape varied by species and prey type. In within-subjects tests, *Gammarus* escaped more easily than *Daphnia*, with particular relationships varying by predator species. Here, prey escape success is displayed as a proportion of initial captures that resulted in a prey item escaping. Error bars=1 SD.

Table 2-4. Mean values of total capture success by prey type and odonate species.

Total *Gammarus* and *Daphnia* capture success means along with error and confidence intervals for all dragonfly species. All values are transformed proportions of attacks that resulted in prey capture and consumption. These have a range between 0.00 and 1.52

Species	Prey	Mean Total Capture Success		
		Mean	Std. Error	95% C.I.
<i>Anax</i>	<i>Gammarus</i>	0.499	0.049	0.402-0.597
	<i>Daphnia</i>	0.252	0.094	0.067-0.438
<i>Erythemis</i>	<i>Gammarus</i>	0.616	0.050	0.518-0.715
	<i>Daphnia</i>	0.794	0.095	0.605-0.983
<i>Libellula</i>	<i>Gammarus</i>	0.439	0.052	0.336-0.543
	<i>Daphnia</i>	0.899	0.100	0.700-1.097
<i>Pachydiplax</i>	<i>Gammarus</i>	0.369	0.037	0.296-0.441
	<i>Daphnia</i>	0.812	0.070	0.673-0.951
<i>Tramea</i>	<i>Gammarus</i>	0.693	0.047	0.600-0.785
	<i>Daphnia</i>	1.038	0.089	0.861-1.215

Table 2-5. Strike speed by odonate species and prey type.

This displays the means for strike speed for all dragonfly species against both prey types; with error and confidence intervals. Values are in mm/sec.

Species	Prey	Mean Strike Ppeed (mm/sec)		
		Mean	Std. Error	95% C.I.
<i>Anax</i>	<i>Gammarus</i>	108.407	6.034	96.463-120.350
	<i>Daphnia</i>	59.556	6.395	46.898-72.214
<i>Erythemis</i>	<i>Gammarus</i>	77.973	6.126	65.849-90.097
	<i>Daphnia</i>	62.856	6.492	50.007-75.705
<i>Libellula</i>	<i>Gammarus</i>	91.388	6.436	78.648-104.127
	<i>Daphnia</i>	60.654	6.821	47.153-74.155
<i>Pachydiplax</i>	<i>Gammarus</i>	66.382	4.565	57.347-75.418
	<i>Daphnia</i>	57.044	4.838	47.468-66.619
<i>Tramea</i>	<i>Gammarus</i>	76.967	5.751	65.583-88.350
	<i>Daphnia</i>	54.418	6.095	42.354-66.482

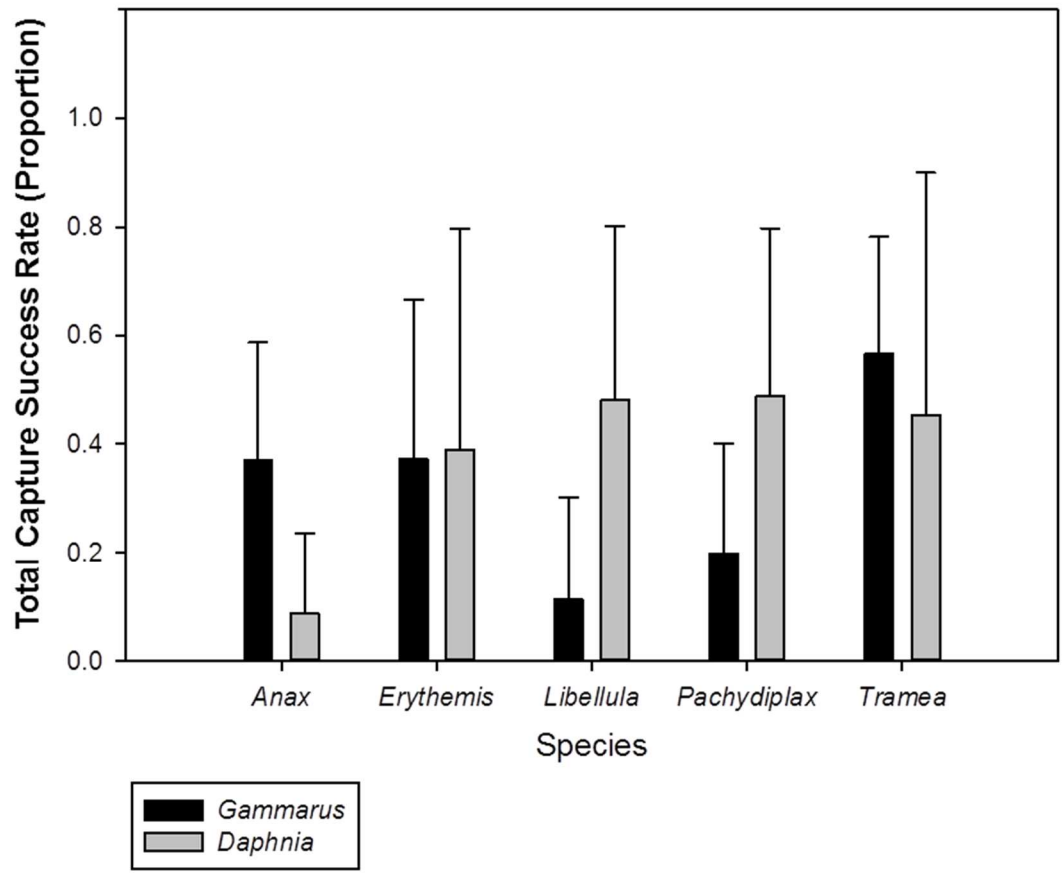


Figure 2-16. Total prey capture success varies by prey and species. Total prey capture in within-subjects tests varied by both prey type and dragonfly species. Whether *Gammarus* or *Daphnia* was easier to catch and then consume differed between dragonfly species and the degree of difference between the two also varied by species. Recapture post-escape was scored as a separate attack. Capture success is displayed as a proportion of attacks that resulted in prey capture and consumption. Error bars=1 SD.

Strike speed varied by predator species and prey type ($df=4$, $F=5.528$, $P<0.001$) with predators striking more slowly when attacking *Daphnia* compared to *Gammarus* (Table 2-5, Figure 2-17). For both prey types, head width was also significantly related to strike speed, with different relationships by prey type ($df=1$, $F=15.739$, $P<0.001$, $Y_{\text{Gammarus}}=19.957x-3.446$, $P_{\text{Gammarus}}<0.001$, $Y_{\text{Daphnia}}=7.653x+23.583$, $P_{\text{Daphnia}}=0.005$).

When regressions were run using pooled *Anax* data, strike speed ($Y=0.001x+1.035$, $P=0.034$) is positively related to initial capture of *Gammarus*, and head width is negatively related ($Y=-0.073x+1.035$). These relationships explained a combined 22.5% of observed variance (Figure 2-18). Nothing was significantly related to *Gammarus* escape, but strike speed was positively related to total predatory success ($Y=0.002x+0.405$, $P=0.033$), explaining 11% of the variation in this response variable (Figure 2-19). Strike speed was measured in mm/sec, and regularly reached speeds in excess of 100 mm/sec or higher, which is much larger in magnitude than most other variables, and thus small coefficients are still significantly different from zero.

Initial capture of *Gammarus* by the non-*Anax* group was positively related to head width ($Y=0.032x+0.748$, $P=0.041$) though the weak relationship only explained 1.5% of the observed data variation. However, post-capture escape by *Gammarus* became less likely the larger the heads of non-*Anax* odonates became ($Y=-0.178x+1.8$, $P<0.001$), and as strike speed increased ($Y=-0.002x+1.8$, $P=0.049$). These relationships explained a total of 33.7% of the variation in this variable. It also translated to total capture success, with this response variable positively related to both odonate head width ($Y=0.123x-0.172$, $df=1$, $P<0.001$) and strike speed ($Y=0.002x-0.172$, $P=0.043$) which together accounted for 30.8% of the variation in these data (Figure 2-20).

Regressions were performed using pooled data for attacks by species with cup-shaped labial masks against *Gammarus*. These showed that initial capture was positively related to the length of the palpal lobes ($Y=0.465x+1.263$, $P=0.008$), and negatively related to both prementum width ($Y=-0.392x+1.263$, $P=0.008$), and palpal setae density ($Y=-0.022x+1.263$, $P=0.008$). However, all these relationships were weak (R^2 of 0.044).

Gammarus post-capture escape success was positively affected by the length of predator palpal lobes ($Y=1.044x+0.459$, $P=0.001$), and the density of mental setae ($Y=0.098x+0.459$, $P<0.001$). It was negatively affected by the width of the palpal lobes ($Y=-1.364x+0.459$, $P<0.001$), and mean attack speed ($Y=-0.002x+0.459$, $P=0.088$), with an R^2 of 0.422.

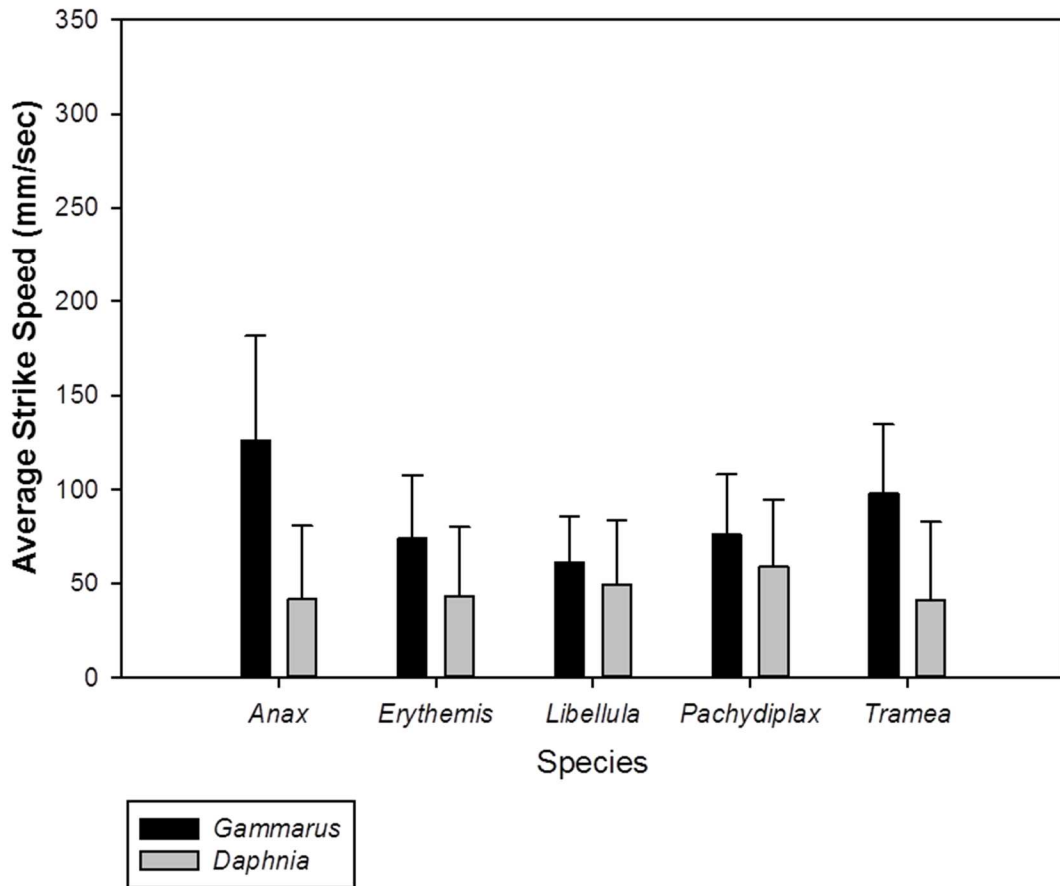


Figure 2-17. Strike speed differs between species and individuals shift strike speed.

Because these are within-subjects tests, this indicates that dragonfly nymphs attacked more slowly when attempting to capture *Daphnia* than they did when attempting to capture *Gammarus*. Error bars=1 SD.

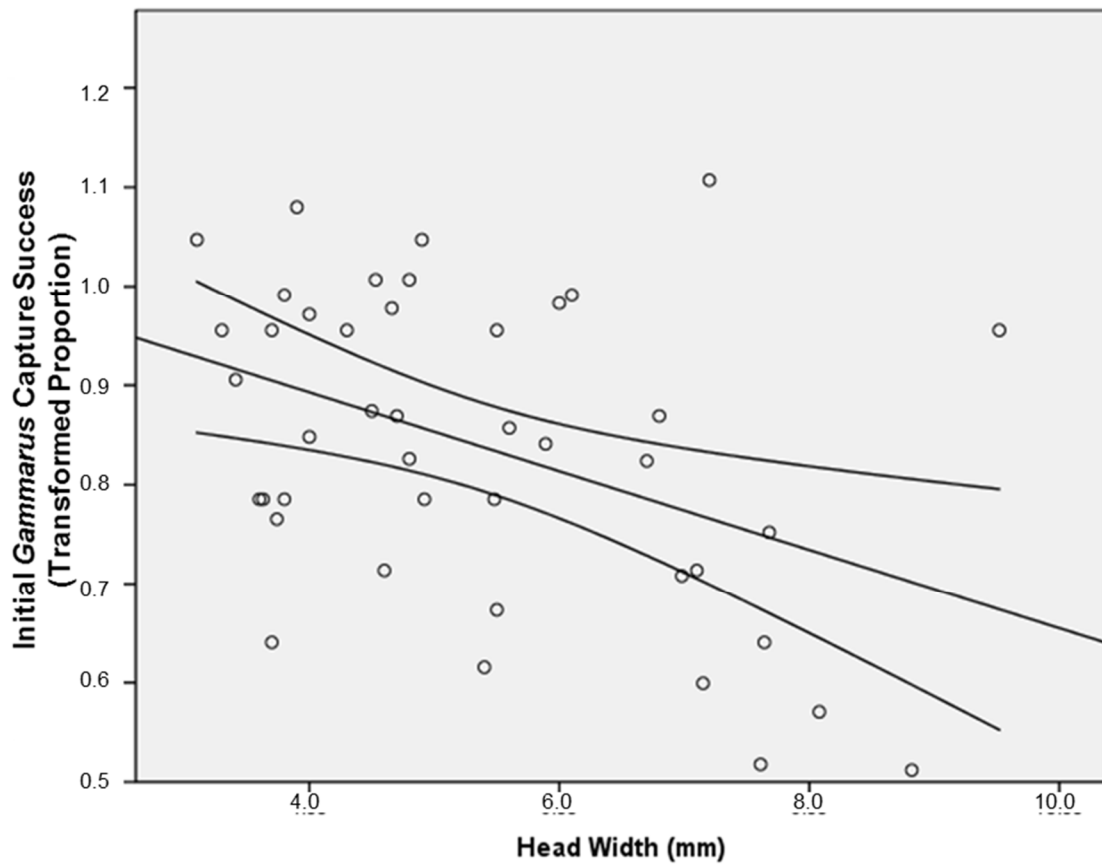


Figure 2-18. *Anax* head width negatively affects initial capture of *Gammarus*. From data pooled from between and within-subjects tests, *Anax* still displayed a negative relationship between initial *Gammarus* capture and *Anax* size. Curves denote a 95% confidence interval around the best fit line.

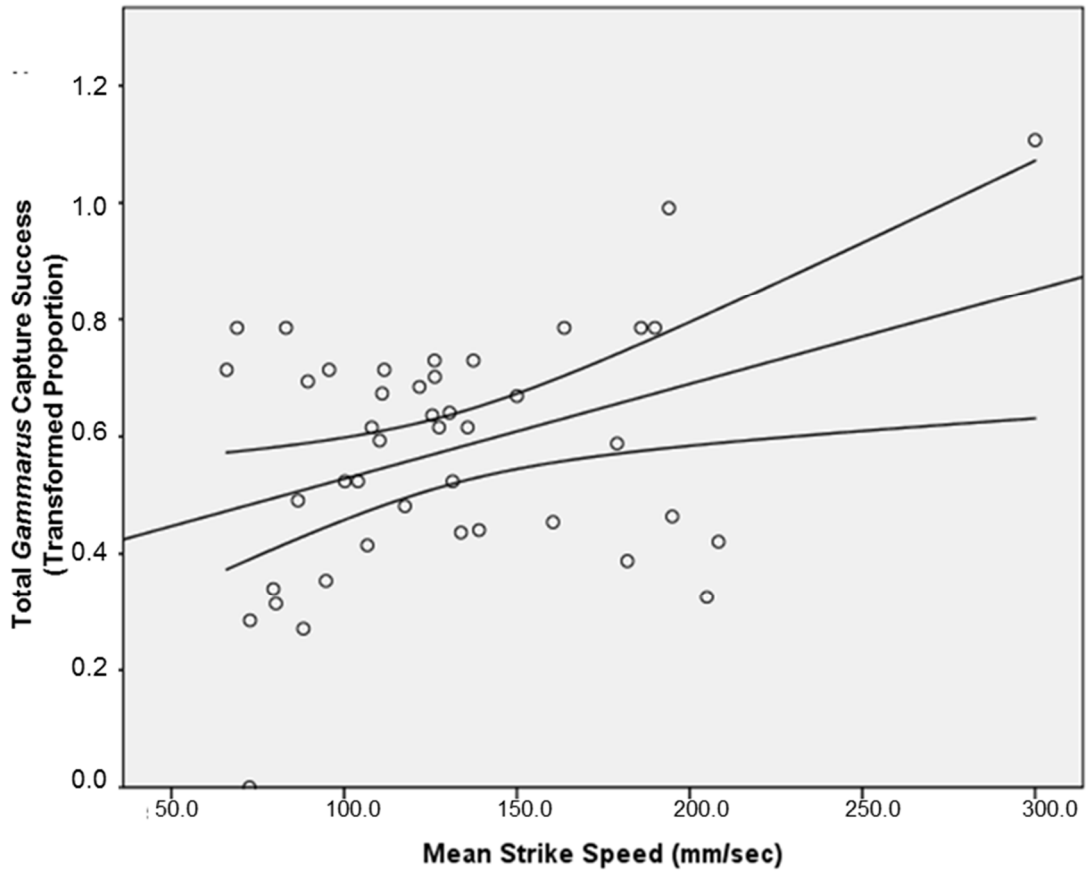


Figure 2-19. Total *Gammarus* capture success by *Anax* varies positively with strike speed. In data pooled from between and within-subjects tests, while attacking *Gammarus*, *Anax* was a more successful predator when its attack speed increased. Curves denote a 95% confidence interval around the best fit line.

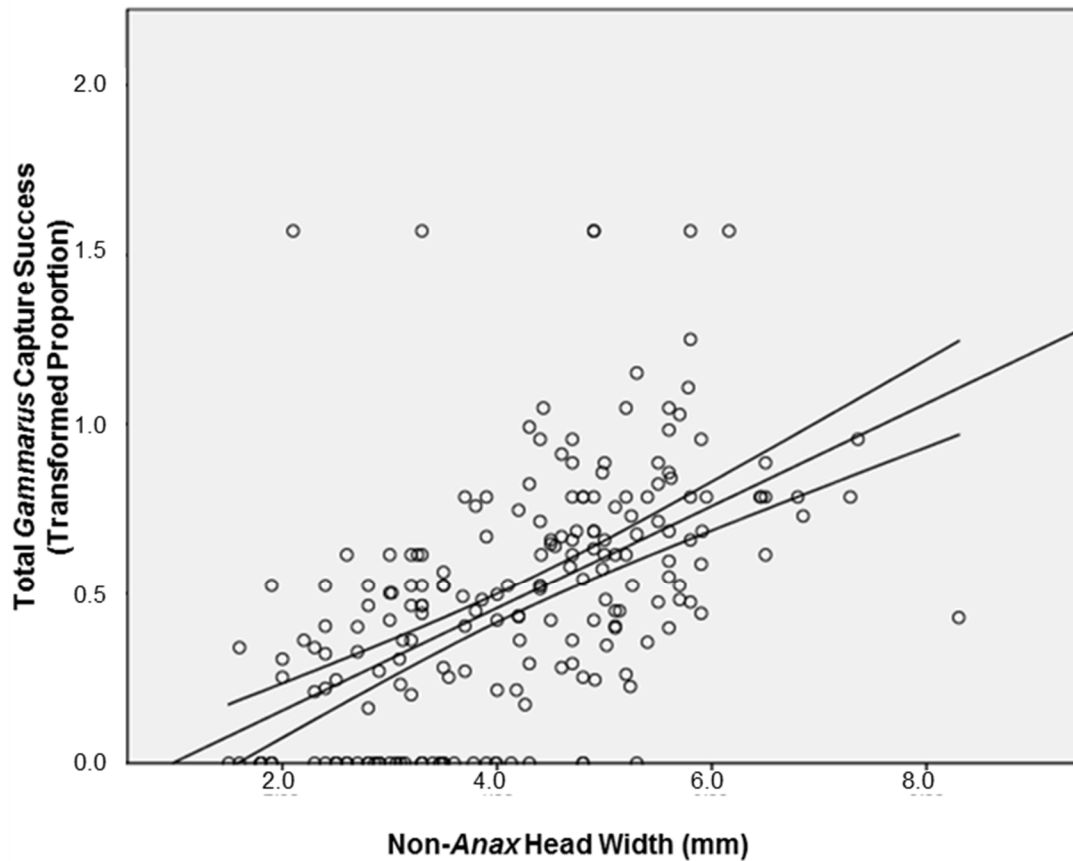


Figure 2-20. *Gammarus* capture success by non-*Anax* species varies with head width. From pooled data, *Gammarus* became easier to catch and consume as the head width of species other than *Anax* increased. Curves denote a 95% confidence interval around the best fit line.

Total predatory success was positively affected by palpal lobe width ($Y=0.903x+0.779$, $P<0.001$), and average strike speed was near-significant ($Y=0.002x+0.779$, $P=0.055$). Both the density of mental setae ($Y=-0.069x+0.779$, $P<0.001$), and the length of the palpal lobes ($Y=-0.698x+0.779$, $P=0.003$) were negatively related to predatory success against *Gammarus*. In total these relationships explained 36.8% of observed variance (Figures 2-21, 2-22). When all non-*Anax* species were excluded and *Daphnia* used as prey in regressions, neither size nor attack speed affected initial capture success. The same is true of *Daphnia* escape, and total predatory success.

When *Anax* was excluded, initial capture of *Daphnia* was not affected by head width or strike speed, but prey post-capture escape is negatively affected by strike speed ($Y = -0.002x + 0.399$, $P = 0.007$), explaining 3.3% of the variance. This translated to a positive relationship with predatory success ($Y = 0.002x + 0.75$, $P = 0.024$) that explains 2.1% of observed variance. In the morphology regressions, initial capture of *Daphnia* was not affected by any predictor variable. Prey escape on the other hand was correlated with attack speed ($Y = -0.003x + 0.738$, $P = 0.004$), palpal lobe length ($Y = -0.082x + 0.738$, $P = 0.017$), and palpal setae density ($Y = -0.026x + 0.738$, $P = 0.004$), all of which negatively affected escape. The amount of variation explained was 7.4%. Total predatory success was positively affected by palpal lobe length ($Y = 0.081x + 0.725$, $P = 0.014$), explaining 2.5% of observed variance (Figure 2-23).

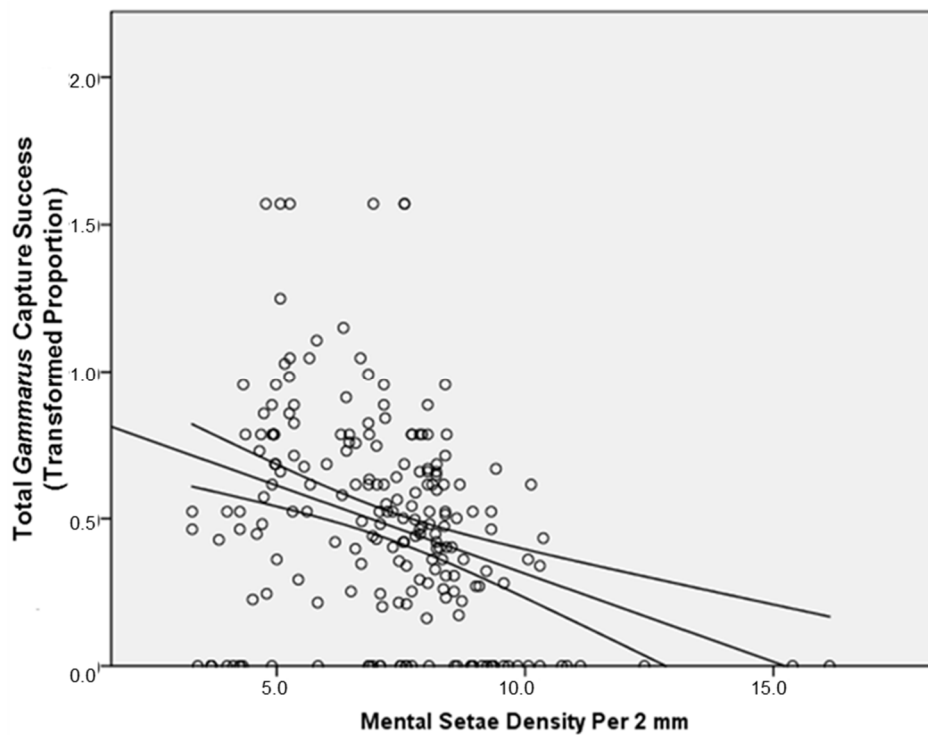


Figure 2-21. Pooled *Gammarus* captures by non-*Anax* varies negatively with mental setae.

From data pooled from between and within-subjects tests, as mental setae density decreased capture success against *Gammarus* by species other than *Anax*. Curves denote a 95% confidence interval around the best fit line.

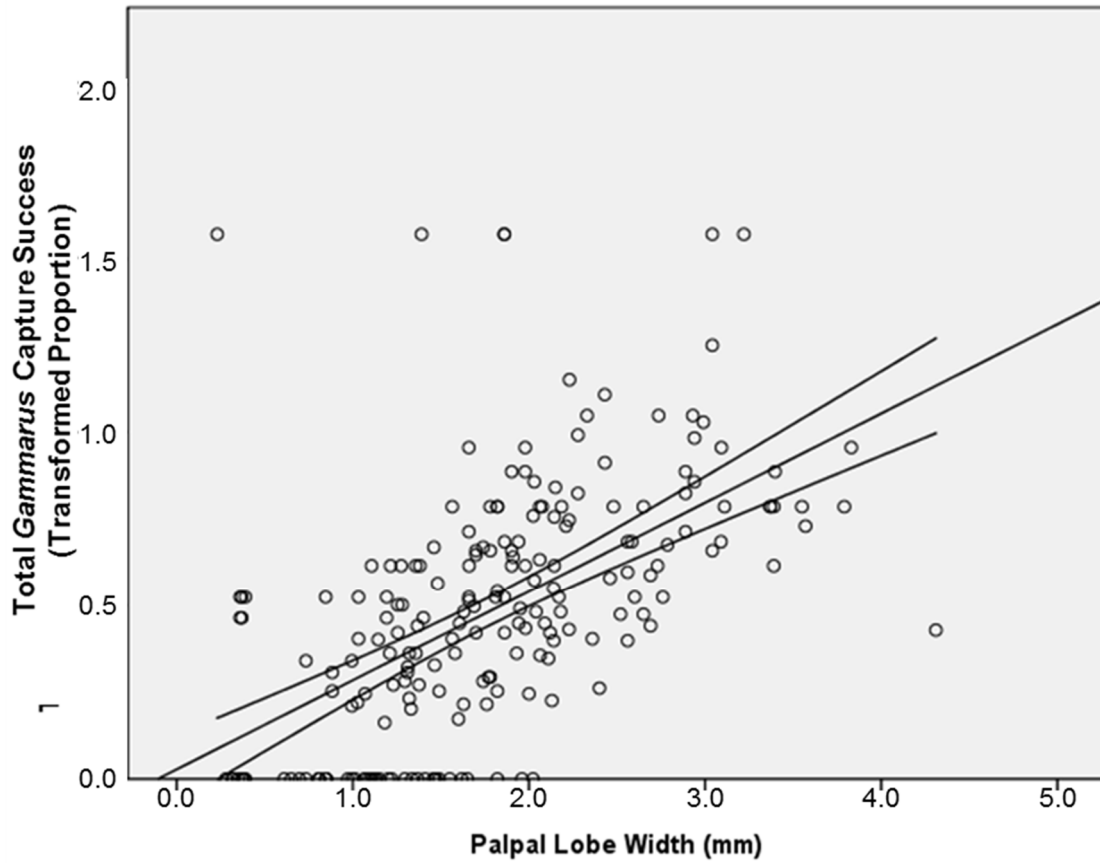


Figure 2-22. Total *Gammarus* capture success by all non-*Anax* varies positively with palpal lobe width.

Data that are pooled from between and within-subjects tests indicate that with increasing size, *Gammarus* became easier to capture and consume. Curves denote 95% confidence interval around the best fit line.

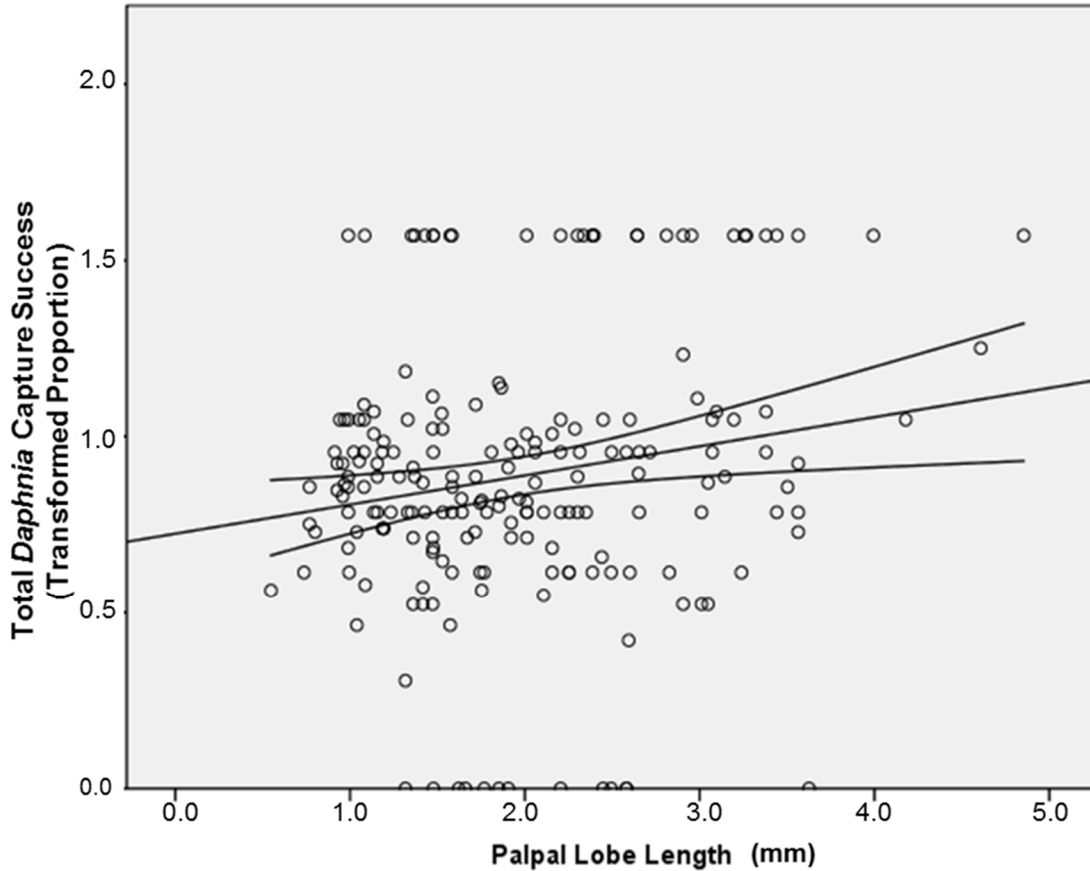


Figure 2-23. Total *Daphnia* capture success by non-*Anax* varies positively with palpal lobe length.

Data that are pooled from between and within-subjects tests indicate that the palpal lobe length of non-*Anax* species was positively related to *Daphnia* capture success.

Curves denote 95% confidence interval around the best fit line.

Discussion

Gape Limitation

This work shows that prey capture success in the Odonata depends strongly on the size of prey (Schael et al. 1991) as well as on morphological differences between predators (Yamada and Boulding 1998). The capture success rates of species with a cup-shaped labial mask (i.e.,

Pachydiplax longipennis and *Tramea lacerata*) increases as a function of head size. Conversely, the opposite trend was observed for species with a flat labial mask; capture success rates declines with head size. These divergent trends are likely due to differences in the initial capture phase of predation, and in post-capture escape. For instance, *Anax* forages by attempting to capture prey by impaling animals with the movable hooks on its palpal lobes, or by gripping prey between the opposing surfaces of the proximal edge of the palpal lobes and the distal edge (Corbet 1999) of the prementum (Figure 2-24). This arrangement is well suited for large prey items, but small prey items are easily missed by the contact surfaces. Thus the success rate of this strategy declines as *Anax* gets larger relative to its prey.



Figure 2-24. Contact points for attacks by *Anax junius*.

Contact points for prey at the distal tips of the palpal lobes (purple circles), and between the medial edge of the palpal lobes and distal prementum (indicated in red and green, respectively).

For all the species with a cup-shaped labial mask from *Erythemis* to *Tramea*, the larger they became, the more difficult it became for *Gammarus*—the larger prey item—to escape once initially caught, and the easier it was for them capture *Daphnia*. Both of these translated to increase prey-capture success for the respective prey.

Strike Speed

Strike speed did not influence initial prey capture for species with a cup-shaped labial mask, but did have a positive effect on the initial capture rate of *Gammarus* by *Anax*. These results were surprising as previous work has shown that a faster strike enhances initial capture success (Webb 1984, Dangles et al. 2006, Meager et al. 2006, Clark et al. 2012). One potential reason that a connection between strike speed and prey capture was not observed is that predator strikes create a wake that precedes the attack in aquatic environments (Young 1991). This may alert prey (Lenz and Yen 1993, Heuch and Karlsen 1997, McHenry et al. 2009) and/or possibly physically propel smaller prey away from the attacking predator (Webb and Weihs 1986, Dodson and Ramcharan 1991, Giambattista et al. 2007). This is a common hypothesis regarding the evolution of suction feeding (Luczkovich et al. 1995, Wainwright et al. 2001). On the other hand, strike speed in *Anax* was positively related to capture success. This is likely because the cross-sectional area moving through the water is very small when they are fully extended (Figure 2-25), which minimizes advance warning of an impending predatory strike to prey. Species with cup-shaped palpal lobes potentially produce larger wakes than *Anax*. However, further study is needed to determine whether this is the case.

One way strike speed does increase prey capture success is in preventing the escape of prey after they are initially seized. This is likely due to positioning of the prey items. Once an attack is initiated, the prementum of a dragonfly nymph is at full extension in, on average, 41.2 milliseconds (N: 218, Mean: 41.2, SD: 11.3). Many prey items are unlikely to be able to get outside the catchment volume of the labial mask in that time (C.O'Keefe et al. 1998, Van Buskirk et al. 2003), but if an attack is on the slower end of that distribution, they might be able to put themselves in a position to escape after they are grabbed. Thus, the faster the strike, the more secure the dragonfly nymph's grip is likely to be, and the less likely a prey item is to get away. One thing worth noting is that dragonfly nymphs irrespective of species modify their strike speed in response to prey species, and this may be a behavioral adaptation that optimizes their strike velocity for different prey (Anderson 1993).



Figure 2-25. Color negative of *Libellula* labial mask at full extension.

This shows the extension of a cup-shaped labial mask at full extension. The cross-sectional area of each lobe is low, reducing the pressure wake in advance of a strike, barring turbulence from drag.

Morphology

Morphological characteristics had significant impacts on prey capture success at different stages of the predation process (Table 2-6). The density of mental setae is positively related to *Gammarus* escape, and higher mental setae densities reduce end capture success against *Gammarus* for dragonfly nymphs. Given their location and orientation, it is reasonable to suspect that setae on the prementum would act as a backstop that prevents *Gammarus* from escaping toward the proximal end of the labial mask and allowing prey to be removed using the nymphs mandibles (Pritchard 1965). However, given that these data indicate that the mental setae help prey escape it may be the case that the setae serve only a sensory function (Gaino and Reborá 2001, Sahlen et al. 2008). If so, they might permit *Gammarus* to escape by providing a micro-refuge inside the catchment volume, holding them against the prementum, but safe from the mandibles of the nymph until the predator tries to manipulate them, giving them a chance to escape. Alternatively, the setae might keep a prey item out of the catchment if the nymph

overshoots (Figure 2-26). Future works needs to determine the mechanistic connection between mental setae and prey escape rates.

The palpal lobes themselves are interesting. The longer they are the easier initial capture of *Gammarus* and *Daphnia* is, which makes intuitive sense. The longer they are, the more reach a given nymph has, and the farther a prey item has to travel in order to avoid the attack, at least along a horizontal vector. However, long palpal lobes also permit *Gammarus* to escape more easily post-capture. This may be a leverage issue.

The adductor muscle that closes the labial palp likely has very limited leverage (Figure 2-27) due to the short lever arm it is attached to (Tanaka and Hisada 1980), while an object pressing against the distal end of the palpal lobe is going to have comparatively high leverage due to the long lever arm on its side of the fulcrum. A prey item like *Gammarus* can exert force on the lever arm, facilitating escape. This is also the likely reason that capturing *Gammarus* is easier with wider palpal lobes. Leverage is not an issue with the width, but the larger surface creates a larger distance the crustacean must travel in order to avoid predation, both in the initial capture phase and in the post-capture phase. Its entire body is potentially enveloped by these lobes and fluid pressure upon labial mask withdrawal forces them against that surface and prevents escape.

Daphnia being very small and with a more limited ability to exert force against the water or hard surfaces have more difficulty escaping from predators. This is likely because the longer palpal lobes increase catchment volume, and its ability to escape after it is within that catchment volume is negatively related to the distance it must travel to escape. A larger volume means it has to travel a longer distance between the time the palpal lobes close, and the time the labial mask is withdrawn.

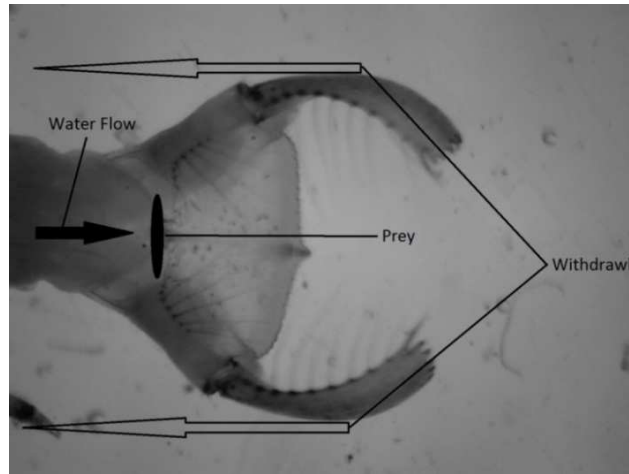


Figure 2-26. Diagram of water flow and prey during a prey-capture overshoot. During an overshoot, a prey item such as *Gammarus* may be blocked from entering the labial mask upon withdrawal by the mental setae.

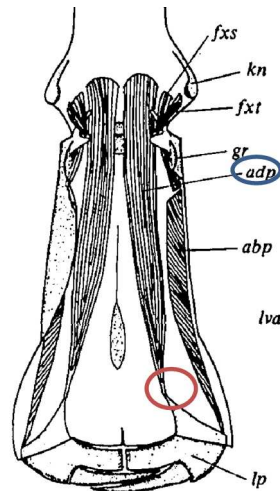


Figure 2-27. Adductor muscles and its attachment site on the labial palp. Adductor muscles (circled in blue) that close the palpal lobes are attached to a very short lever arm (circled in red), that limits the amount of force that can be applied to close the labial mask. Modified from Tanaka and Hisada (1980).

Table 2-6. Effect of morphological variables on prey capture across prey and species. Here, Exp1 is the between-subjects tests only. Exp2 consists of data pooled across the between-subjects and within-subjects tests, - and + denote negative and positive relationships (respectively) between the morphology and prey-capture stage in question.

		<i>Anax</i>			<i>Non-Anax</i>		
<i>Prey=Gammarus</i>		Initial Capture	Prey Escape	Total Capture	Initial Capture	Prey Escape	Total Capture
Head Width	Exp1	-				-	+
	Exp2	-			+	-	+
Attack Speed	Exp1						
	Exp2	+		+		-	+
Prementum Width	Exp1				-		
	Exp2				-		
Palpal Lobe Length	Exp1				+		
	Exp2				+	+	-
Palpal Lobe Width	Exp1					-	+
	Exp2					-	+
Mental Setae	Exp1					+	
	Exp2					+	-
Palpal Setae	Exp1						
	Exp2				-		
		<i>Anax</i>			<i>Non-Anax</i>		
<i>Prey=Daphnia</i>		Initial Capture	Prey Escape	Total Capture	Initial Capture	Prey Escape	Total Capture
Head Width	Exp1	-			+		+
	Exp2						
Attack Speed	Exp1					-	+
	Exp2					-	+
Prementum Width	Exp1						
	Exp2						
Palpal Lobe Length	Exp1				+		
	Exp2					-	+
Palpal Lobe Width	Exp1						
	Exp2						
Mental Setae	Exp1						
	Exp2						
Palpal Setae	Exp1						
	Exp2					-	

There are certain limitations to these data. Intraspecific variation in morphology was almost non-existent once size was accounted for, so all variation observed in morphological variables was a result of the linear combination of size and species. In this case, morphological data likely partially account for the variation that is observed in capture success between species. In order to examine morphology further, one of two methods will be required; direct manipulation of morphology such as palpal and mental setae, or using two closely related species that only differ in one aspect of their morphology. Mechanistic examination of the effects of dragonfly nymph motion on water flow and their subsequent impact on prey could also be done using high speed photography and particulate tracers (Peng and Dabiri 2009, Gemmell et al. 2014).

Competition and Intraguild Predation

This research revealed differences in prey capture abilities that are correlated with interspecific differences in the morphology of the labial mask. Such results have important implications for competitive interactions and the persistence of intraguild predation. First, these results imply that prey specialization may be mediated by morphology (Schluter and McPhail 1992, Svanback and Bolnick 2007). Morphological variation between may affect diet composition, even when active prey choice is not occurring. This can lead to specialization (Seed and Hughes 1995, Labropoulou and Eleftheriou 1997). If this is occurring, it may relieve the pressure of competition, and increase the parameter space within which intraguild predation is stable. If active choice is involved, then it is possible that dragonfly nymphs will shift their dietary preferences toward prey species that they are better able to exploit when in the presence of competitors (Bonesi et al. 2004, Hin et al. 2011), reinforcing this effect.

There is another way in which these results might bear on intraguild predation, *Anax* and its relatives within the Aeshnidae all have very similar morphology (Soltesz 1998, Merrit et al. 2008). Intraguild predation is size-structured among odonates, with larger individuals being more likely to attack and consume smaller individuals irrespective of species (Crumrine 2005, Crumrine 2010). As *Anax* increases in size, its ability to capture small prey decreases. This might create an

inverse size refuge from intraguild predation from *Anax* that relieves the threat of predation on younger instars, and permits them to reach a size where they can compete with heterospecifics, aeshnids often overwinter as nymphs in at least one year (Corbet 1999). In permanent ponds, individuals from other species metamorphose out or migrate in during spring and early summer, then lay eggs (Corbet 1999). Their offspring would be exposed to the much larger aeshnids such as *Anax*. When they are very small, the larger aeshnids may not capture them very effectively.

Most models of intraguild predation assume equal risk for all size classes (Polis et al. 1989, Holt and Huxel 2007), and those that incorporate size-structure find a feedback loop between size and the ability to consume both shared prey and the other predator species (Mylius et al. 2001, van de Wolfshaar et al. 2006). These results show that this feedback loop does not necessarily exist, and that a disparity can be expected to exist—at least in some systems—between the competitive ability of intraguild predator and prey. This disparity may permit coexistence between IG predator and IG prey (Mylius et al. 2001).

Chapter 3

Prey Consumption, Diet Choice, and Predator Attraction.

Introduction

Intraguild predation does not often consist solely of a single intraguild predator and single intraguild prey sharing one prey species (Remsburg and Turner 2009). An IG predator and IG prey are both predators that share other prey. Often, multiple IG prey species co-exist with one or more IG predator species, and this may provide a mechanism by which intraguild predation is maintained. In systems where multiple IG prey species exist, those species will vary in competitive ability, either due to behavioral or morphological differences between species (Relyea 2000, Relyea and Auld 2004, Hoverman et al. 2005, Relyea and Auld 2005). In systems with symmetric predation on IG prey species that are all targeted equally by IG predators that are likely to be unstable, the winner (the species that might survive) will be the species that, when in demographic equilibrium, depresses prey availability to the point that the other species cannot survive. This can be because their requirements are low per individual, or because they are highly effective consumers (Holt et al. 1994). Once this happens, the system may reach equilibrium with the competitive exclusion of the IG predator at low shared prey density or the IG prey at high shared prey density (Holt and Polis 1997). However, IGP does not need to be symmetrical. If superior competitive ability also makes an IG prey species more vulnerable to IGP, then those species may be preyed upon more often than the competitively inferior species. If this happens, then exclusion of a competitively inferior IG prey species by a competitively superior IG prey species may not occur due to suppression of their population by the IG predator (Relyea 2000, Smith 2006).

The presence of alternate IG prey may also prevent the competitive exclusion of the IG predator at low shared prey availability (Kang and Wedekin 2013), and prevent the exclusion of all IG prey at high shared prey availability due to predation. In order for preferential predation to be a mechanism for IGP stability competitive ability and vulnerability to IGP must correlate. There

are several possible mechanisms, with this chapter focusing on the sharp end of predation: the act of attacking and consuming prey.

The examination of this must begin with an understanding of the dragonfly sensory system. The compound eyes of dragonflies are very good for detecting movement, sensing light, and calculating range (Corbet 1962, Pritchard 1966, Sakamoto et al. 1998), but have poor resolving power at distance (Land 1997). So, while their vision is very good for an insect, they still rely on movement to detect prey. There are mechanoreceptors on nymph legs and antennae that are used to detect movement in the water column outside their visual field or in conditions where vision is hampered by poor light or high turbidity (Gaino and Rebola 2001, Sahlen et al. 2008), and chemoreceptors on the antennae that may help detect prey and predators (Gaino and Rebola 2001).

The propulsion and prey-capture mechanisms of dragonfly nymphs are the same. Water is taken in through the rectum where it contacts the gills, and is then expelled by muscular contraction as a form of pulsed jet propulsion, or the rectum is closed off and those same muscular contractions used to increase fluid pressure behind the prementum, throwing it forward in a predatory strike (Tanaka and Hisada 1980). Both movement and pressure disturbances are produced that make the nymph detectable by other nymphs through vision and mechanoreception. This means that predatory strikes by IG prey nymphs have the potential to increase their risk of predation. In addition, because dragonfly nymphs have chemoreceptors, there is the possibility that the incidental release of bodily fluids by shared prey while they are being eaten can attract IG predators (Wisenden et al. 1999, Eklov 2000, Cashner 2004). IG predators may be attracted by these visual, chemical, and pressure cues released by other nymphs feeding in a manner not dissimilar to predator attraction to "Schreckstoff" (Frisch 1942, Cashner 2004). This provides a proximate mechanism by which superior resource competitors might be preferentially targeted for IGP. It follows from this that an IG prey species that consumes more prey items may be more vulnerable than one that consumes fewer prey.

This model is complicated by the fact that foraging behavior modes are not necessarily fixed. Organisms often change their behavior in response to predation risk that can have broad ecological effects. In herbivores such as ungulates (Ripple and Beschta 2004, Laundre 2010) this “ecology of fear” is typified by changes in prey movement and foraging patterns that suppress extensive localized feeding on vegetation (Skarpe and Hester 2008). IG predators might do something similar, changing patterns of prey selection to avoid being eaten, or to increase their energy intake in the face of competition (Barnard and Brown 1981). So the competitively superior species in an IG predator-free context might find itself competitively inferior when IG predators are present, and possibly safer than it would be without a competitor in the face of the same IG predator.

Alternative Prey and Prey Selection

Prey selection is often modeled as a zero-one rule, with prey either included or not included in the diet based on an energy intake calculation (Pyke 1978) such that in a two prey system, the most profitable prey is consumed until its abundance drops below a threshold density, at which point prey preference switches to the more abundant but less profitable prey species (Krebs et al. 1977, Pyke 1978). Although clearly simplistic, this basic model recapitulates some, but not all features of a large majority of systems to which it has been applied (Sih and Christensen 2001). Profitability is generally parameterized in terms of the ratio of benefit to cost, with benefit being defined as caloric value, and cost as search and handling time (Davies 1977, Pyke 1978). Partial preferences, where foragers sometimes take a given prey item and sometimes do not, are rarely modeled very well, which is a shortcoming, given that many studies of foraging demonstrate partial preferences (Krebs et al. 1977, McNamara and Houston 1987, Berec and Křivan 2000, Křivan 2010). There is some work that predicts competitors will partially include less profitable prey in their diet (Křivan 2010), and that partial preferences may exist due to non-omniscience on the part of foragers (Berec 2000, Berec and Křivan 2000).

Most applications of foraging theory deal explicitly in active diet choice (Pyke et al. 1977), not necessarily what ends up in the diet (Power et al. 1992, Labropoulou and Eleftheriou 1997, Downes 2002). There is not much of a difference for prey that cannot defend themselves; such as seeds or sessile insects (Krebs et al. 1977). Predators that feed on active prey that may escape are a different matter, and what a predator wants is not necessarily the same as what it can catch (Sih and Moore 1990, Sih and Christensen 2001). Predators know this, either because they are capable of learning it (Stimac et al. 1982, Suboski 1990, Paradise and Stamp 1991), or innately (Rilling et al. 1959, Prete 1990, Wootton et al. 2007). For example, aeshnids have shown complex prey-specific behaviors that appear to take advantage of their morphologically-based ability to capture and consume prey that are less vulnerable to other predators, such as snails (Rowe 1987) and midge larvae (Power et al. 1992). They have also been demonstrated to learn preferences for prey they have experience catching (Bergelson 1985). Whether these behaviors are learned or the result of innate prey preferences is beyond the scope of the current treatment, but the results should be the same for most prey items commonly found with the odonates under consideration, and very difficult to differentiate for nymphs that are not raised from very early instars with controlled prey availability. Dragonflies are gape-limited and as they become larger, larger prey become easier to catch, and handling time often drops (Werner 1974, Thompson 1975, Scharf et al. 1998). As a result, larger prey should be preferred irrespective of species, but the degree of that preference should be modulated by interspecific differences in ease of capture.

When there is the risk of predation, IGP or otherwise, prey preferences might shift. When attacked or consumed prey species often release a variety of chemical and mechanical cues into the environment (Eklov 2000, Laforsch et al. 2006, Schoeppner and Relyea 2009) that may either be incidental to prey capture or released as explicit signals to conspecifics warning of predation risk (Loennstedt and McCormick 2011). These cues may attract other predators that eavesdrop and interfere with prey-handling (Chivers et al. 1996, Nilsson and Brönmark 2000, Wisenden and Thiel 2002, Cashner 2004), possibly lethally. IG prey species may try to avoid IG predators by changing to less-preferred prey (Elliott 2004, Siddon and Witman 2004, Svanback and Bolnick

2007). This may be done by taking smaller prey that releases fewer detectable cues into the water column or prey with shorter handling times, or by increasing preference for easy prey so that a larger proportion of attacks justify the predation risk. IG prey may also reduce movement rates (Babbitt 2001, Ferris and Rudolf 2007), and the total number of predatory attacks in order to avoid being consumed.

Prey availability might also play a role in shaping behavior (Lawton et al. 1980, Johansson 1993). As prey become more abundant, the energy cost of foraging drops (Hirvonen 1999, Greeff and Whiting 2000). So at high prey availability, IG prey species should be more likely to reduce foraging activity or switch preferences toward less risky prey, because the costs of doing so are decreased (Babbitt 2001).

I tested the following predictions:

- 1) Anti-predator responses of IG prey (which is a predator that is fed upon by other predators) will be to reduce strike rate on shared-prey, and switch to smaller prey that releases fewer IG predator-attracting cues.
- 2) Due to predator attraction, strike rate and the consumption of prey on the part of IG prey will increase the probability of attack by an IG predator.
- 3) IG Predators will disproportionately target the IG prey species that displays higher strike rates (the rate at which shared prey is attacked over time) against shared prey and that consumes higher shared prey biomass.

Methods and Results

Prey Choice When The IG Predator Is Restrained

Several different sets of experiments were conducted to test these predictions. The first experiment tested for changes in prey choice based on non-lethal heterospecific presence (i.e., predators that could potentially prey upon one another were placed together but prevented from physically interacting), and for differences in prey selection on the basis of size and ease of capture. To do this, *Libellula lydia*, *Erythemis simplicicollis*, and *Pachydiplax longipennis* were

used as focal individuals. These species were used in all experiments in this chapter because they all co-occur with each other and the chosen IG predators in the same ponds, and occupy the same regions of the littoral zone within patches of vegetation. So they are in direct competition with each other and are exposed to the same IG predators used in these experiments. Each individual was randomly assigned to one of four treatment groups: no IG predator, conspecific, *Anax junius*, or *Tramea lacerata*. The latter two are IG predators. This created a 3x4 factorial experiment with 10-15 replicates; each replicate used a single individual. All trials took place in 90 mm petri dishes divided down the middle using a barrier created from nylon mesh stretched over an aluminum frame.



Figure 3-1. Experimental setup visualization.

Focal nymphs are placed toward the middle of the frame along with prey items, with an IG predator nymph (if any) on the other side.

The nylon mesh divider permitted potential chemical cues to diffuse through the water, and was partially transparent to visible light, so focal individuals should have been able to detect individuals on the other side of the divider. At the beginning of each trial, individuals were placed on their respective sides and a 5 minute acclimation period was allowed, following which 10 individuals of *Gammarus* sp. and 10 individual *Daphnia* sp. were placed on the focal individual's side as prey items (Figure 3-1). Each trial was filmed using a Nikon L610 camera at 30 frames per second with a resolution of 1920x1080 pixels for ten minutes. All analyses were performed in

Kinovea (Version 1.21, 2014). Body length and head width were measured digitally for all focal individuals. All attacks, initial captures, escapes and then final consumption were scored as in Chapter 2, above. In addition, contact encounters were recorded. Contact encounters were defined as the number and type of prey items occupying an arc from the distal end of the second pair of legs at full extension and extending out past the head, at the time of attack (Figure 3-2). These were summed for each individual and prey species.

Data analysis was a within-subjects ANCOVA of arcsine square root transformed predatory success rates against each prey type by species. Body length was used as a covariate in this analysis.



Figure 3-2. Strike range utilized to determine contact encounter rates.

Prey that are counted are circled in aquamarine, while the green arc denotes the range, determined by the length of the middle leg pair at full extension.

The second analysis directly tested for prey choice between species and IG predator treatment. This was done by testing for deviation from randomness in prey choice. The contact encounter rates taken from video were used to generate an expected value for predatory attacks, with the assumption that attacks are random and thus should be congruent with the proportion of prey types occupying the nymph's strike range when it attacks. The observed and expected

values were used to calculate the chi-squared statistic, which was sign-reversed to indicate the direction deviated from randomness, with negative values indicating a preference for *Daphnia*. This was normalized into a Prey Choice Index (Equation 3-1) following Wilson and Hilferty (1931).

Let: W be the Prey Choice Index, Y be the chi-squared statistic and n be the degrees of freedom. This normalization is monotone and preserves sign once centered so that 0 indicates no prey preference. These data were analyzed using ANCOVA by species and IG predator, using body length as a covariate.

$$W(Y) = \frac{\left(\frac{Y}{n}\right)^{1/3} - \left(1 - \left(\frac{1}{9}\right)\left(\frac{2}{n}\right)\right)}{\sqrt{\left(\frac{1}{9}\right)\left(\frac{2}{n}\right)}}$$

Equation 3-1

Within-subjects tests of prey capture success indicated that species differ significantly in their ability to capture *Gammarus* and *Daphnia* (Figure 3-3). Capture success rates differ between prey type (df=1, F=27.409, P<0.001), and there was an interaction between prey type and focal individual body length (df=1, F=10.454, P=0.002), along with prey type and species (df=2, F=3.192, P=0.045). There was a significant relationship between prey type and both focal species (df=2, F=5.796, P=0.004) and IG predator (df=3, F=5.51, P=0.001) but not nymph body length. The total R² of these relationships is 0.22 (Figure 3-4).

Omnibus Methods

The next set of experiments were all conducted using a physical methodology that is identical save for the treatment groups used and the statistical tests that apply. All trials took place in 90 mm petri dishes, with a single focal nymph, along with each set of prey, IG predator, or competitor that was required for the experiment in question. After a five minute acclimation period, trials were filmed for 10 minutes using a Nikon L610 camera at a resolution of 1920x1080, 30 frames per second. Video analysis was done using Kinovea (Version 1.21, 2014). Body

lengths, and head widths were all measured digitally. All attacks on shared prey (non-guild prey) were recorded, and converted to attack and consumption rates.

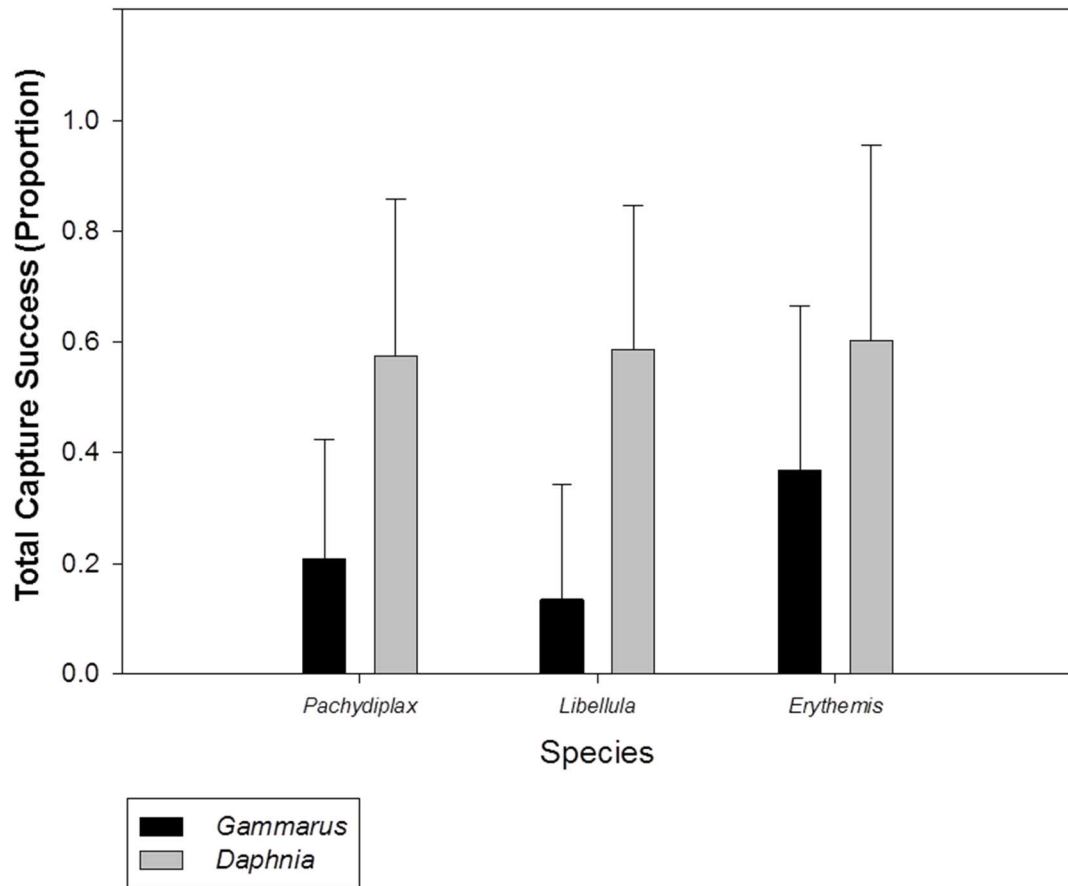


Figure 3-3. Prey capture success varies between prey and dragonfly species
Prey capture success against the two prey types was different between the three focal species of IG prey nymph, with *Daphnia* being generally easier to capture and consume. The data displayed are the proportion of attacks that lead to prey capture and consumption. Error bars=1 SD.

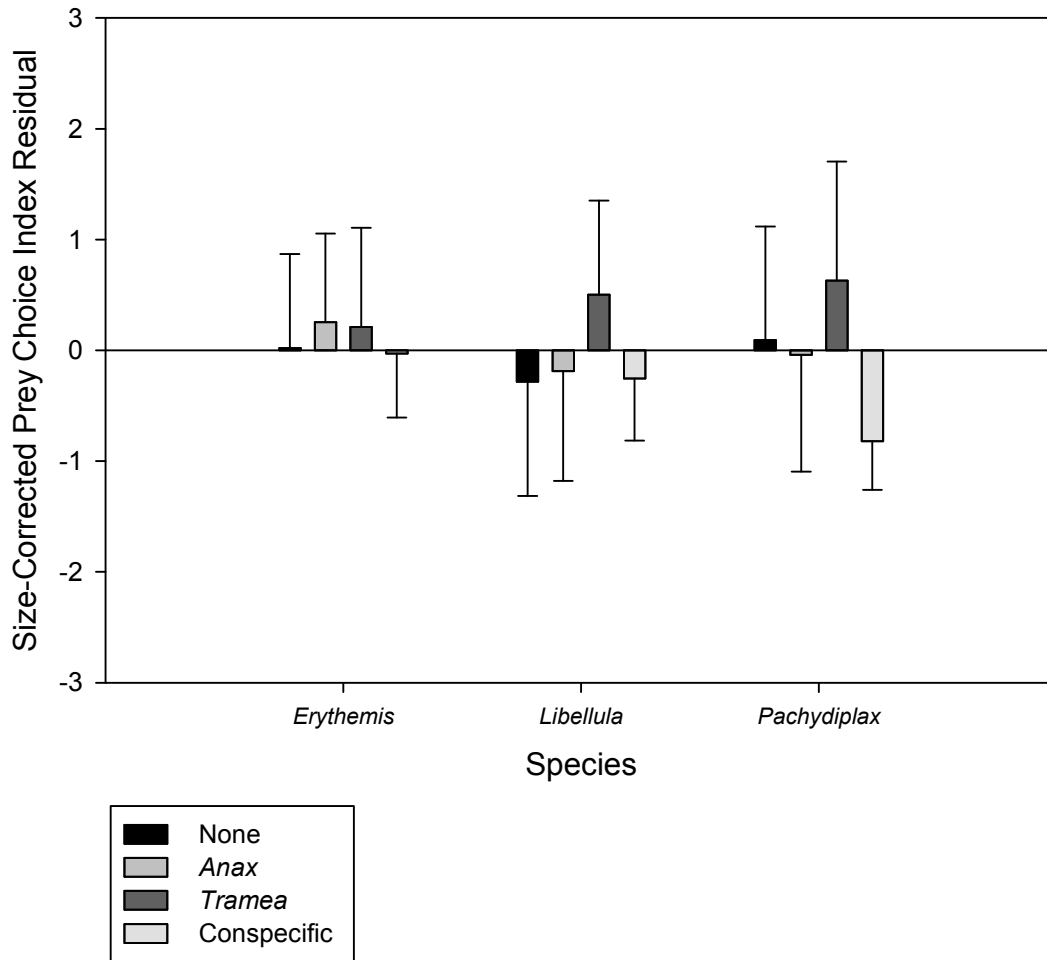


Figure 3-4. Prey choice varies between IG prey species and restrained IG predator. This shows changes in preference for the three focal species (*Erythemis*, *Libellula*, and *Pachydiplax*) based on non-lethal exposure to an IG predator (*Tramea*, *Anax*, and a conspecific). Displayed is the residual of the Prey Choice Index after regression over the width of the focal nymphs head in order to correct for individual nymph size. The Prey Choice Index is a unitless monotonic transformation of a Chi Squared statistic that has been sign reversed to show the direction of a preference. Low values (in the negatives) indicate a preference for *Daphnia*, high values (positive values) indicate a preference for *Gammarus*. Error bars=1 SD.

Time to death by IG predation was recorded for all IG prey nymphs, truncated at 600 seconds when the trial ended. Where relevant, prey choice was calculated for all focal individuals as above. Lastly, a subset of consumed prey items (the ones that could be measured given camera angle) had their volume estimated (under the assumption that they approximate a cylinder and all prey types are equal in their density), and averaged. This volume was used as a proxy for biomass consumption (referred to herein as biovolume) for every individual based on how many of each prey type they consume, and was tabulated both separately for each prey type, and summed.

On occasion, certain statistical techniques were used that might have notations that are unfamiliar. Logistic and Cox regressions for example utilize the coefficient B which denotes the relationship between the predictors and the response variable in its regression model. The ratio between B and its standard error (denoted: S.E) determines the Wald Chi Squared statistic (denoted: Wald). Wald when combined with the degrees of freedom (denoted: df) determines the degree of significance for hypothesis testing (denoted: Sig). Bexp (and ExpB, depending on the analysis) is the odds ratio change in the odds of the event of interest (e.g. death) for a one unit change in the value of the predictor variable. AIC is the Akaike information criterion, which is a measure of model fit. Smaller is better within a given set of competing models. Another measure of model fit that is often used is the -2 log-likelihood statistic (sometimes denoted: -2LL) which is also in smaller-is-better form.

Prey Choice When The IG Predator Is Unrestrained

Here, competition and changes in movement and prey choice between simple intraspecific competition and IG predation were tested in lethal conditions (i.e., an IG predator had direct access to IG prey, and non-guild shared prey). To do this, *Erythemis simplicicollis*, *Libellula lydia*, and *Pachydiplax longipennis* were used as focal species. These were randomly assigned to one of two prey density treatments and one of two competitor/IG predator treatments (hereafter referred to as IG predator), for a 3x2x2 factorial design with 10-12 replicates. Prey

density treatments consisted of a low prey density treatment with 10 *Daphnia* and 10 *Gammarus*, while the high density treatment used 20 of each. The IG predator treatment consisted of either a conspecific, or *Anax junius*. Data were collected as per the Omnibus Methods above.

The Prey Choice Index was used as a response variable in an ANCOVA between species, prey density, and IG predator with body length and strike rate used as covariates, with non-significant terms discarded until R^2 was maximized. Strike rate was also used in an ANCOVA by species, prey density, and IG predator; as was biovolume consumption and movement rate. Then, because no IG predation occurred between conspecifics, they were excluded in order to perform a logistic regression on IG predation attacks. Predictors in this analysis included IG prey species, IG predator species, prey density, IG predator prementum/IG prey length ratio (hereafter referred to as the prementum ratio), Prey Choice Index, summed strike rate and biovolume consumption, run in a backward selection procedure. Cox regression was used to examine mortality rates between IG prey species and the impact of IG predator identity on mortality rates using a similar set of predictor variables.

Prey choice was affected by total strike rate ($Y=3.839x-0.295$, $df=1$, $F=15.381$, $P<0.001$), body length ($Y=0.019x-0.295$, $df=1$, $F=10.351$, $P=0.002$), and IG prey species ($df=2$, $F=6.820$, $P=0.001$). There was also a significant interaction between IG predator and initial prey density ($df=1$, $F=8.270$, $P=0.005$), and a nearly significant species by IG predator interaction ($df=2$, $F=2.715$, $P=0.069$). In total, 20.5% of prey choice variation was explained by these relationships (Figure 3-5). Strike rate varied by species ($df=2$, $F=17.146$, $P<0.001$), initial prey density ($df=1$, $F=5.514$, $P=0.02$), and by the interaction between species, IG predator, and prey density ($df=2$, $F=7.772$, $P=0.001$). These relationships maximized R^2 at 0.218 (Figure 3-6). Biovolume consumption varied with prey choice ($Y=0.084x -0.05$, $df=1$, $F=25.057$, $P<0.001$), IG prey body length ($Y=0.005x-0.05$, $df=1$, $F=14.853$, $P<0.001$), and species ($df=2$, $F=8.569$, $P<0.001$). There were marginal interactions between species and initial prey density ($df=2$, $F=2.898$, $P=0.058$), and between species, IG predator, and initial prey density ($df=2$, $F=3.030$, $P=0.051$). R^2 was maximized at 0.297 (Figure 3-7).

IG predatory attacks did not differ between focal species or any other variable with the exception of the prementum ratio ($df=1$, $B=4.756$, $B_{exp}=116.239$, $Wald=3.914$, $P=0.048$, $-2 \log$ likelihood=83.063). Cox regression indicated that the probability of death for an IG prey species (as distinct from the shared prey species) was affected only by its body length ($df=1$, $B= -0.191$, $B_{exp}=0.826$, $Wald=5.427$, $P=0.02$, $-2 \log$ likelihood=103.012) and movement ($df=1$, $B=0.135$, $B_{exp}=1.145$, $Wald=6.937$, $P=0.008$, $-2 \log$ likelihood=103.012).

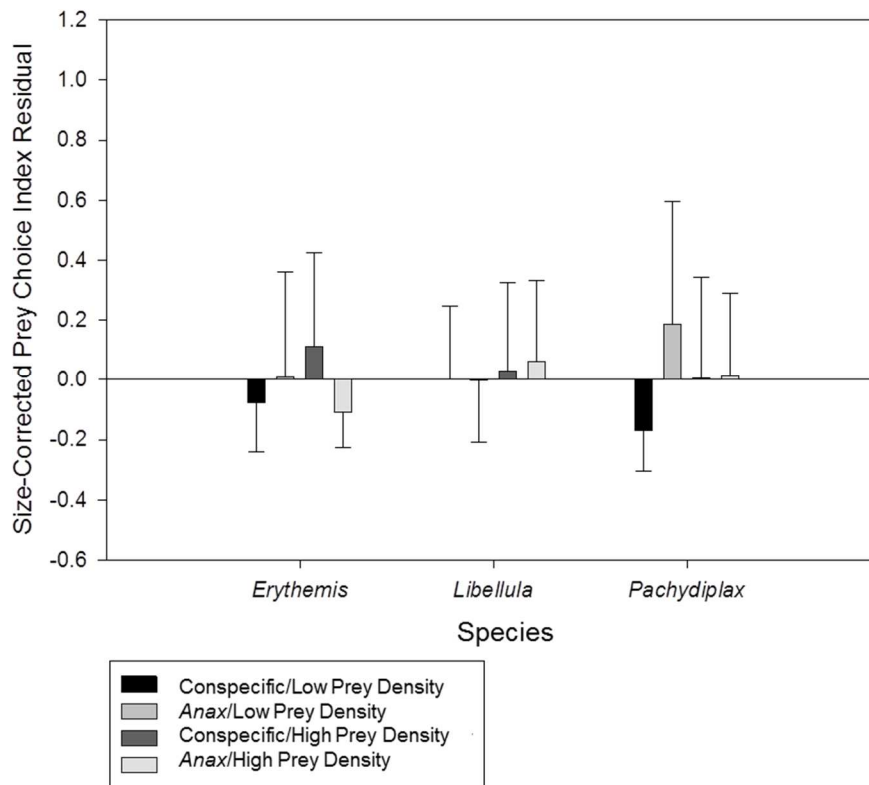


Figure 3-5. Prey choice varies by species, prey availability and lethal IG predator.

Prey selection changes for the three focal species exposed to an *Anax* or to a conspecific at high or low shared prey density. The response variable is a size-corrected Prey Choice Index where larger values translate to *Gammarus* preference. Error bars=1 SD.

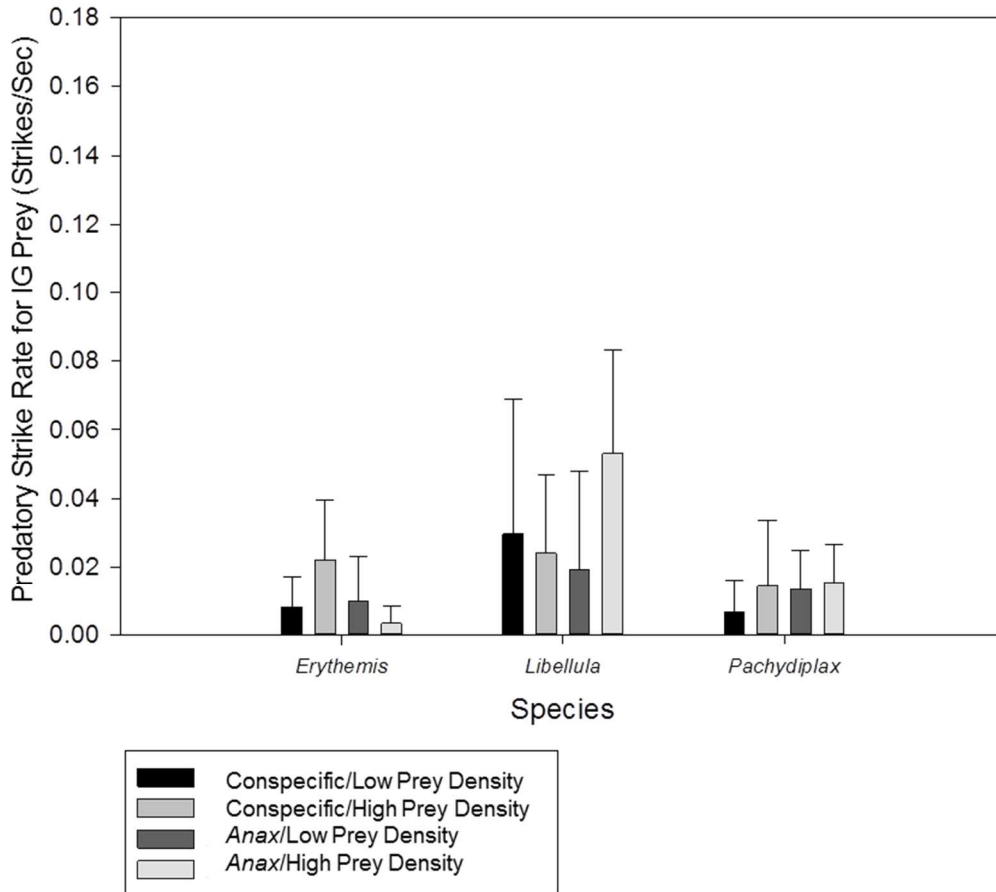


Figure 3-6. Strike rate varies between species, IG predator, and prey density. Dragonfly nymph strike rates (the rate at which focal nymphs attack shared prey items) changed as a consequence of potentially lethal exposure to *Anax* or to a conspecific, at high or low prey density. Error bars=1 SD.

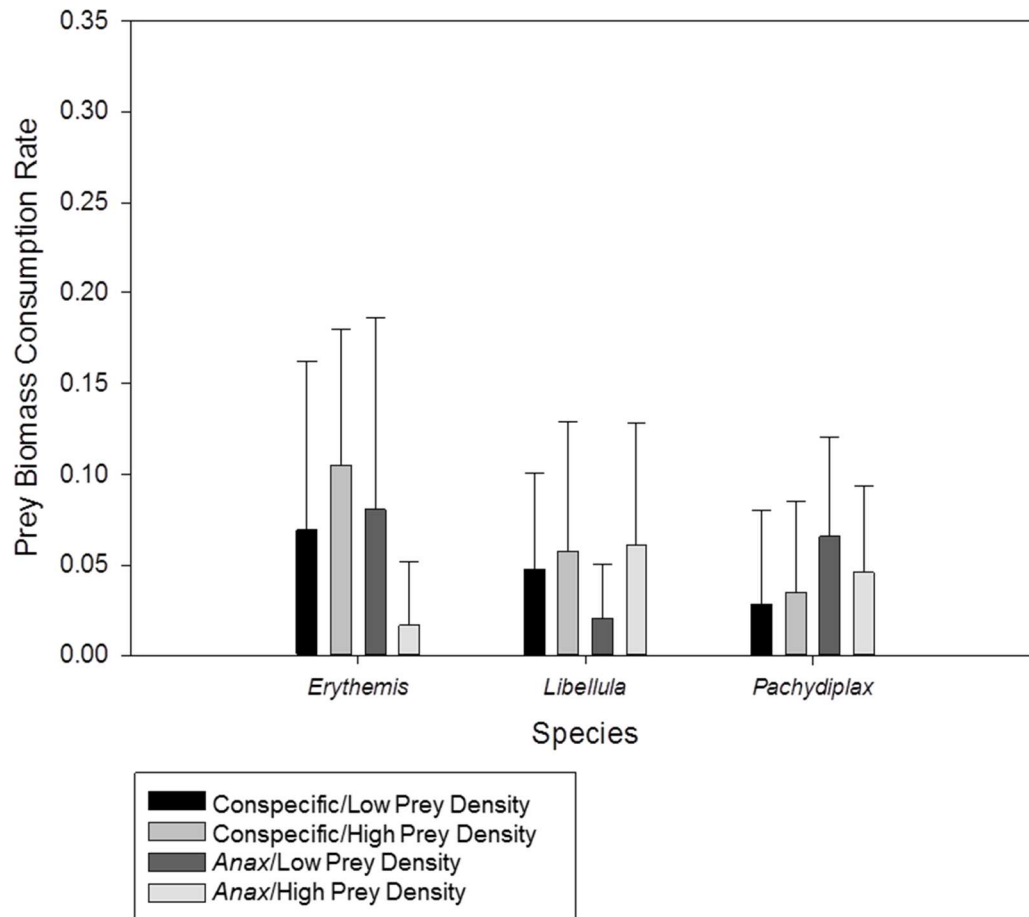


Figure 3-7 Biovolume consumed varies by species, IG predator and prey density. Biovolume is the calculated volume of prey items consumed, and is used as a proxy variable for biomass. This graph shows how the rate at which that volume was consumed by dragonfly nymphs that were exposed to predation risk from *Anax* or from a conspecific, at both high and low shared prey density. Error bars=1 SD.

Prey Composition and Mortality Methods

The third experiment tested for the effects of prey composition on competitive and IG predatory interactions between species. *Libellula lydia* and *Erythemis simplicicollis* were used as focal species, randomly assigned into a prey composition treatment consisting of 10 individuals of *Daphnia* sp., 10 individuals of *Gammarus* sp., or 10 of each shared prey species, then into an IG predator treatment consisting of a conspecific, *Anax junius*, or *Tramea lacerata*. This set up a 2x3x3 factorial design with 10-12 replicates. Data were recorded in accordance with the Omnibus methods above. IG predator attacks on IG prey focal species were analyzed using logistic regression between treatment groups and utilizing the same covariates as above.

Logistic regression including prey composition, species, IG predator and prementum ratio as predictors of the probability of attack found significant effects of IG predator ($B_{Anax}=2.004$, $df=1$, $Wald=11.599$, $P=0.001$) and prementum ratio ($B=4.303$, $df=1$, $Wald=6.52$, $P=0.011$), with a near-significant effect of prey composition ($df=2$, $Wald=5.370$, $P=0.068$; $B_{Gammarus}=1.216$, $df=1$, $Wald=3.726$, $P=0.057$; $B_{Both}=1.232$, $df=1$, $Wald=4.734$, $P=0.03$). This minimized AIC at 131.12. When this was performed again using focal species, IG predator, prey composition, movement rate, strike rate, IG predator strike rate, and biovolume consumption, the results were somewhat different. The resulting model included IG predator ($B_{Anax}=1.851$, $df=1$, $Wald=8.735$, $P=0.003$), prementum ratio ($B=4.678$, $df=1$, $Wald=7$, $P=0.008$), strike rate ($B=63.666$, $df=1$, $Wald=8.222$, $P=0.004$), and movement rate ($B=-276$, $Wald=10.65$, $P=0.001$). In this extended model, AIC improved to 118.344.

Cox regression of mortality utilized these variables as predictors, in addition to focal species in order to account for species-specific differences in predator attack success that may exist. The same variables were included in the final model, with focal species being non-significant (Table 3-1, Figure 3-8). The -2 log-likelihood for this model was 162.071.

Whether or not an IG prey nymph was attacked was affected by IG predator ($B=2$, $df=1$, $P=0.001$). There was no difference in attacks on IG prey nymphs between *Gammarus* and both shared prey treatments (*Gammarus* + *Daphnia*), but *Daphnia* treatments led to significantly lower

rates of IG predator attack on IG prey nymphs ($B=1.232$, $P=0.03$). As the ratio of IG prey body length ($B=4.303$, $P=0.011$) and IG predator prementum width increased, the probability of an attack by the IG predator also increased. -2LL (the -2 log-likelihood statistic) was 123.784 (Figure 3-9).

Table 3-1. Cox regression included variables.

Cox regression was used to determine what variables affected the probability of death for focal nymphs. This indicates that size-differences between IG predator and IG prey nymphs, IG prey strikes on shared prey, IG prey movement rate, and IG predator identity affected the risk of death for IG prey nymphs.

	B	SE	Wald	df	Sig.	Exp(B)
Species	0.174	0.493	0.124	1	0.725	1.190
Premontum Ratio	4.115	1.286	10.242	1	0.001	61.249
Strike Rate (strikes/sec)	37.333	11.439	10.651	1	0.001	1.635E16
Movement Rate (mm/sec)	0.122	0.040	9.396	1	0.002	1.130
IG Predator	1.590	0.604	6.941	1	0.008	4.904

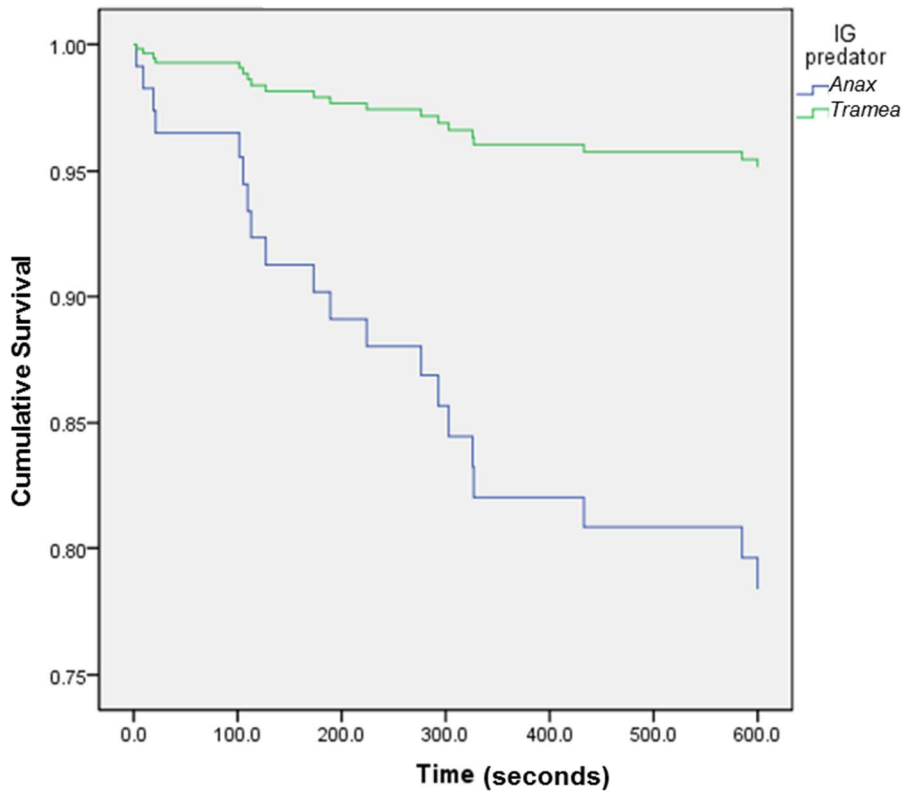


Figure 3-8. Cumulative survival curve for IG prey nymphs exposed to *Anax* and *Tramea*. This is the Cox regression curve that shows survival over time for IG prey nymphs (such as *Erythemis*) when they are the potential prey of an IG predator (in this case *Anax* or *Tramea*, conspecifics were excluded). *Anax* was more lethal over time than *Tramea* was for all IG prey nymphs.

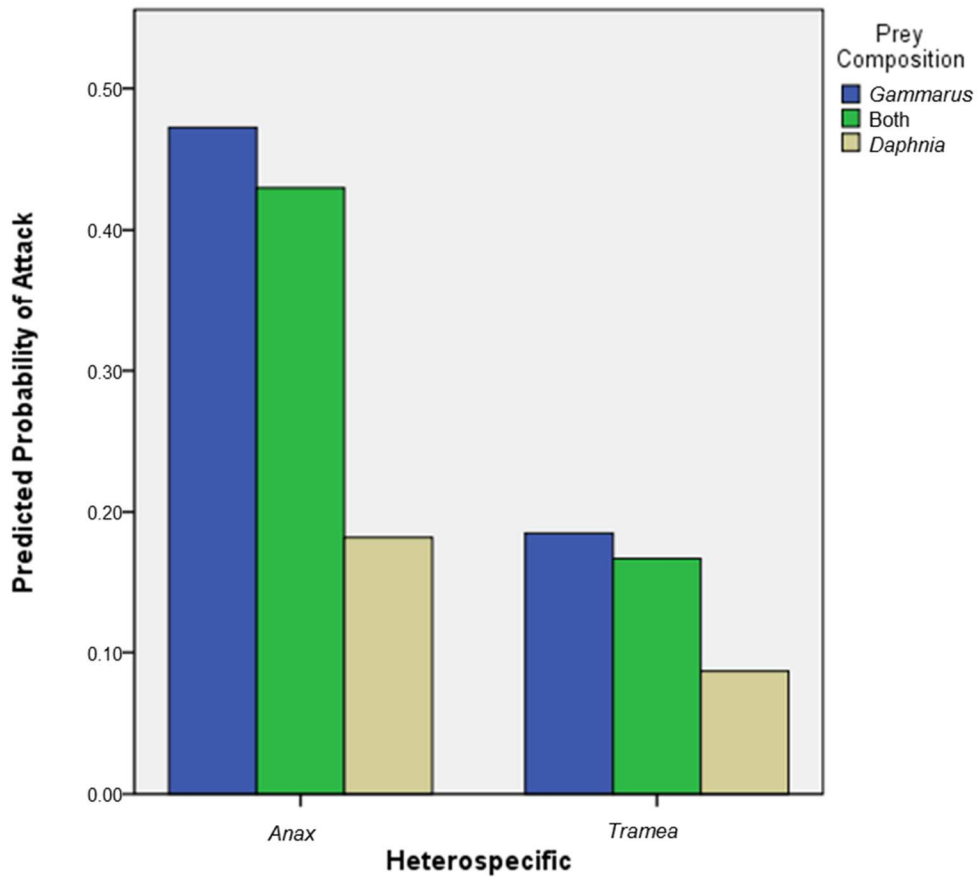


Figure 3-9. Probability of attack varies with IG predator and prey composition. This is a model based on a binary logistic regression. The response variable was a 0 or 1, denoting whether or not a given nymph was attacked over the course of a trial by another nymph. Predictor variables for this particular model were the species of the attacker and the prey composition: *Daphnia*, *Gammarus*, or both. The proportions denoted here is the calculated probability that a given nymph would be attacked over the course of a trial.

Competition and IGP Methods

This experiment tested for the effect of intra- and interspecific competition on IGP. It utilized a 2x2x2x2 design with the first factor being Species A (*Pachydiplax longipennis* or *Libellula lydia*), a second species denoted Species B (so any given Species A is exposed to either a conspecific or a heterospecific IG prey species). The third factor was an IG predator treatment consisting of either no predator or *Anax junius*. The final factor was a prey density treatment (high and low) that included both *Gammarus* and *Daphnia*. The batteries of statistical tests are otherwise identical to those for prior experiments; save that competitor (Species B) biovolume consumption is included as a covariate in tests of strike rate and biovolume consumption.

Competition and IGP Results

Prey choice varied between IG prey species (df=1, F=11.333, P=0.001) and body length (Y=0.018x-229, df=1, F=15.022, P<0.001), as well as strike rate (Y=5.686x-229, df=1, F=35.691, P<0.001). There was also an interaction between IG prey species, competitor species, and IG predator (df=1, F=4.141, P=0.035). These relationships explained 17.4% of the variation in prey choice (Figure 3-10). Strike rate was affected by focal species (df=1, F=6.011, P=0.015) and two interactions: a competitor by predator interaction was identified (df=1, F=10.798, P=0.001), and a species by predator by initial prey density interaction (df=1, F=4.548, P=0.034). These relationships explained 9.5% of variation in strike rates (Figure 3-11).

Biovolume consumption varied with IG prey body length (Y=0.004x-0.053, df=1, F=6.903, P=0.009), prey choice (Y=0.084x-0.053, df=1, F=12.862, P<0.001), and strike rate (Y=1.057x-0.053, df=1, F=9.13, P=0.003). These relationships explained 15.9% of the variation in these data. Movement rate varied by species (df=1, F=15.119, P<0.001), IG predator (df=1, F=3.957, P=0.048), and the prementum ratio (Y=-6.838 X-2.002, df=1, F=4.009, P=0.046), with a model R² maximized at 0.067 (Figure 3-12).

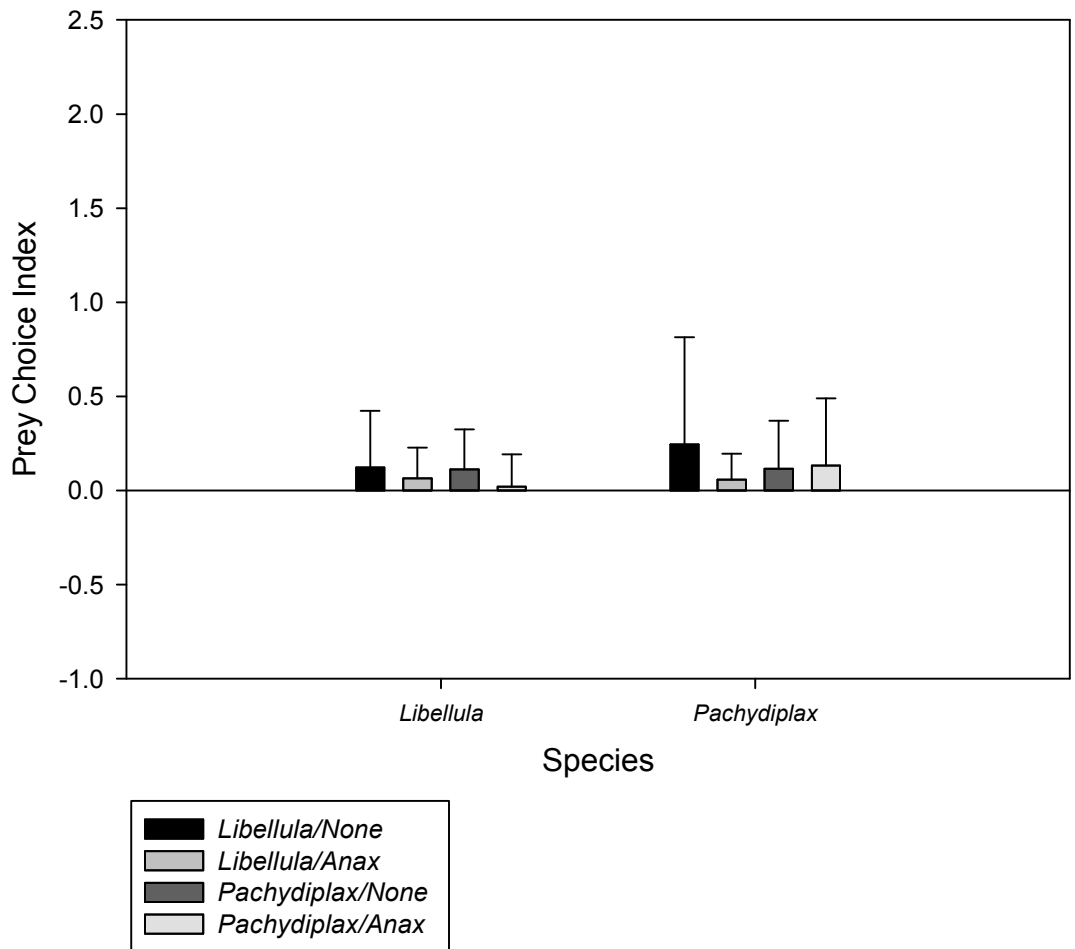


Figure 3-10. Prey choice varies by competitor and IG predator. This shows how prey choice varied between species IG prey species (either *Libellula* or *Pachydiplax*, X axis) in response to combinations of IG prey competitors (either *Libellula* or *Pachydiplax*) and the presence or absence of an IG predator (*Anax* or None). Positive values of the Prey Choice Index indicate a preference for *Gammarus*.

Error bars=1 SD.

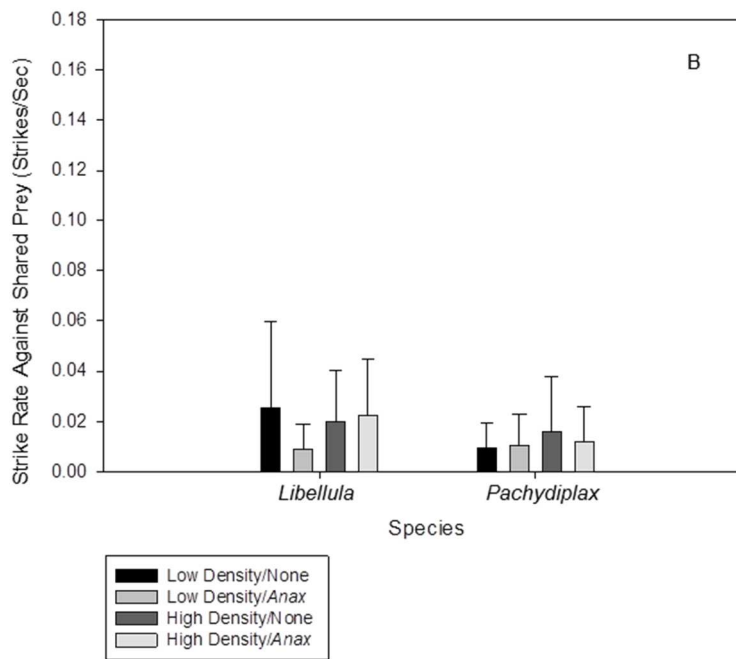
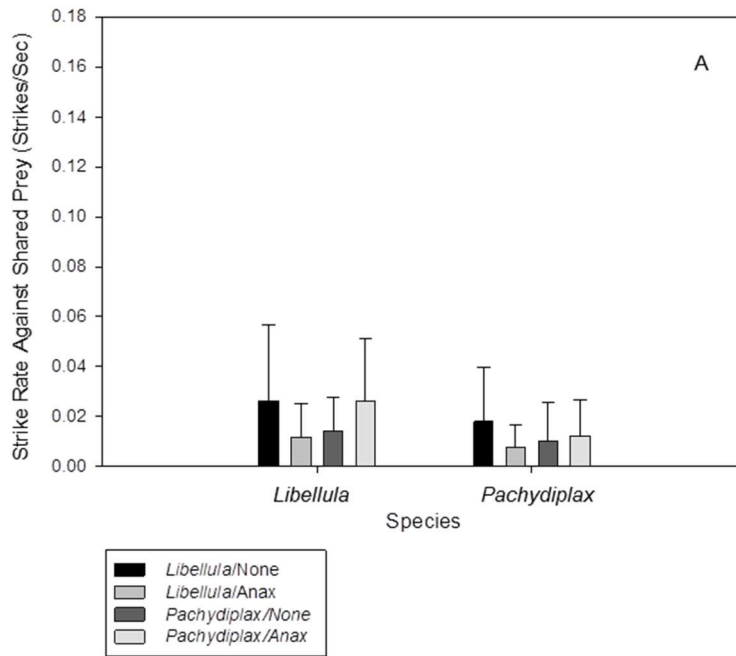


Figure 3-11 Strike rate varies with competitor, prey density, species, and IG predator.

A=Strike rate response by IG prey species (X Axis) to an IG prey competitor and an IG predator (e.g., *Libellula*/None). B=IG prey species (X Axis) by prey density and IG predator (e.g., Low Density/*Anax*). Error bars=1 SD.

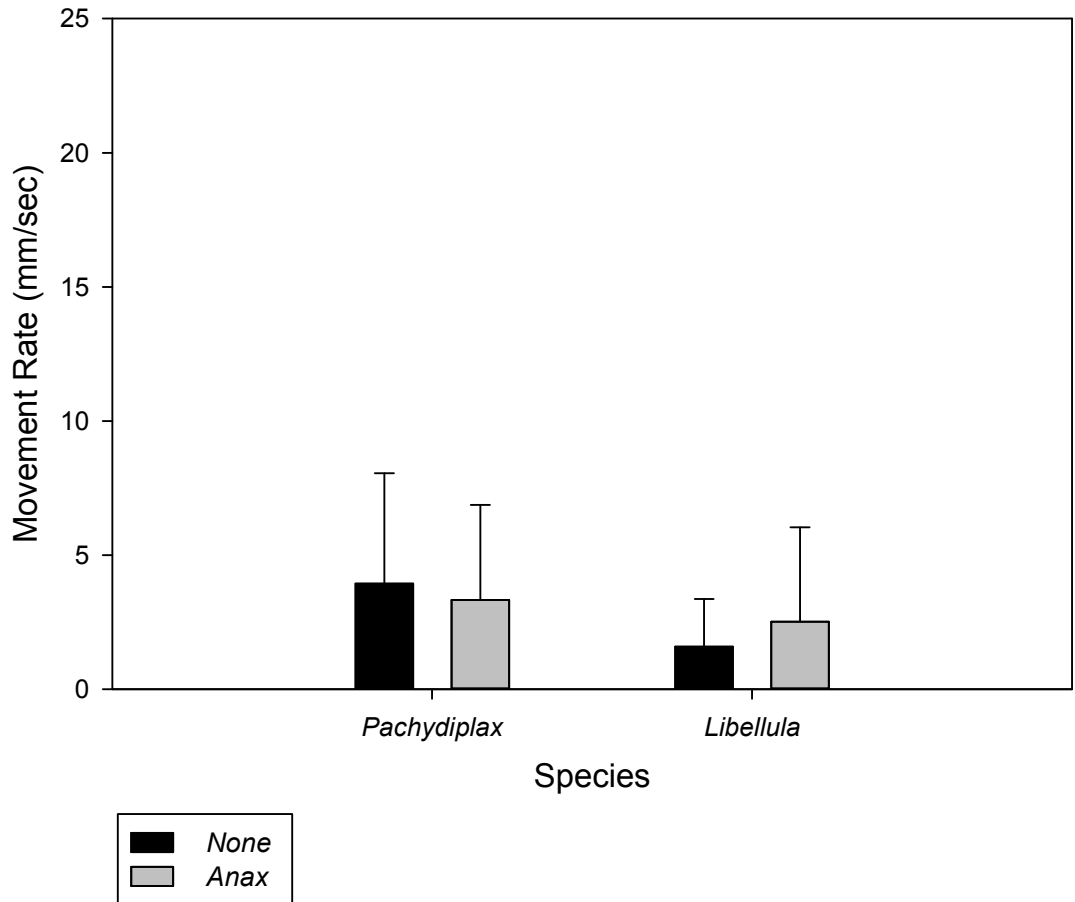


Figure 3-12. Movement rate varies by predator and species. This shows how movement rate (in mm/sec) changes in response to predation risk. *Pachydiplax* does not respond very strongly, though has a higher baseline movement rate in close quarters, whereas *Libellula* increases movement in response to predation risk. Error bars=1 SD.

The probability of being attacked varied only with the rate at which the IG predator struck at shared prey ($B=-15.541$, $df=1$, $Wald=6.730$, $P=0.009$). AIC was minimized at 165.39. The probability of death was not modified by any variable save movement rate, with a -2 log likelihood of 273.049 (Table 3-3). Though when body size, predator prementum, and competitor species

were accounted for (Table 3-4), there is a detectable difference between species, with *Libellula* being more likely to die ($B_{exp} = 2.316$, $B = 0.840$, $df = 2$, $Wald = 3.963$, $P = 0.047$).

Table 3-2. Death probability logistic regression.

The probability of an IG prey nymph being killed by an IG predator was increased by the movement rate (in mm/sec) of the IG prey nymph.

	B	SE	Wald	df	Sig.	Exp(B)
Move	0.127	0.042	9.166	1	0.002	1.136

Table 3-3. Effect of IG prey species and competitor species mortality probability

The probability of being killed by an IG predator differed between species and competitor species, in combination with the ratio of predator prementum to IG prey

	B	S.E.	Wald	df	Sig.	Exp(B)
Species (<i>Pachydiplax</i>)			8.592	2	0.014	
Species(<i>Erythemis</i>)	-0.355	0.346	1.050	1	0.306	0.701
Species(<i>Libellula</i>)	0.459	0.332	1.911	1	0.167	1.582
Premmentum Ratio	2.556	1.045	5.985	1	0.014	12.889
Competitor (<i>Pachydiplax</i>)			6.419	3	0.093	
Competitor(<i>Erythemis</i>)	-0.766	0.367	4.359	1	0.037	0.465
Competitor(<i>Libellula</i>)	-0.180	0.339	0.282	1	0.595	0.835
Competitor(None)	0.026	0.360	0.005	1	0.943	1.026
Constant	-1.146	0.442	6.718	1	0.010	0.318

Final Omnibus Test

The last experiment used every individual of *Erythemis simplicicollis*, *Libellula lydia*, and *Pachydiplax longipennis* that had been exposed to risk from predation by *Anax junius* in earlier experiments, pooling prey type and prey composition treatments that are not individually related to attack and mortality probability. The only variables of concern were IG prey species, competitor (another IG prey species, which included an entry for none), and scale covariates such as the prementum ratio, strikes per second by IG prey and IG predator (both toward shared prey), biovolume consumption rate for IG prey, and IG prey movement rates. These were used in logistic regression of attack probability, and Cox regression.

The initial logistic regression indicated significant differences between IG prey species in the probability that the IG prey will be attacked by *Anax*, and a marginal difference in the probability that the IG prey will be attacked by *Anax* while also in the presence of another IG prey species (Table 3-4). The prementum ratio was also important. AIC was 448.015. Here, *Pachydiplax* was the reference category, while *Erythemis* was least likely to be attacked ($B=0.-355$, $B_{Exp}=0.701$), and *Libellula* most likely ($B=0.459$, $B_{Exp}=1.582$). The marginal effect of the competitor species was such when *Pachydiplax* was set to baseline (as the reference category in logistic regression), no competitor was more likely to result in an attack than *Pachydiplax* ($B=0.026$, $B_{Exp}=1.026$), *Erythemis* was the least likely competitor to result in an attack compared to *Pachydiplax* ($B=-0.766$, $B_{Exp}=0.465$), and *Libellula* was intermediate ($B=-0.180$, $B_{Exp}=0.835$).

When strike rate, movement rate, IG predator strike rate (against shared prey), and consumed biovolume were included, the effect of the competitor disappeared completely. IG prey species, movement rate, predator strike rate, consumed biovolume and prementum ratio were all significant. AIC was minimized at 390.075 (Table 3-5, Figure 3-13). When Cox regression was performed, species, movement rate, prementum ratio, and predator strike rate were all significant (Table 3-6, Figure 3-14). The -2 log-likelihood was 903.505.

Table 3-4. Logistic regression of IG predator attacks against IG prey.

The probability of being attacked by an IG predator differed between species, and was modified by the rate at which IG prey species consumed shared prey biovolume, their movement rate, and the rate at which the IG predator attacked shared prey; this last likely act as measure of the IG predator's hunger.

	B	S.E.	Wald	df	Sig.	Exp(B)
Prementum Ratio	3.386	1.156	8.584	1	0.003	29.556
Biovolume Consumption Rate (mm ³ /sec)	5.234	2.606	4.032	1	0.045	187.537
Movement rate (mm/sec)	0.152	0.037	16.627	1	0.000	1.165
IG predator strike rate (strikes/sec)	17.407	4.138	17.697	1	0.000	3.63E7
Species (<i>Pachydiplax</i>)			6.973	2	0.031	
Species(<i>Erythemis</i>)	-0.385	0.341	1.275	1	0.259	0.681
Species(<i>Libellula</i>)	0.467	0.313	2.222	1	0.136	1.596
IG prey strike rate (strikes/sec)	-7.712	8.701	0.786	1	0.375	0.000
Constant	-2.548	0.523	23.735	1	0.000	0.078

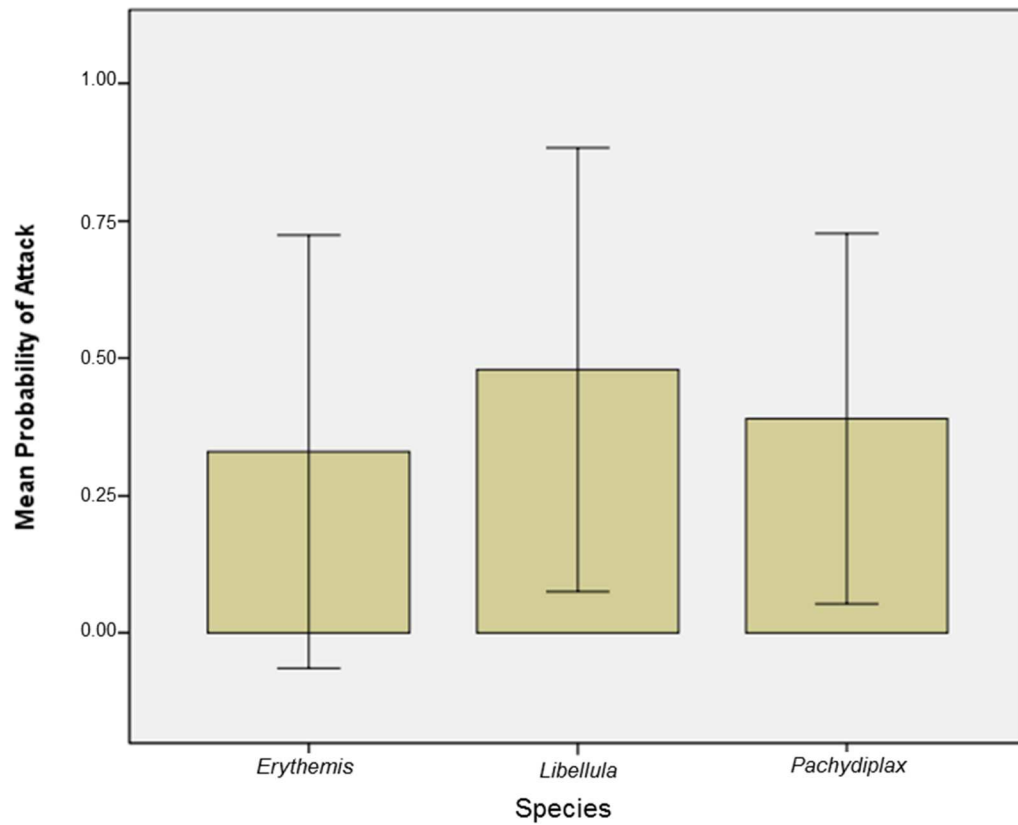


Figure 3-13. Attack probability on IG prey by *Anax* varies by IG prey species.

This shows that the probability of being attacked by *Anax* over the course of a trial varied between species, with *Libellula* being the most likely to be attacked. Error bars are at +/- 2 SD.

Table 3-5. Cox regression of death probability for all species.

Cox regression was used to determine what variables affected the probability of death for focal nymphs. This indicates that IG prey species, the size-differences between IG predator and IG prey nymphs, IG prey strikes on shared prey, IG prey movement rate, and IG predator strike rate against shared prey affected the risk of death for IG prey nymphs.

	B	SE	Wald	df	Sig.	Exp(B)
Prementum Ratio	3.041	0.846	12.915	1	0.000	20.921
Movement Rate (mm/sec)	0.138	0.022	39.159	1	0.000	1.148
Species (<i>Pachydiplax</i>)			8.309	2	0.016	
Species(<i>Erythemis</i>)	0.107	0.336	0.101	1	0.751	1.113
Species(<i>Libellula</i>)	0.733	0.303	5.844	1	0.016	2.082
Predator Strike Rate (strikes/sec)	9.521	2.141	19.785	1	0.000	13645.562

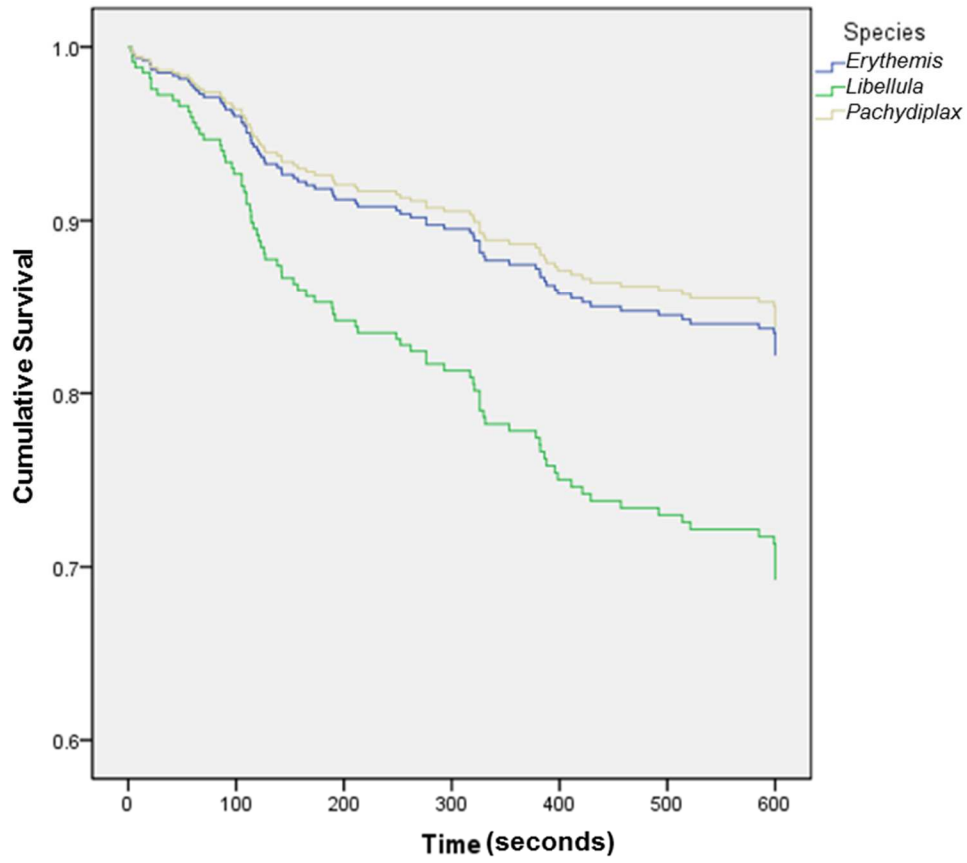


Figure 3-14. *Libellula* has the lowest survivorship of all IG prey species when at risk from *Anax*. s is the cumulative survival curve for IG prey dragonfly nymphs over time. It indicates that *Libellula* suffered the highest mortality rate over time due to attack by *Anax*, compared to *Pachydiplax* and *Erythemis*.

Discussion

Prey selection

Behavior often changes in response to predation risk, either within a species (Peckarsky 1996, Laurila and Kujasalo 1999, Hoverman et al. 2005, Meutter et al. 2005) or among closely related species living in different environments (Brodin and Johansson 2004, Johansson and Suhling 2004, McCauley 2008). The most common forms of behavior that are studied are activity rate associated with foraging and foraging patch occupancy (Eklov and Halvarsson 2000, Babbitt 2001, Mogali et al. 2012). Foraging activity is typically reduced in the presence of a predator to avoid detection (Martel and Dill 1995, Relyea 2001). This leads to a foraging/predation risk tradeoff that in many ways structures herbivore communities (Stoks 1999, Anholt et al. 2000, Smith 2006), and affects IGP as well (Walls 1995, Yurewicz 2004, Bruce 2008).

For predators under threat of predation themselves, prey selection might also be relevant. This is because when predation occurs, there are a variety of cues released into the environment. There are scents, sounds, visual information, and other cues that their own predators can potentially detect (Hogstedt 1983, Mathis et al. 1995, Chivers et al. 1996, Wisenden and Thiel 2002), which puts the initial predator at risk of predation. This is called predator attraction (Cashner 2004). Unfortunately, little is known about how this phenomenon affects behaviors like prey selection in predators generally, or its application to IGP in particular.

When free of predation risk, a predator should prefer more profitable prey items (Krebs et al. 1977, Sih and Christensen 2001), which will generally be a larger prey item presuming that it can still be caught (Werner 1974, Werner and Hall 1974, Barnard and Brown 1981). In an aquatic environment, larger prey items have a larger volume of bodily fluids that diffuse into the water column (Schmidt-Nielsen 1984) and their struggling produces more turbulence that can be detected by mechanoreception (Légier-Visser et al. 1986, Pohlmann et al. 2004, Rebora et al. 2004). As a result, larger prey should also attract more predators. A potential anti-predator strategy for IG prey species might be to actively select smaller prey items that reduce their risk of detection by a larger predator when predators are present.

Evidence for changes in prey selection by IG prey was inconsistent. There were significant differences between tests where the IG predator was unrestrained (lethal tests) and those where the IG predator was restrained (non-lethal tests). In non-lethal tests there was little-to-no change in prey selection between being alone vs. in the presence of *Anax* IG predators for any focal species. This is despite the fact that increased strike rates and high rates of biovolume consumption increased the probability of attack by *Anax* when unrestrained. *Tramea* predators are another matter. The response by IG prey was in the opposite direction than that which was expected; *Libellula* and *Pachydiplax* increased their preference for *Gammarus* in response to *Tramea* rather than shifting toward *Daphnia* as part of an anti-predator strategy (Siddon and Witman 2004). The same was true when comparing conspecific treatments to *Anax* treatments. Preference for *Gammarus* increased or stayed the same when *Anax* was present in the non-lethal tests. In the lethal tests at high prey density, *Erythemis* increased their preference for *Daphnia* in the presence of *Anax* while the other species preferences stayed the same, compared to when a conspecific was present. At low prey density, preference for *Gammarus* increased or stayed constant across all IG prey species.

There are several possible reasons why lethal and non-lethal tests differed in this respect. The first is a lack of information possessed by the focal nymphs in the non-lethal tests. Many defensive behaviors performed by prey organisms scale with predation risk because the defensive behavior has a cost associated with it (McLean and Godin 1989, Wisenden et al. 1994, Martín and López 1999). As a result of this cost, behavioral anti-predator strategies are often distance dependent (Blumstein 2003, Cooper Jr et al. 2008). If a dragonfly nymph can detect the presence of a predator but not its size or location, it might use a different strategy than what it would use to reduce what it perceives as an imminent risk of death (Abrams 1994, Lima and Bednekoff 1999). Behind a mesh divider, an IG prey nymph may know that an IG predator is present due to chemoreception (Wisenden 2000, Rebora et al. 2012), but the perceived risk may be muted (McLean and Godin 1989, Kramer and Bonenfant 1997, Relyea 2001). The mesh divider used in the non-lethal tests kept shared prey on one side, and permitted the passage of

water and potential chemical cues. A dragonfly nymph may not also be able to resolve images through it (Pritchard 1966, Land 1997). The mesh might also dampen or diffuse any mechanical cues that propagate through the water column. So the nymphs might detect an IG predator, but not necessarily respond the same way as in the absence of the barrier.

In the lethal tests, a tradeoff with foraging becomes important in explaining the difference between high and low prey density. At low prey density, prey preference stayed the same or shifted toward a preference for *Gammarus* in the presence of *Anax* compared to a conspecific. Dragonfly nymphs have to balance two competing needs. They need to avoid being eaten, and they need to grow and develop (Stoks and Johansson 2000, Wellborn 2002) in an aquatic environment that is often temporary (Bridges 2002, Stoks and McPeck 2003a). Moreover, growth can lead to a size-refuge from at least a portion of their predators (Olson 1996, Urban 2007a). Every time they reduce energy intake to avoid an imminent risk of death, they may be increasing their risk of death later (Ludwig and Rowe 1990).

When prey density was high, *Daphnia* may be abundant enough that they were worth targeting as a response to predation risk (Caraco et al. 1980, Barnard and Brown 1981). At low prey density, rates of encounter with *Daphnia* were low, they are smaller and represent less food value, and IG prey nymphs have to balance their need to feed against predation risk (Babbitt 2001, Yurewicz 2004, Stav et al. 2010). Given that at low prey density IG prey nymphs prefer *Gammarus* more than they do at high prey density, shifting further toward that preference makes sense. At high prey density, they can afford to pass up *Gammarus* to reduce predation risk because *Daphnia* are abundant, but when *Daphnia* encounter rates drop too low, rather than risk starvation they reduce inclusion of *Daphnia* in their diet. This is analogous to risk-sensitive patch-foraging wherein foragers running below energy reserves should select patches based on their variance in the hope that they find a patch containing sufficient food to put them into positive energy balance, rather than selecting for reliable but potentially insufficient patches (Caraco et al. 1980, Caraco 1981). Here, every attack they make on a prey item increases their risk of death, feeding on *Daphnia* would not allow them to sustain their energy reserves, so they target

Gammarus. They are effectively increasing their risk of death in the short term in order to reduce their risk of death in the long term (Ludwig and Rowe 1990).

When another IG prey species was combined with the risk of predation, prey selection changed again. When *Anax* was not present, prey selection moved toward greater *Daphnia* preference when a heterospecific competitor was present, compared to a conspecific. When *Anax* was present this response became even stronger. However, when a conspecific was combined with *Anax* rather than a heterospecific competitor, there was no change from when a conspecific alone was present. Examining this in more detail species by species, *Pachydiplax* and *Libellula* displayed different strategies. *Pachydiplax* did not change its prey selection when a conspecific competitor was present, and did not respond to the IG predator *Anax*. When *Libellula* was present, it shifted toward a preference for *Gammarus* prey when *Anax* was not present and toward *Daphnia* when *Anax* was present. *Libellula* shifted toward a preference for *Daphnia* in the presence of *Anax*, irrespective of the identity of its IG prey competitor. One possibility is that these nymphs are competing to not be eaten (Arnold and Wassersug 1978, Brodie Jr and Formanowicz Jr 1983, Lawler 1989, McPeck 1990a). In other words, they may sacrifice short-term foraging gains in order that the other nymph will be detected and eaten first (Relyea 2002), potentially satiating the IG predator (Mathavan 1976). All other things being equal, there should be no change between conspecific and heterospecific treatments. It does not matter to the individual if the other individual trying to evade the proverbial tiger is one of their own species or not. They and their genes are just as dead if they fail and group selection is nonsense (Smith 1964, West et al. 2007). *Libellula* followed this pattern, *Pachydiplax* did not. So, either this explanation needs to be rejected and something other than an anti-predator response proposed; or the hypothesis needs to be modified. One possible modification is that these animals are not only competing to not be eaten, but they are competing for food as well (Cothran 2013, Relyea 2000). In much the same way that differences between predators shape anti-predator responses (Wilson 2005, Kishida 2005) anti-competitive behavior may be influenced by the identity of a competitor. When exposed to combined predation and competition, the best possible response a

dragonfly nymph can exhibit may be sensitive to the behavior and capabilities of the competitor as well as the predator (Relyea 2004, Grand 2002, Grether 2009). This may explain why the behavior observed in these two species differs.

Attempting to explain the observed trends this way with existing data risks becoming an *ad hoc* fallacy, but there are ways of testing it. The easiest is to expand the species under consideration to include a third species that differs substantially in its prey capture success or other foraging behavior, such as *Erythemis simplicicollis*. If either *Libellula* or *Pachydiplax* exhibit a third set of prey preference shifts when they have this (or another) IG prey species as a competitor under otherwise similar experimental conditions then it would lend support to this hypothesis. Even better if a fourth species were included that is not sympatric with these species. The nymphs would be evolutionarily naïve to this competitor species (Kiesecker 1997), and with the inclusion of a negative control, should show no foraging response to the competitor if this hypothesis is true.

Mortality

For prey choice changes to be beneficial to the individual they must increase fitness, which in this experimental system most likely means reducing mortality from predation, or increasing growth rate through energy intake. When single shared prey type tests and dual prey type tests were compared there was no effect on the mortality of the IG prey. When *Daphnia* was the only shared prey species, there was an effect on attack rates, but this did not lead to differences in mortality. However, strike rate and consumed biovolume of shared prey did affect mortality rates. Low strike rates and low biovolume consumption (independent of strike rate) correlated with reduced mortality rates. Moreover, the shared prey (*Gammarus* or *Daphnia*) attacked by the IG predator was also a useful predictor. As that attack rate climbed, the likelihood of IG prey nymphs being attacked by the IG predator tended to increase. This means that, at least on the time-scales and prey quantities under consideration, IG predators (and *Anax* in

particular) were not easily satiated by shared prey (Sentis et al. 2013), and this variable was likely a measure of how hungry the IG predator happened to be.

This appears to be evidence of the predator attraction hypothesis discussed above (Cashner 2004). These data demonstrate that IG predators were attracted to IG prey nymphs by the predatory activities of those same nymphs, and provides a mechanism by which a tradeoff between foraging and predation risk can exist in IG predators that is not reliant on movement but directly on their capacity to engage in consumptive competition (Lima et al. 1985, Cowlshaw 1997, Verdolin 2006). There are multiple interacting aspects of foraging behavior that can be independently modified in response to predators and competitors. Each has its own benefits and drawbacks on short and long timescales.

The quantity consumed (biomass or biovolume) is a practical measure of resource intake for a predator (Pollard 1988, Preston 1990), provided different prey types do not differ too much in nutrient content/availability (Belovsky 1981, Hjeljord et al. 1982, Mayntz et al. 2005). Increased energy intake over time leads to faster growth rates (Lawton et al. 1980), which can reduce the time it takes to reach a size refuge from predation (Aljetlawi et al. 2004, Rudolf and Armstrong 2008), and reduce the time it takes for dragonfly nymphs in particular to reach adulthood (Lawton et al. 1980, Pickup and Thompson 1990). But at least at short spatial ranges and time scales, prey consumption appears to increase the risk of attack, and thus the risk of being killed by a predator. This is likely due to chemical cues released into the water during handling (Nilsson and Brönmark 2000, Cashner 2004).

Independent of this is strike rate, which likely increases the risk of IG predation through the movement and water column perturbations it creates (Tanaka and Hisada 1980, Sahlen et al. 2008), thus increasing the probability of detection. All other things being equal, decreasing strike rate should tend to decrease the number of prey consumed, but this is not necessarily the case. Dragonfly nymphs can decrease their strike rate by shifting prey selection in the direction of prey they can more easily catch and that produce less detection risk, and they did in some cases without appreciably altering the quantity of prey they were able to consume.

Differential Mortality and IGP

Where differential mortality between IG prey species is concerned, particularly when in pairwise interspecific combinations, *Libellula* was the most likely to be killed by IG predators. The number of prey consumed was higher than for *Pachydiplax*, though slightly lower than for *Erythemis*. The movement rate of *Libellula* when exposed to predation by *Anax* was high, likely increasing the probability of attack because it increases the chance of being detected (Heads 1985, Stoks et al. 2003). Its strike rate against shared prey was also high, which likely further increases risk of detection. Yet, its success rate against shared prey, and *Gammarus* in particular, was low. It seemingly compensated for a low success rate by increasing the number of attempts and succeeded; yet doomed itself to predation in the process.

Overall, it appears that the central hypothesis is supported, specifically, that individuals and species with superior competitive abilities were more likely to be consumed by IG predators, which is in line with predictions (Holt et al. 1994), that preferential consumption by predators of superior resource competitors may stabilize IGP.

There are several questions brought up by these results that can be addressed in future work. The first is a more detailed look at prey choice under conditions of risk. These experiments used only IG predators capable of attacking and consuming the IG prey. Another way IGP may be stabilized at the community level is through ontogenetic shifts in diet, as well as predation risk (Hin et al. 2011). IG predators may be IG prey at smaller sizes (Hin et al. 2011), which may reduce their population recruitment into size classes dangerous to other species in high productivity habitats where apparent competition would predominate (Holt and Polis 1997).

However, there is another aspect of that. When they are small, it seems likely that a species like *Anax* may follow the same prey-selection dynamics that *Pachydiplax* and other IG prey species do. *Anax* can grow from a first instar nymph to an adult in as little as three months (Corbet 1999, May 2013) and many IG prey species take much longer to develop (Corbet 1999), which means that an *Anax* that survives to a larger size will be able to prey upon nymphs that attempting to consume it when it was first hatched. IG prey nymphs would also have every

reason to attack and kill them, to prevent *Anax* from eventually growing in size to prevent future predation risk as well as to obtain energy and nutrients. It stands to reason that they would prefer to consume young *Anax* (for example) over their other prey.

Chapter 4

Movement and Space Use

Introduction

Just as differential predation on the basis of direct consumptive competition can potentially stabilize IGP (Chapter 3), other aspects of IG prey behavior can influence the risk of predation. If these result in preferential predation on stronger competitors, IGP can be stabilized (Holt et al. 1994, Walls 1995). In predator-prey interactions, activity and foraging often respond to variation in predation risk based on a foraging/predation tradeoff in which the responses to predation risk negatively affect foraging, and foraging increases predation risk (Wellborn et al. 1996, Wissinger et al. 1999, Relyea 2000). This is often seen through movement and patch use (Cowlshaw 1997, Eklov and Halvarsson 2000, Verdolin 2006).

Movement permits animals to seek food items if they become locally scarce (Nolet et al. 2006, Stav et al. 2010) and avoid encounters with predators (Arias-Del Razo et al. 2012), but it can also make them more easily detected if they are within range of whatever sensory modalities those predators happen to use (Link et al. 1986, Wheeler 1989, Martel and Dill 1995, Shine and Sun 2003). IG prey must balance the competing demands of foraging, avoiding encounters with predators, and avoiding detection if an encounter occurs. This leads to patterns of behavior for many taxa that vary with the risk of predation, the form that risk takes, prey availability, and the urgency with which they must feed in order to avoid starvation, grow, and develop (Morton et al. 1995, Bridges 2002, Carlson et al. 2015). In dragonfly nymphs, typical solutions are most commonly studied among closely related species that vary in their co-occurrence with fish (McPeck 1995, Stoks and McPeck 2003b, Mikolajewski et al. 2010).

In ponds with predatory fish, dragonfly nymphs typically have low activity rates relative to species that inhabit fishless habitats (ClausWalker et al. 1997, Baker et al. 1999) because fish are extremely lethal (McPeck 1990b) and easily detect movement. They have a lateral line system sensitive to movement (Montgomery and Macdonald 1987, McHenry et al. 2009) and vision is well-developed in most predatory species (Hairston et al. 1982, Miller et al. 1993).

Avoiding detection by fish is a high priority for prey species that co-occur with them, and there is less urgency to leave a pond that is permanent enough for fish to inhabit. Compared to this, species that occupy fishless habitats are more active (Mikolajewski et al. 2010), and other insects, such as aeshnid dragonflies are often the top predators (Johnson 1991). Insects are less dangerous than fish (Albecker 2011), likely because the range at which they can detect a prey item is much shorter (Hairston et al. 1982, Land 1997, Reborá et al. 2004). In temporary ponds, other small nymphs need to mature rapidly before the temperature rises, oxygen depletes, and the pond dries. For these nymphs, the risk of pond drying outweighs the risk of predation (Laurila and Kujasalo 1999, Johansson and Suhling 2004).

This suite of behavioral and life history adaptations is often generalized as a slow-fast continuum (Johansson 1991, Hirvonen 1999). Slow developing relatively sedentary species are on one end, while fast developing and relatively active species are on the other. These ends of the continuum correlate strongly with perennial and ephemeral water-bodies respectively (Johansson 2000). A dragonfly nymph living in a temporary body of water must develop quickly in order to eclose and leave the aquatic environment before drying occurs. On the other hand, in permanent bodies of water, that urgency is not present and instead activity is reduced to facilitate predator avoidance (Stoks et al. 2003, Wohlfahrt et al. 2006). This tradeoff exists because activity rate affects the probability of encounter with and detection by a potential predator, and thus the probability of being consumed, but also increases the rate of encounter with food sources (Peacor and Werner 1997, Anholt et al. 2000, Eklov and Halvarsson 2000, Babbitt 2001).

However, many species are not entirely restricted to one type of habitat (Corbet 1999, McCauley et al. 2008, Petrin et al. 2010). Some are generalists (Hopper 2001, Petrin et al. 2010), whereas others have a limited ability to assess habitat quality (Michiels and Dhondt 1990, Horváth et al. 2007, Kriska et al. 2009). This limitation can be as extreme as laying eggs in crude oil (Horváth et al. 1998). Dragonflies detect oviposition sites through the use of horizontally polarized light, and have little ability to assess other habitat characteristics (Waage 1987, Wolf and Waltz 1988, Michiels and Dhondt 1990). Distribution patterns appear to follow neutral theory

for dispersion, with survival in any given location being determined by local conditions congruent with a niche model (McCauley et al. 2008). Consequently, species that are primarily adapted for different habitats often co-occur (Hopper 2001, McCauley et al. 2008). Due to uncertainty in habitat occupancy despite adaptation to particular environments, dragonfly nymphs often exhibit phenotypic plasticity to adapt to local variation in community composition and habitat quality (Arnqvist and Johansson 1998, Block and Stoks 2004, Stoks et al. 2012). The degree to which a given species can respond to different conditions varies, and it is this variation that is of interest with respect to IGP. When two or more IG prey are present with different foraging activity rates and anti-predator responses, the species that is more active in the presence of an IG predator should generally be competitively superior, and also the most vulnerable to IGP (Johansson 1993, Walls 1995). They encounter prey more frequently (Formanowicz 1982), but also encounter IG predators more frequently (Crowl 1989).

Microhabitats used by odonates are highly variable and include tree-holes and bromeliads (Fincke 1994). However, most species in North American pond assemblages can be classified as belonging to one of two groups: climbers, living and hunting in aquatic macrophytes, and sprawlers, occupying the bottom of the littoral zone (Corbet 1999, Cordoba-Aguilar 2008, Hc and De Marco Jr 2008). Climbing in macrophyte beds or simply using them as structural refugia is also used as protection from predators (Crowder and Cooper 1982, Tarr and Babbitt 2002). However, it can work in both directions and predators can use structural complexity to approach or ambush their prey (Schultz et al. 2009). Thus, a defense against one predator can expose an individual to risk from another predator (Atwood et al. 2009, Schultz et al. 2009).

Some empirical examples illustrate this. *Epitheca cynosura* not only reduce their foraging activity, but increase their use of spatial refugia inside aquatic macrophyte beds (ClausWalker et al. 1997), and this same strategy works to reduce fish predation. When the risk of cannibalism and interference competition increases with refuge use as it does within *Ischnura verticalis*, there is no safe place to go, and space use does not change even when predatory fish are added (Elkin and Baker 2000). *Pachydiplax longipennis* is driven into aquatic macrophyte beds by fish, but

there is a drawback because they are placed at risk of predation by larger species such as *Anax* that use the same macrophytes. As a result they are excluded from habitats containing both fish and large *Anax*. *Anax* are present in these ponds because they breed earlier in the season or overwinter, and thus *Pachydiplax* may not be excluded in assemblages composed entirely of late-breeders, or where early-breeders are themselves excluded by fish (Morin 1984, Wellborn and Robinson 1987). It is worth noting that they can exist with one or the other form of top-predator, just not always both (Hopper 2001, Crumrine 2005).

Another complication is that the use of cover can decrease foraging efficiency (Corbet 1999). For some species, the use of macrophytes as refuge from predation can decrease energy intake. This is dependent on the type of prey. A prey item that swims in open water out of the vegetation may be more difficult for a predator that inhabits said vegetation to prey upon. Alternatively, bottom dwelling prey species that use detritus as cover might be more difficult for climbing species to prey upon because their location in the water column is different. If the use of spatial refugia or location in the water column both protects a dragonfly nymph from IG predators and hinders foraging, then when two IG prey species (remember, also a predator) differ in these traits—particularly at high prey availability—then it may serve as a mechanism for IGP stability.

In order to investigate this, the following hypotheses were tested:

- 1) Movement and space use will vary between IG prey species, and they will respond to prey availability, predation risk from IG predators, and competing IG prey.
- 2) Variation in movement and space use will translate to variation in predation risk.
- 3) More active IG prey species and those that do not utilize structural and spatial refuges will suffer higher predation risk in absolute terms, and relative to heterospecific competitors that utilize refuges and are less active.

Methods and Results

Baseline Activity and Climbing Propensity

The first experiment established a baseline for activity level and climbing propensity between different species. Individual nymphs of the species *Agrigomphus submedianus*, *Anax junius*, *Libelula lydia*, *Epitheca princeps*, *Erythemis simplicicollis*, *Pachydiplax longipennis*, and *Tramea lacerata* were placed alone (1 nymph per container) in a 2.5 liter tank containing 12 or 24 *Gammarus* (prey density of 4.8 or 9.6 prey items per liter), which was set up as a 2.5 cm three-dimensional grid. Small wooden dowels (~2.5 mm) simulating aquatic plants were placed at the center of grid squares on the X/Y plane (Z is vertical). After a 15 minute acclimation period, the nymphs were observed every ten minutes for a total of nine observations of location and movement in three-dimensional space. At least 10 individuals of each species were used for each treatment group per species without re-use. Analysis of variance was used to test for an effect of species and prey density on movement rate and climbing propensity.

When movement rate was defined as mean travel distance there was a significant effect of species (df=6, F=7.185, P<0.001) and a species by prey density interaction (df=6, F=4.384, P<0.001) that in total explained 25.2% of data variance (Figure 4-1). When defined as the square root transformed number of relocations, there was a significant effect of species (df=6, F=4.857, P<0.001), and a significant species by prey density interaction (df=6, F=5.393, P<0.001) that in total explained 21.5% of the observed data variance (Figure 4-2). Climbing propensity was affected by species (df=6, F=28.838, P<0.001) and prey density (df=1, F=10.009, P=0.002), with no significant interaction. R² was 0.489 (Figure 4-3).

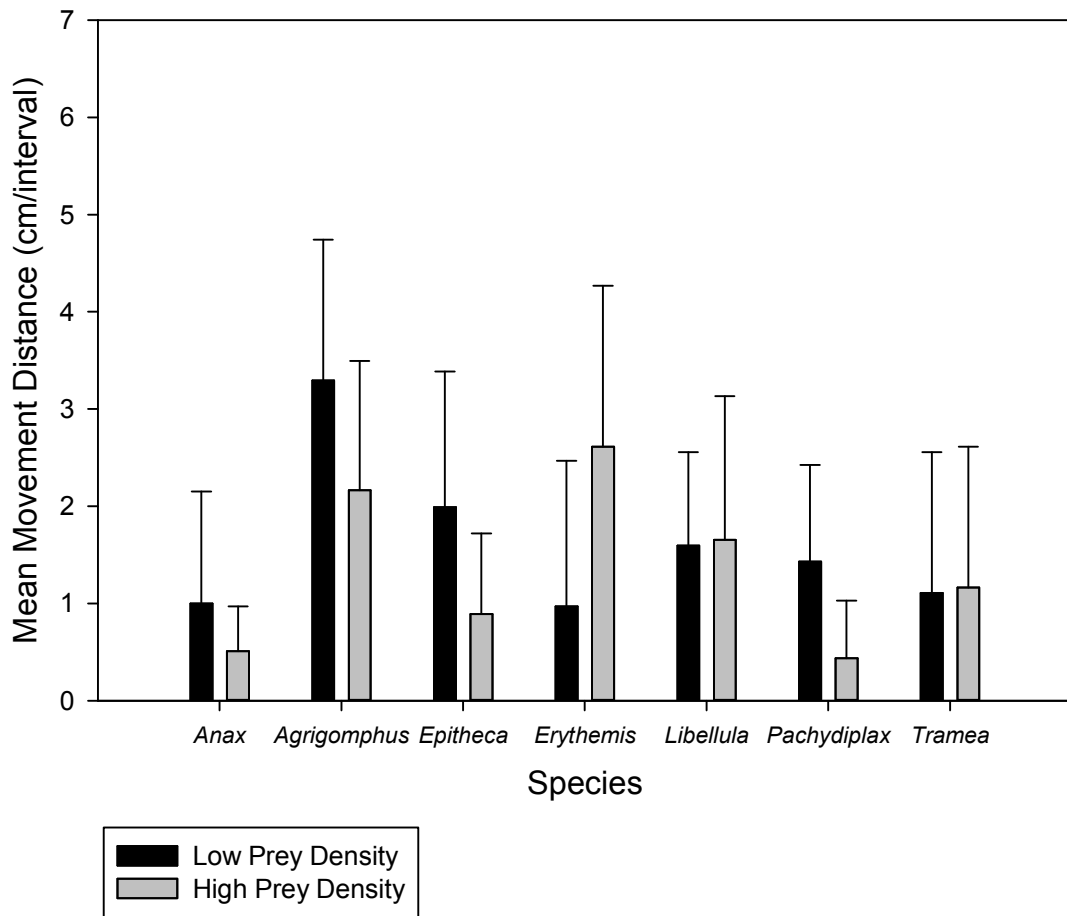


Figure 4-1. Movement distance varies by species and prey density. The mean distance moved per time interval changed between prey density treatment groups. Most species moved more at low prey density, though this changed for *Libellula* and *Erythemis*. Error bars=1 SD.

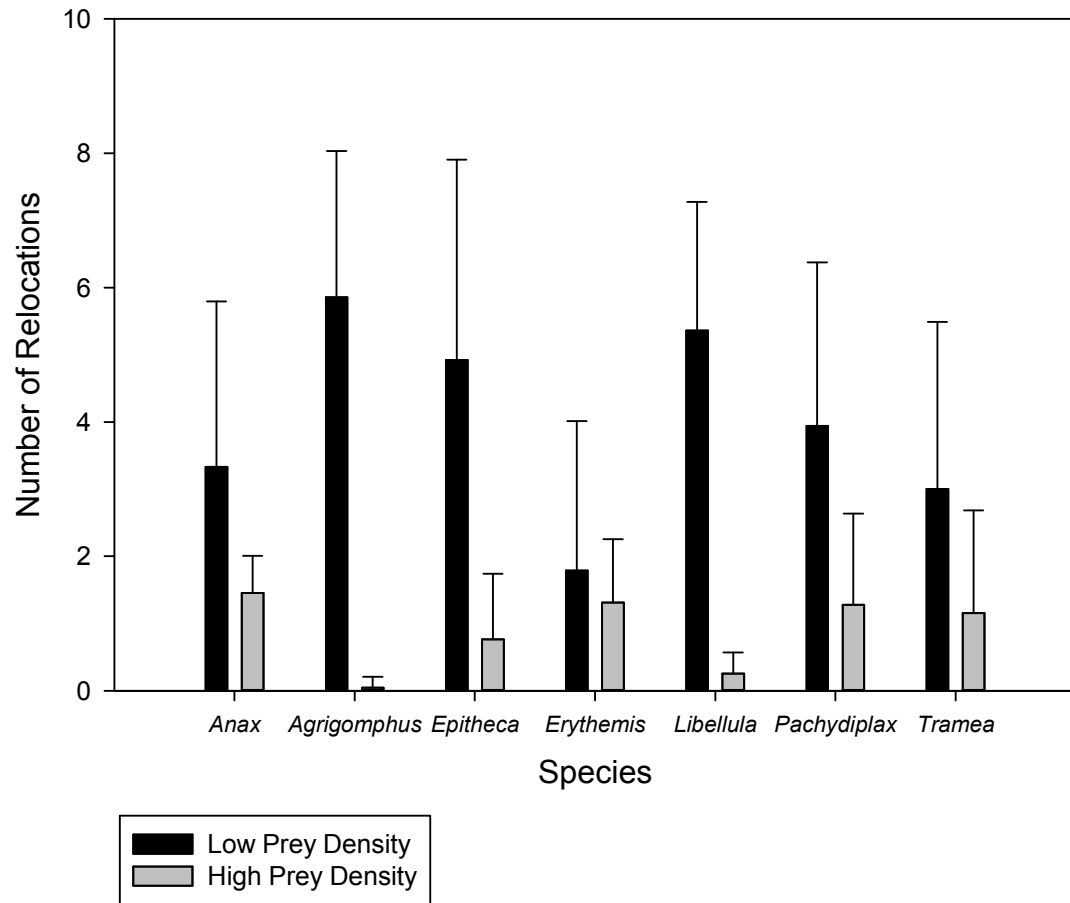


Figure 4-2. Relocations vary by species and prey density.

When relocations were used as a measure of movement, all species relocated more often at low prey density. Error bars=1 SD.

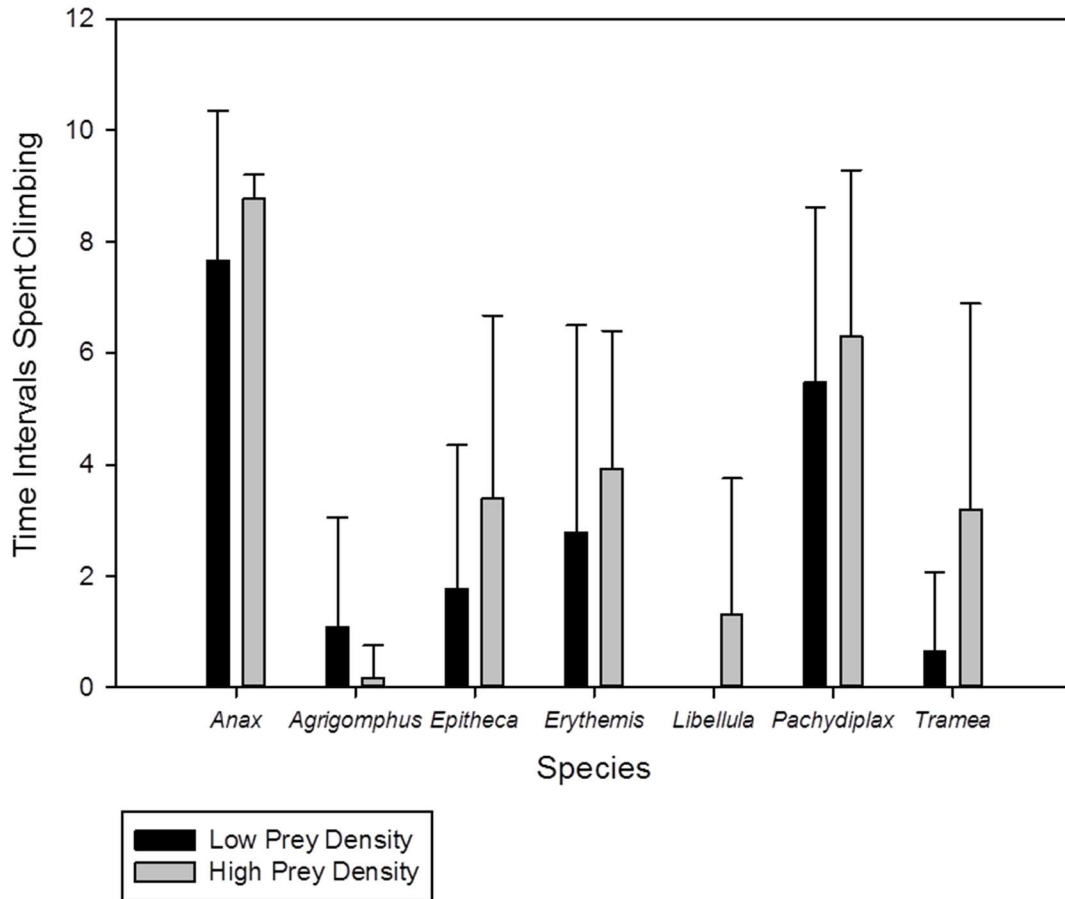


Figure 4-3. Climbing time varies by species and prey density.

Climbing was measured as time intervals spent above zero on the vertical axis. It varied between species, and was usually higher when prey density was higher. Error bars=1 SD.

Non-Lethal Conditions Movement and Climbing Responses

The second experiment tests for anti-predator responses in combination with prey-density. It took place in 2.5 liter aquaria divided into a 2.5 cm 3D grid with a bare substrate. Plastic plants were set into the center of squares on the X,Y plane on one half of the aquarium using silicon sealant. The experiment itself was a 3x2x5 complete block design with ten replicates per IG prey species. Species used as IG prey (Factor 1) were *Erythemis simplicicollis*, *Libellula lydia*, and *Pachydiplax longipennis*. Factor 2 was a prey-density treatment at 4.8 (low density) and 9.6 (high density) *Gammarus* per liter, while Factor 3 was a IG predator treatment using no predator, *Anax junius*, or *Tramea lacerata* which in all cases was large enough to consume the focal individual. Predators were contained within a cage made of a fine aluminum mesh, and were not re-used.

Each trial consisted of a single individual of a focal IG prey species, fasted for two days, photographed for later measurement, and then placed in the experimental aquarium along with the caged predator. *Gammarus* were added after a 15 minute acclimation period. Data were then collected every 10 minutes for a total of 10 observations. Location in three-dimensions was recorded at each interval, and was used to derive the number of relocations, distance moved, and time spent using macrophytes.

Data were analyzed using ANCOVA with mean distance moved and number of moves, as well as mean location on the vertical axis, and time spent above 0 on the vertical axis used as response variables between all treatments. Head width was used as a covariate. All count variables were square root transformed in order to meet normality assumptions, as count data are typically Poisson distributed.

Movement, here defined as the mean distance moved per time interval, did not change with predator, but was negatively affected by body length ($Y=-0.05x-3.158$, $df=1$, $F=9.971$, $P=0.002$) and IG prey species ($df=2$, $F=7.597$, $P=0.001$), and an IG prey species by prey density interaction ($df=2$, $F=3.983$, $P=0.02$). In total 17.9% of the variance in these data was explained by these relationships (Figure 4-4).

When movement was defined as the number of relocations, IG prey species ($df=2$, $F=9.387$, $P<0.001$) and prey density ($df=1$, $F=6.931$, $P=0.009$) were significant, while IG predator and body length was not. R^2 was 0.135 (Figure 4-5). Climbing was affected by species only ($df=2$, $F=42.053$, $P <0.001$) and this explained 43.1% of the variation in these data (Figure 4-6). The time spent under cover was affected by an IG prey species by IG predator interaction ($df=4$, $F=2.567$, $P=0.04$), though only 9.8% of the variation in data was explained by this relationship (Figure 4-7).

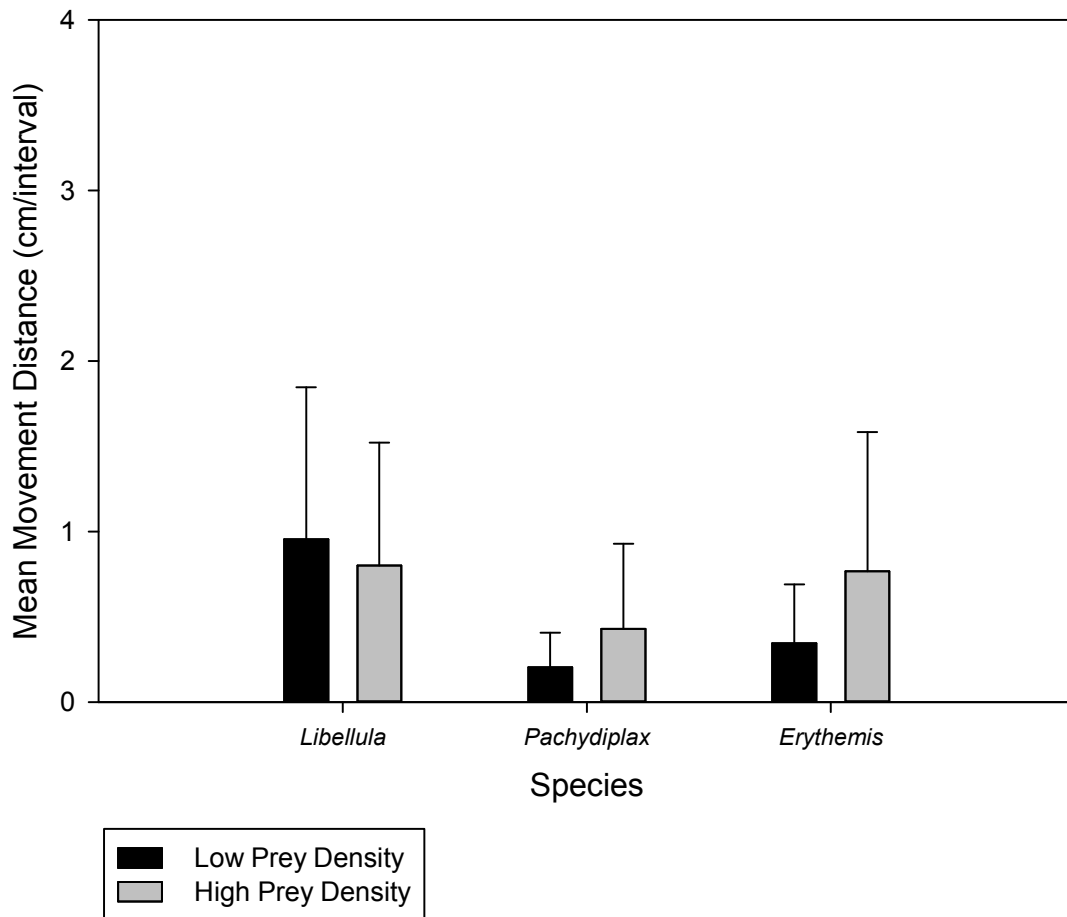


Figure 4-4. Movement distance varies by species and prey density in a complex environment. In a more structurally complex environment, mean movement distance per interval tended to be higher when prey density was higher. Error bars=1 SD.

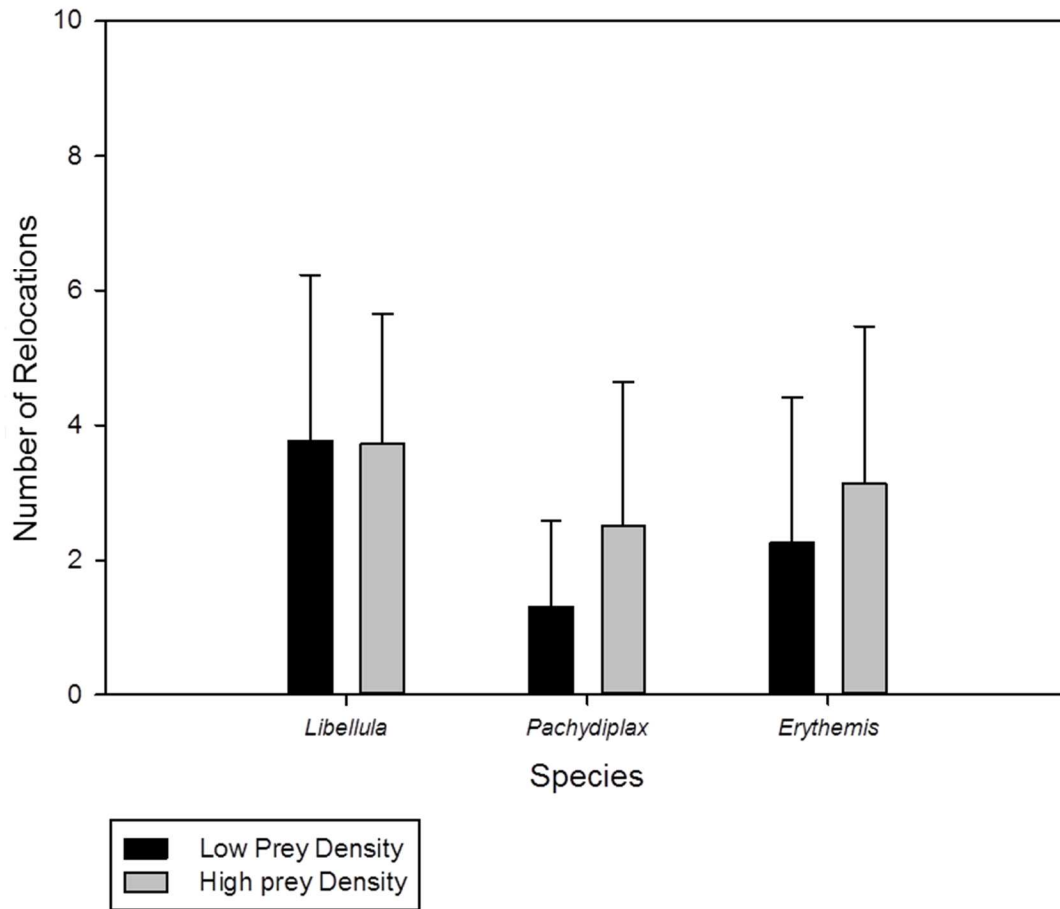


Figure 4-5. Relocations vary by species and prey density in high complexity environment.

The total number of relocations by dragonfly nymphs in a structurally complex environment displayed the same pattern as distance per interval and was higher at high prey density. Error bars=1 SD.

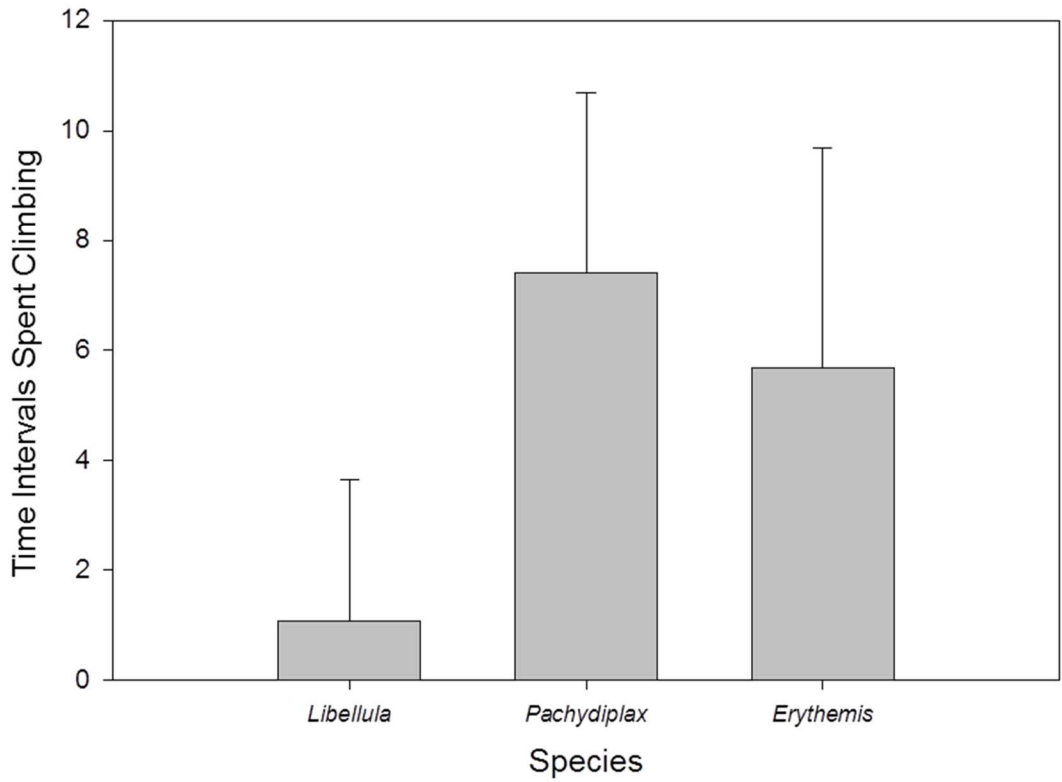


Figure 4-6. Climbing time varies by species.

Climbing time in a complex environment did not vary with prey density, but did differ between species with *Libellula* spending the least amount of time above zero on the vertical axis. Error bars=1 SD.

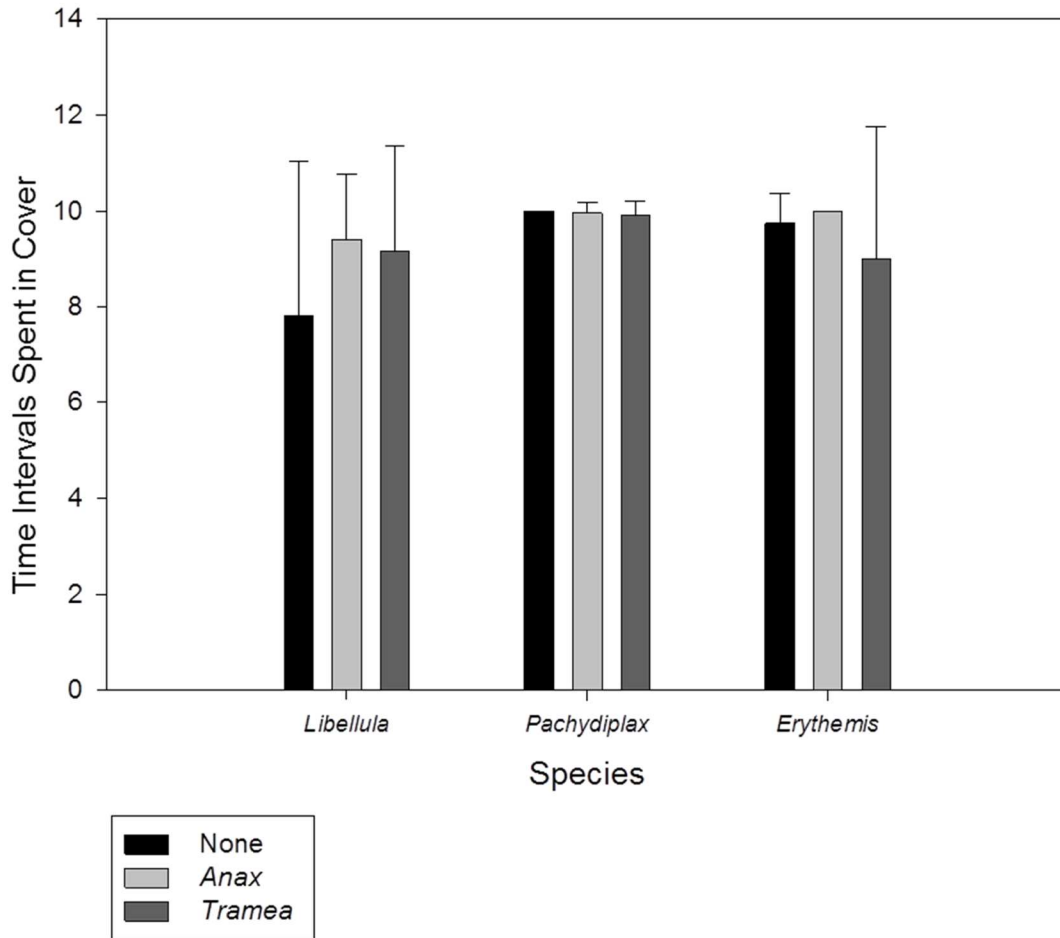


Figure 4-7. Time in cover varies only slightly by species and IG predator.

Most nymphs irrespective of species and IG predator spent the vast majority of their time in cover, but it did vary slightly between species, and by IG predators as an interaction term, but the relationship was very weak. Error bars=1 SD.

Lethal Conditions Movement and Climbing Responses and Mortality

The third experiment tested the effect of behavior on intraguild predation. *Pachydiplax longipennis*, *Erythemis simplicicollis*, and *Libellula lydia* were used as IG prey species, and were fasted for two days to control hunger levels before trials begin. This experiment used 2.5 liter aquaria divided into a 2.5 cm 3D grid with a bare substrate. Plastic plants were set into the center of squares on the X,Y plane on one half of the aquarium using silicon sealant. Hypotheses were tested using a 2x3x3x4 complete block design with 10 replicates for each IG prey species. The first factor was a prey density treatment at 4.9 and 9.8 *Gammarus* per liter. The second factor consisted of a IG predator treatment of no predator, *Anax junius* or a *Tramea lacerata*. The third and fourth factor consisted of all pairwise combinations of IG prey species, individually marked for same-species treatments and including a single-individual control. All individuals had their head-widths measured. Movement and location data were collected by direct observation at 10 minute intervals for a total of 10 observations.

ANCOVA was used between treatment groups using head width as a covariate upon movement and space use variables identically to the second experiment in this chapter, save for the addition of other treatment groups, and examining IG predator movement and space use as well. Negative controls were excluded from a further set to allow IG predator movement to be used as a covariate. Cox regression and logistic regression were used to analyze mortality.

Movement, when defined as the interval probability of relocation was affected by IG prey species (df=2, F=7.968, P<0.001) and initial prey density (df=1, F=20.902, P<0.001). There were also significant interactions between IG prey species and initial prey density (df=2, F=4.128, P=0.017), IG prey species and competitor species (df=6, F=2.544, P=0.019), and competitor species and initial prey density (df=3, F=3.544, P=0.014). These relationships were all weak though, and only explained 7.6% of total variance (Figure 4-8).

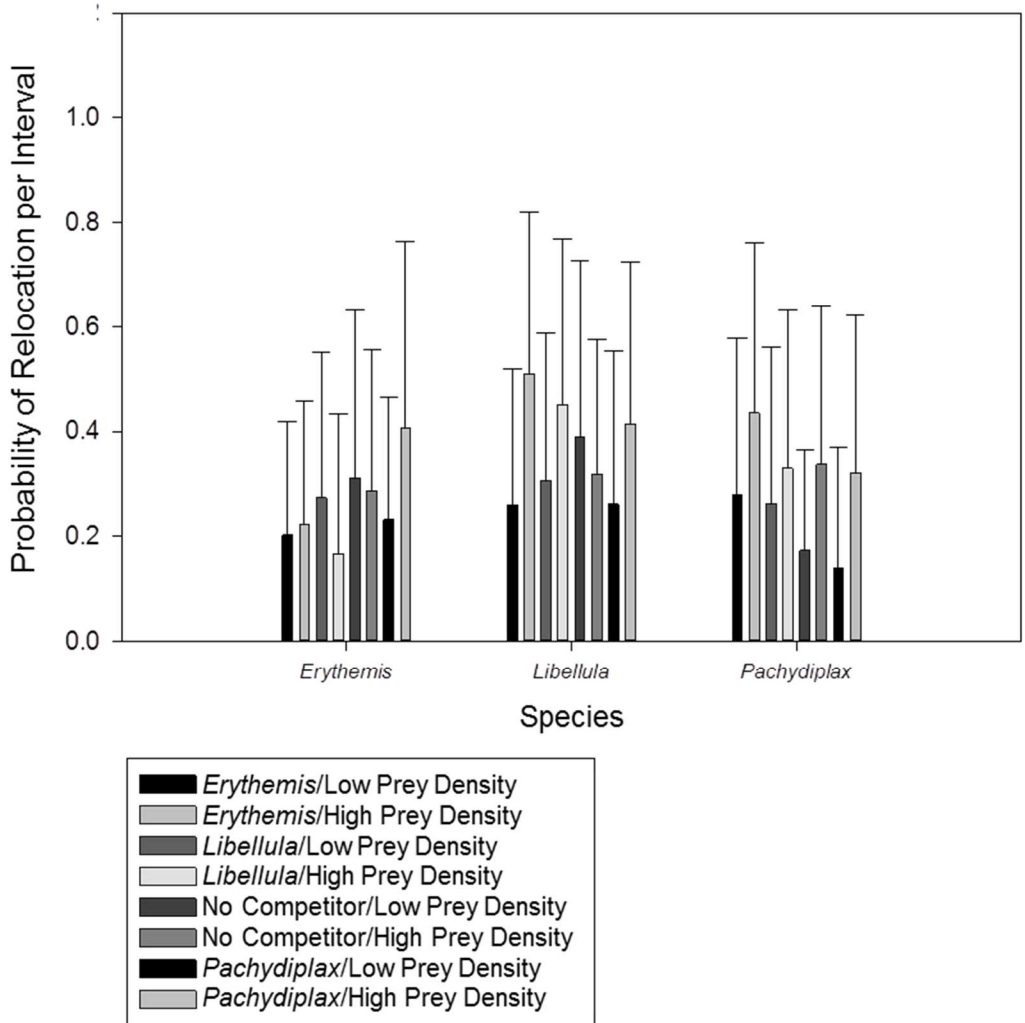


Figure 4-8. Movement varies by species, competitor and prey density.

Movement, here the probability that an individual nymph would relocate during a given time interval, was affected by that nymph's species (X axis), the identity of an IG prey competitor species (which may be a conspecific, or absent), and the density of their prey. The competitor or prey density information is combined in the legend (e.g., *Erythemis*/Low Prey Density indicates that the competitor was *Erythemis* and their prey was at low density). Error bars=1 SD.

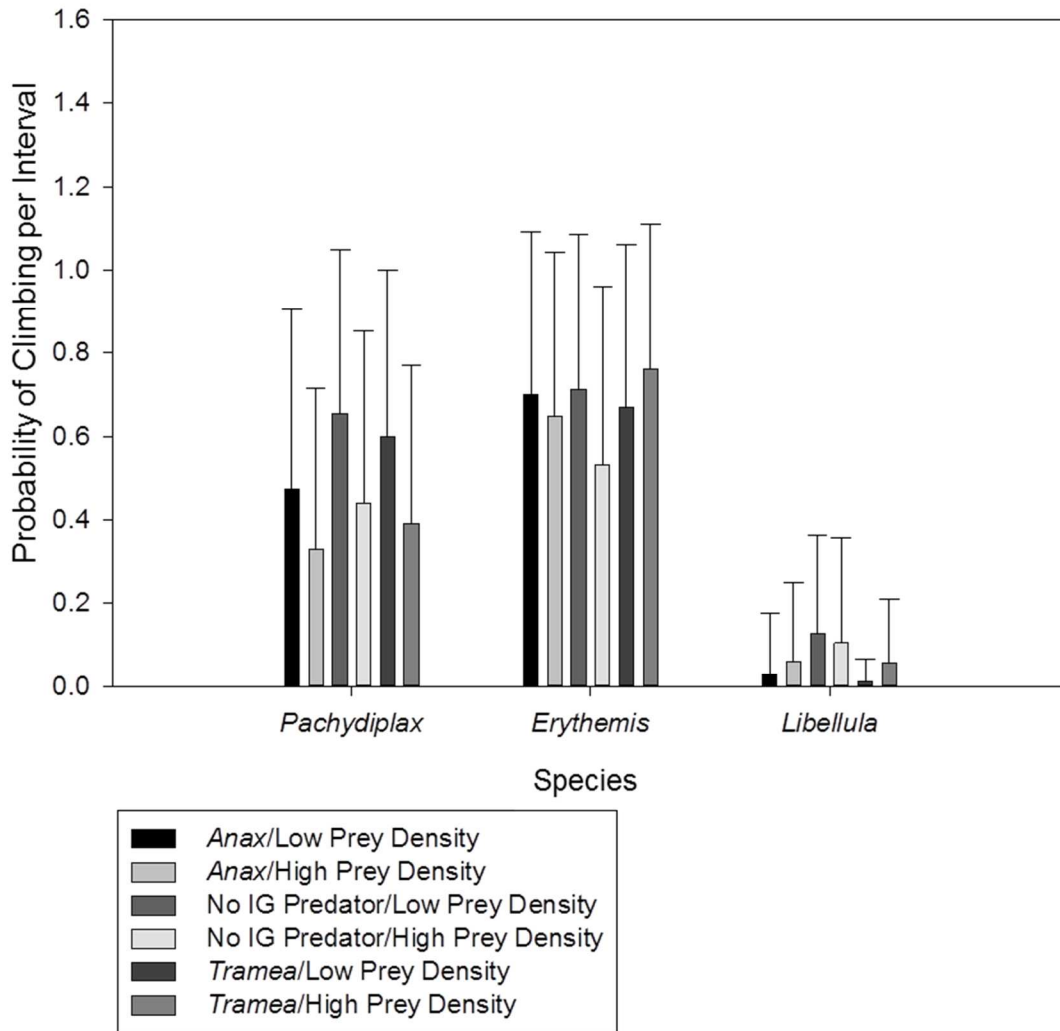


Figure 4-9. Climbing varies by species, predator and prey density.

The probability that an individual would be climbing during a given time interval was affected by the IG prey species identity (X axis), the identity of an IG predator species (which includes a negative control), and the density of their shared *Gammarus* prey.

The IG predator and prey density information is combined in the legend (e.g., *Anax/High Prey Density* indicates that the IG predator was *Anax*, and *Gammarus* was at high density). Error bars=1 SD.

Climbing propensity was positively affected by head width ($Y=0.06x+2.482$, $df=1$, $F=8.16$, $P=0.013$). It also varied by IG prey species ($df=2$, $F=114.206$, $P<0.001$) and initial prey density ($df=1$, $F=6.775$, $P=0.009$). Significant interactions existed for IG prey species and initial prey density ($df=2$, $F=7.087$, $P=0.001$). Lastly, there was a marginal interaction between IG prey species and IG predator ($df=4$, $F=2.351$, $P=0.053$). These relationships explained 38.2% of the variance in these variables (Figure 4-9).

Time spent in cover was modified by body size ($Y=0.013x+2.671$, $df=1$, $F=7.136$, $P=0.008$), IG prey species ($df=2$, $F=31.991$, $P<0.001$), and competitors ($df=3$, $F=4.426$, $P=0.004$). There was also a significant IG prey species by competitor interaction ($df=6$, $F=2.405$, $P=0.026$). Two marginal relationships were also evident by IG predator ($df=2$, $F=2.891$, $P=0.056$) and in a IG prey species by IG predator interaction ($df=4$, $F=2.224$, $P=0.065$). R^2 was 0.118. When body length was excluded in order to test for size-dependent anti-predator responses R^2 dropped to 0.11. However, the IG prey species by IG predator interaction became significant ($df=4$, $F=2.424$, $P=0.047$) (Figure 4-10, 4-11, 4-12).

When Cox regression was performed on mortality data, *Anax* was more likely to kill IG prey than *Tramea* was ($B=1.498$, $Bexp=4.474$, $P<0.001$), IG prey movement probability positive affected mortality ($B=0.83$, $Bexp=2.294$, $P=0.001$), while IG prey climbing negatively affected mortality ($B=-0.437$, $Bexp=0.646$, $P=0.038$). The -2LL statistic was 914.268. When this was performed excluding continuous variables and including only categoricals, only the IG predator was significant and model fit was worse, with a -2LL statistic of 966.423.

When size-ratios were taken into account with the other continuous covariates, IG predator species was significant ($B=1.46$, $Bexp=4.304$, $P<0.001$). The ratio between prey body length and predator head width was also significant ($B=0.951$, $Bexp=2.589$, $P=0.022$), as was IG prey movement probability ($B=0.903$, $Bexp=2.4678$, $P<0.001$). These all increased the probability of death for the IG prey. Climbing propensity decreased the probability of mortality ($B=-0.424$, $Bexp=0.655$, $P=0.046$). The -2LL statistic was 907.593, which made it superior to the first model (Figure 4-13).

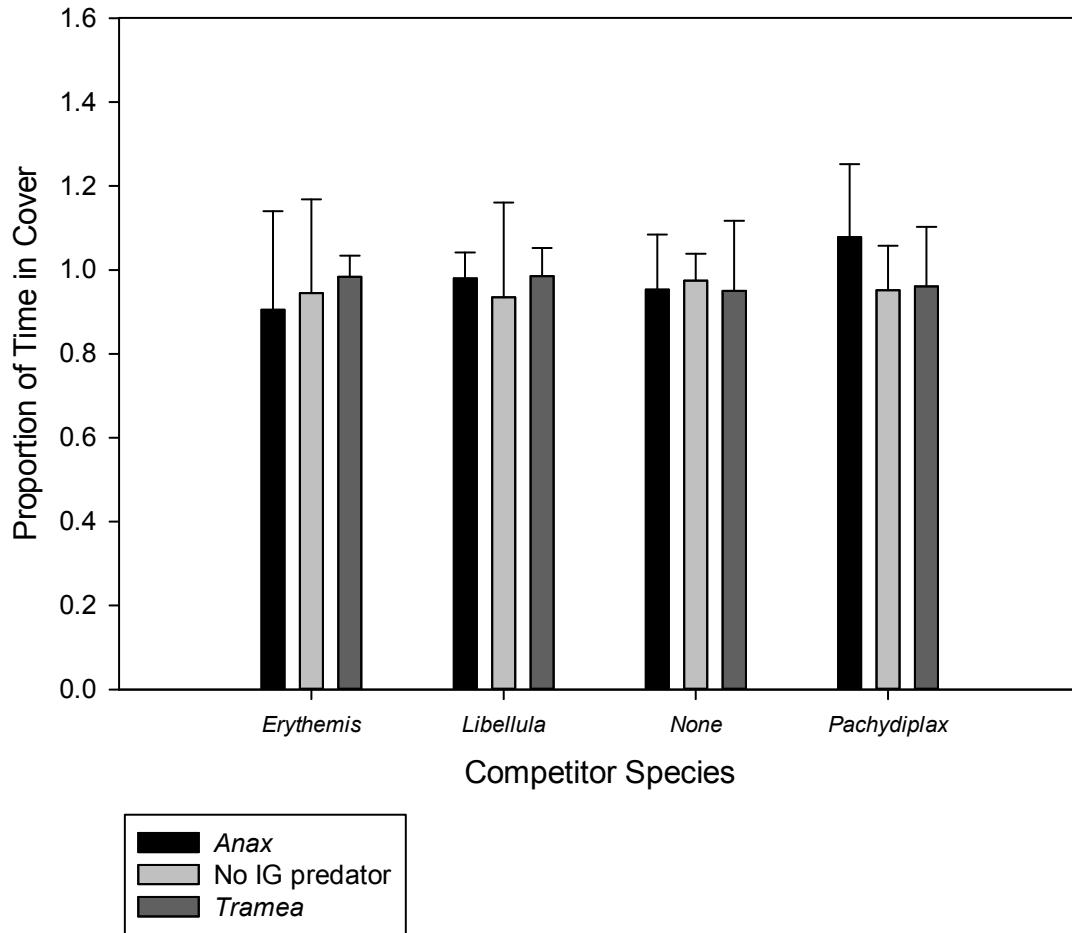


Figure 4-10. Time in cover by competitor species and IG predator treatment in *Erythemis*.

In *Erythemis*, the time spent in cover was not especially variable in response to competitors or IG predators. Error bars=1 SD.

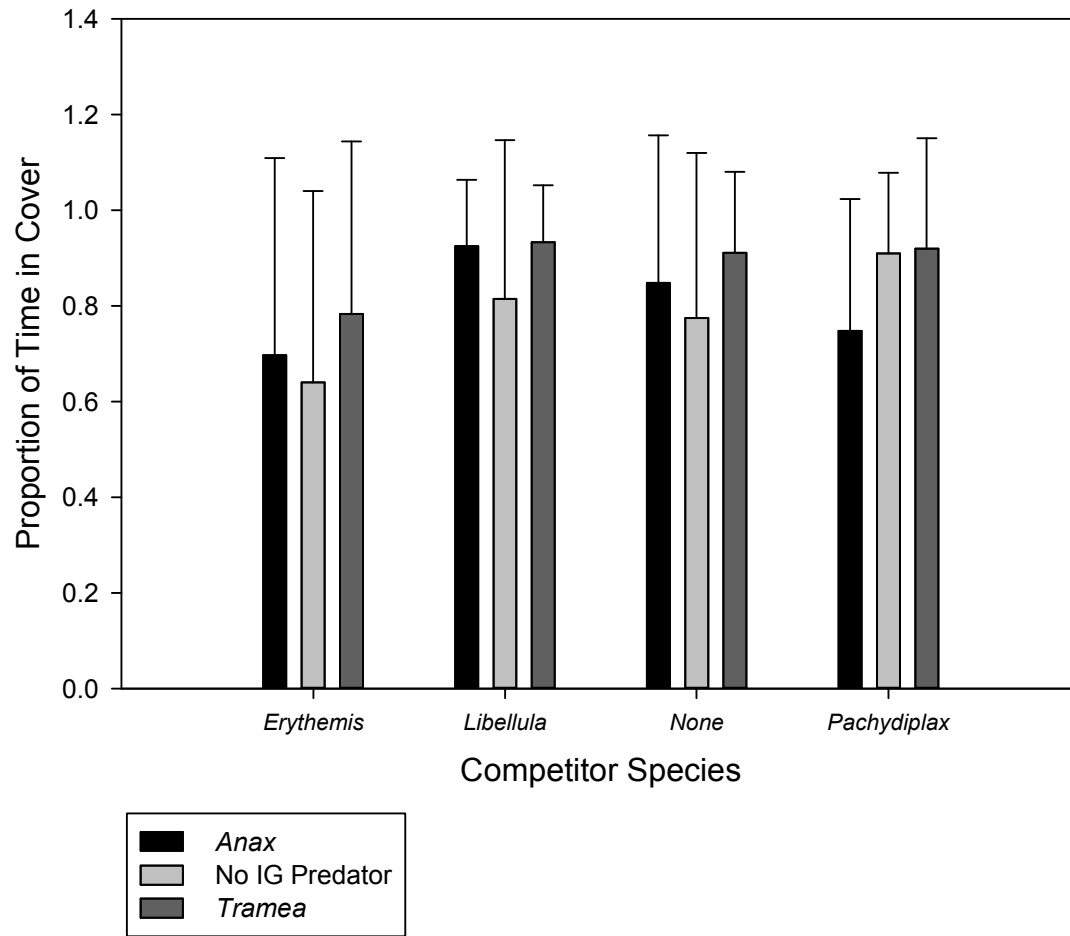


Figure 4-11. Time in cover varies by competitor species and IG predator treatment in *Libellula*.

In *Libellula*, the time spent in cover was affected by an interaction between what competitor was present, and what IG predator was present. Error bars=1 SD.

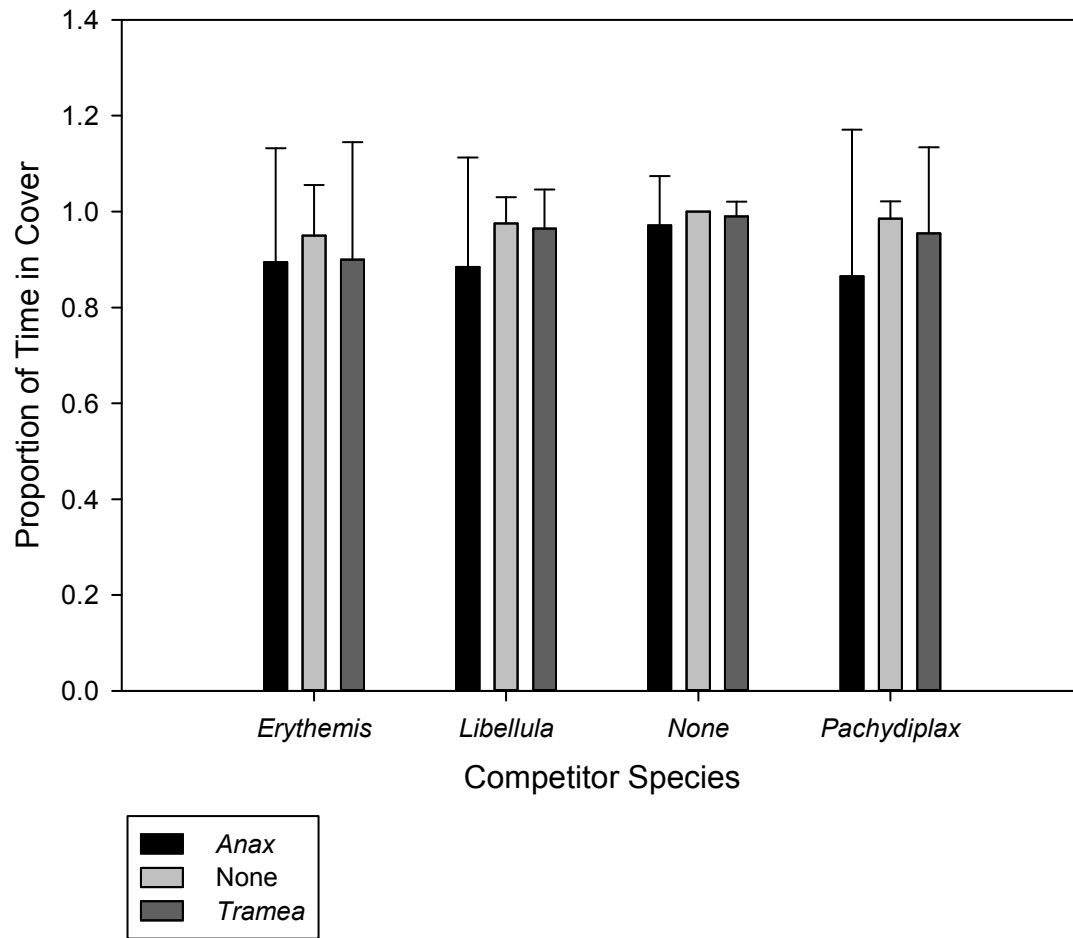


Figure 4-12 Time in cover varies by competitor species and IG predator treatment in *Pachydiplax*.

In *Pachydiplax*, the time spent in cover was affected by an interaction between what competitor was present, and what IG predator was present. Error bars=1 SD, which pushes the display range above 1.0.

When logistic regression was performed, *Anax* killed other nymphs more often than *Tramea* did (B=1.668, Bexp=5.302, P<0.001). Movement rate (B=1.064, Bexp=2.898, P<0.001) and the body-size ratio (B=1.266, Bexp=3.548, P=0.016) increased mortality while climbing decreased it (B=-0.489, Bexp=0.613, P=0.037). -2LL was 362.179. Excluding continuous covariates, only the IG predator species was significant, and the model fit was inferior with a -2LL statistic of 396.023.

When a Generalized Linear Model using a binary logistic function was performed (a procedure similar to Logistic Regression that permits the inclusion of interaction terms in SPSS), the parameter B is sign reversed from a standard logistic regression but is otherwise largely equivalent. Several relationships changed, when continuous covariates related to movement were used, IG prey species was marginally related to mortality rate (df=2, Chi Square=5.48, P=0.065) and the ratio between IG predator head size and prey body length decreased survivorship (B=-1,649, df=1, P<0.001), while *Tramea* killed IG prey less often than *Anax* did (B=-1.778, df=1, P<0.001). IG prey movement rate also decreased survivorship (B=-1.112, df=1, P<0.001). In terms of model fit, AIC was 378.457.

When continuous covariates related to movement were excluded and only body size ratios and categorical variables were included with interaction terms, species became significantly related to survivorship (df=2, Chi Square=7.5, P=0.024). *Pachydiplax longipennis* was set to baseline (reference category), while *Libellula* was killed more often (B=-0.107), and *Erythemis* was killed less often (B=0.176). The same head width to body length ratio negatively affected survivorship as well (B=-1.421, df=1, P=0.01). There was also a significant interaction between IG prey species and competitor species (df=6, Chi-Square=13.241, P=0.039). This model was inferior to the previous model, with an AIC of 390.127 (Figure 4-14).

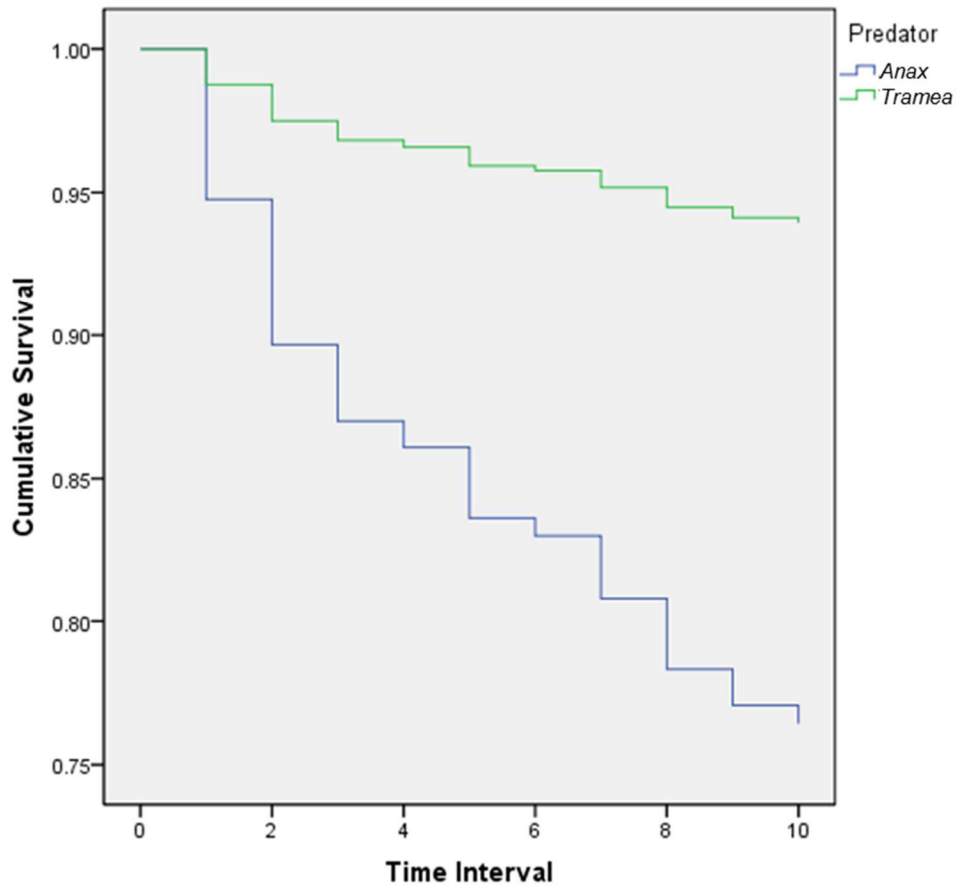


Figure 4-13. *Anax* is more lethal to IG prey than *Tramea*.

In Cox regression, mortality over time indicates that *Anax* is more lethal than *Tramea* irrespective of other factors such as IG prey species or prey density.

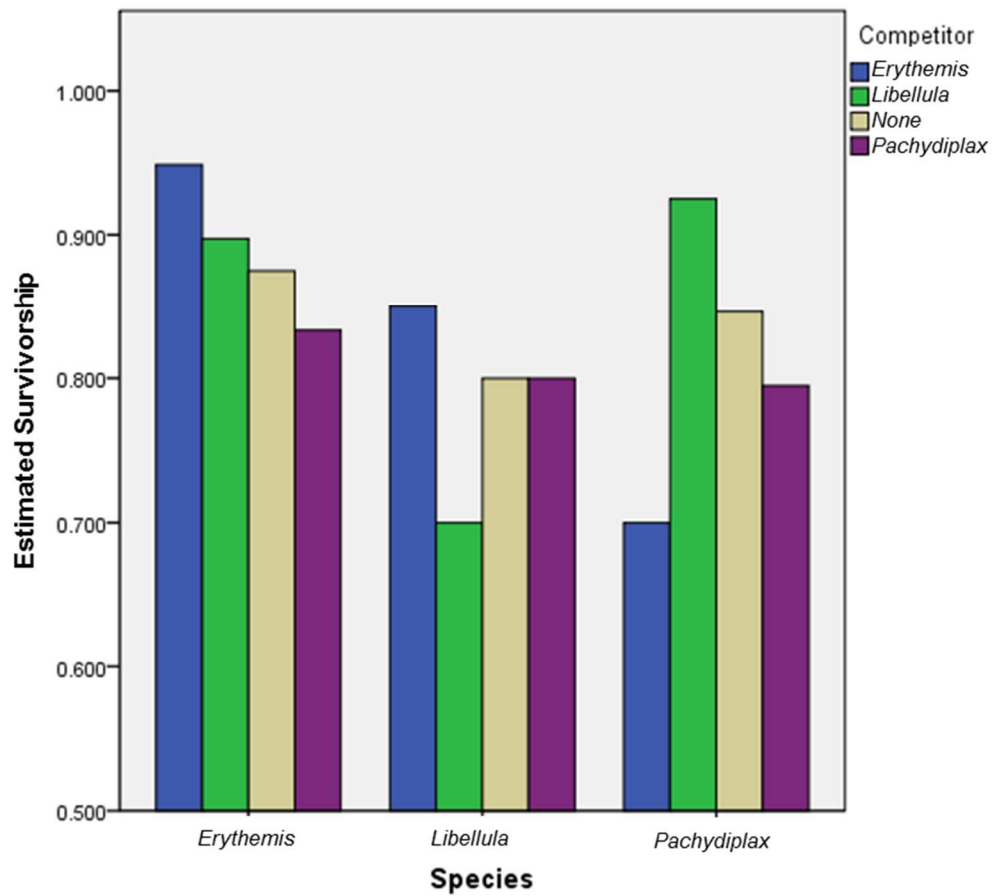


Figure 4-14. Survivorship varies by species and competitor.

Estimated survivorship, here estimated from binary logistic regression, was influenced by an interaction between IG prey dragonfly species, and what competitor species (also an IG prey species) was present.

When IG prey movement was restricted only to those individuals exposed to predation, and predator movement and space use variables included as predictors, movement rate decreased with predator climbing ($Y=-0.100x-2.049$, $df=1$, $F=4.199$, $P=0.041$), and varied between IG predator species ($df=1$, $F=5.795$, $P=0.017$) as well as initial prey density ($df=1$, $F=7.292$, $P=0.007$). These relationships explained 4.7% of the observed variation in data (Figure 4-15).

When IG prey climbing behavior was examined with the inclusion of IG predator movement, which necessitated the exclusion of IG predator negative controls to prevent collinearity in the continuous variable set, there were complex relationships between IG prey species ($df=2$, $F=57.440$, $P<0.001$), IG predator ($df=1$, $F=30.729$, $P<0.001$), and initial prey density that included numerous interaction terms (Table 4-5). The ratio between IG predator and IG prey heads was negatively related to climbing ($Y=-0.104x-3.613$, $df=1$, $F=13.051$, $P<0.001$). Predator use of cover was also negatively related to climbing ($Y=-0.244x-2.292$, $df=1$, $F=5.255$, $P=0.022$), predator climbing ($Y=0.514x+10.322$, $df=1$, $F=106.537$, $P<0.001$) was positively related to IG prey climbing. R^2 for these relationships was 0.528 (Figure 4-16).

Cover use was not affected by IG predator movement, cover use, or climbing behavior. However, the larger the predator was relative to the IG prey, the more time IG prey spent under cover ($Y=0.019x-1.382$, $df=1$, $F=7.029$, $P=0.008$). IG prey species differed in their cover use ($df=2$, $F=3.317$, $P=0.037$), and they responded to competitor species ($df=3$, $F=4.045$, $P=0.007$) and predator identity ($df=1$, $F=6.627$, $P=0.01$). There was a significant competitor by IG predator by prey density interaction ($df=3$, $F=4.105$, $P=0.007$) as well. In total, these explained 9.8% of the variation in these data (Figure 4-17).

When *Anax* was the only predator considered, logistic regression performed on mortality data indicated that IG predator/IG prey size ratio ($B=0.343$, $B_{exp}=1.409$, $P=0.034$), predator movement ($B=0.870$, $B_{exp}=2.388$, $P=0.084$), and prey movement ($B=0.966$, $B_{exp}=2.628$, $P=0.002$) rates had any significant impact on death probability for IG prey, all positive. However, predator movement was marginal. Log-likelihood was 260.848. When *Tramea* was the only

predator considered, IG prey movement ($B=2.277$, $B_{exp}=9.751$, $P=0.002$) increased the probability of death, along with the size ratio ($B=0.845$, $B_{exp}=2.327$, $P=0.008$) Log-likelihood was 94.805.

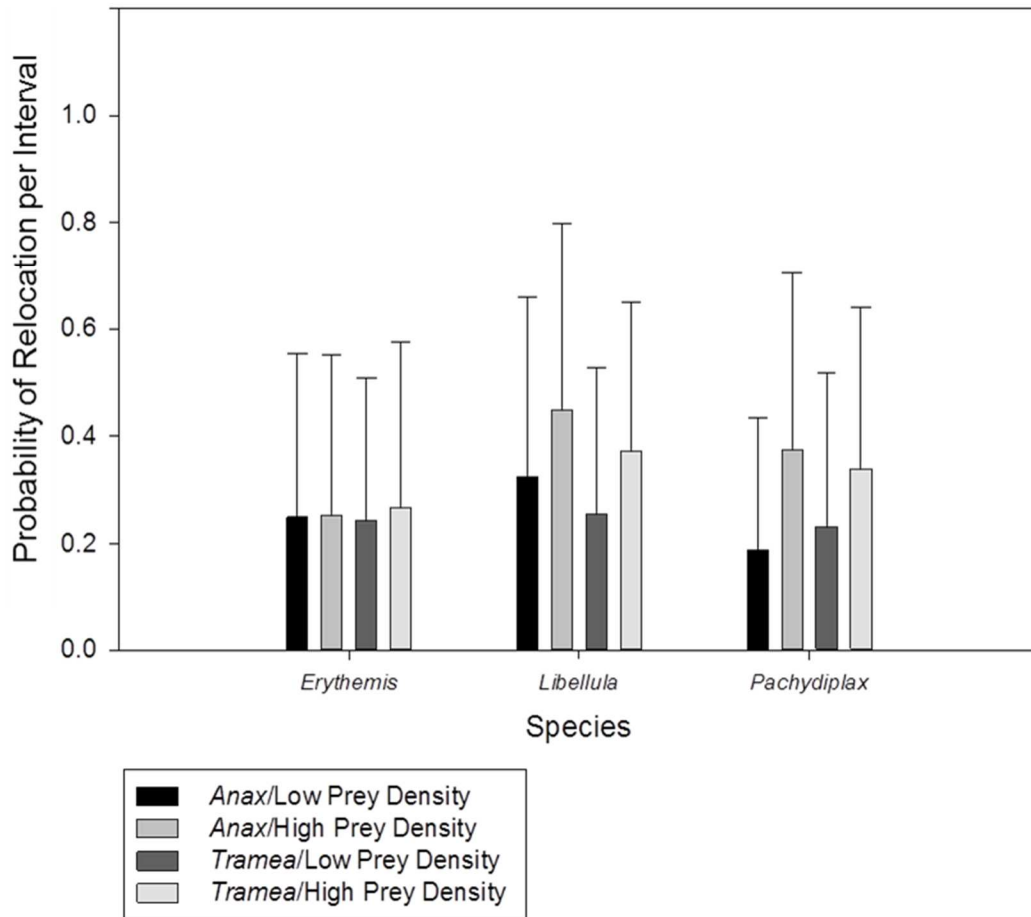


Figure 4-15. IG prey movement varies with prey density and predator without negative controls.

With the negative controls excluded to examine IG prey responses to IG predator movement, IG prey nymphs responded to both IG predator identity as well as prey density (e.g., *Anax*/Low Prey Density). Error bars=1 SD.

Table 4-1. ANOVA table for IG prey climbing behavior with negative controls excluded.

IG prey climbing behavior, without negative controls, was influenced by complex interactions between their species, IG predator identity, competitor, and prey density.

This is in addition to continuous covariates such as IG predator cover use and the size of the IG predator relative to IG prey.

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	114.466	51	2.244	11.388	0.000
Intercept	3.523	1	3.523	17.876	0.000
Pred movement	0.186	1	0.186	0.943	0.332
Pred climbing	20.997	1	20.997	106.54	0.000
Pred cover use	1.036	1	1.036	5.255	0.022
Head ratio	2.572	1	2.572	13.051	0.000
IG prey species	22.641	2	11.320	57.440	0.000
Competitor	0.892	3	0.297	1.509	0.211
IG predator species	6.056	1	6.056	30.729	0.000
Prey density	1.718	1	1.718	8.715	0.003
IG Prey * Competitor	2.491	6	0.415	2.107	0.051
IG Prey * IG Pred	0.477	2	0.239	1.211	0.299
IG Prey * Prey density	7.487	2	3.744	18.995	0.000
Competitor * IG pred	0.939	3	0.313	1.589	0.191
Competitor * Prey density	0.498	3	0.166	0.842	0.471
Pred * Prey Density	4.608	1	4.608	23.383	0.000
IG Prey * Competitor * IG Pred	0.995	6	0.166	0.842	0.538
IG Prey * Competitor * Prey Density	1.664	6	0.277	1.407	0.210
IG Prey * IG Pred * Prey Density	0.257	2	0.128	0.651	0.522
Competitor * IG Pred * Prey Density	0.285	3	0.095	0.482	0.695
IG Prey * Competitor * IG Pred *	0.439	6	0.073	0.371	0.897
Prey Density					
Error	83.366	423	0.197		
Total	381.010	475			
Corrected Total	197.832	474			

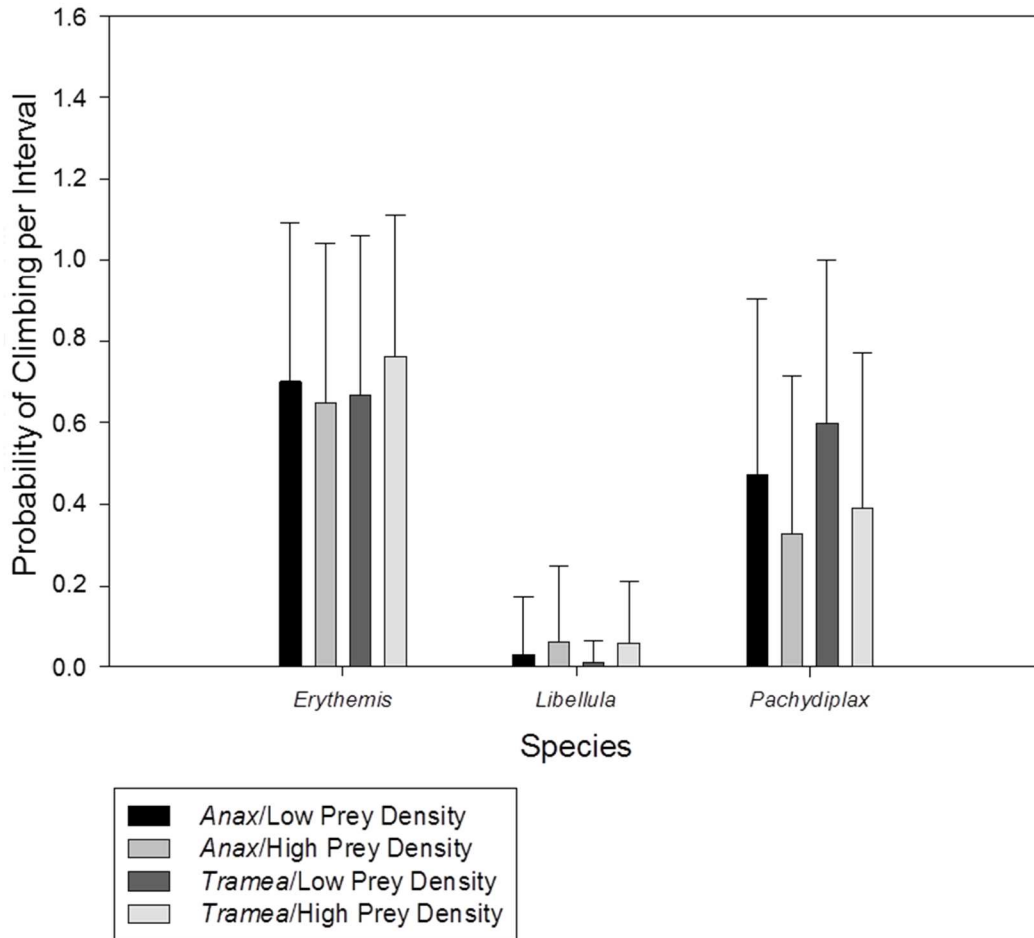


Figure 4-16. IG prey climbing varies by species, IG predator, and prey density. Without negative controls, and accounting for covariates, climbing by IG prey nymphs was influenced IG prey species, IG predator identity, and prey density (e.g., *Anax*/High prey density). Error bars=1 SD, which pushes the display range above 1.0.

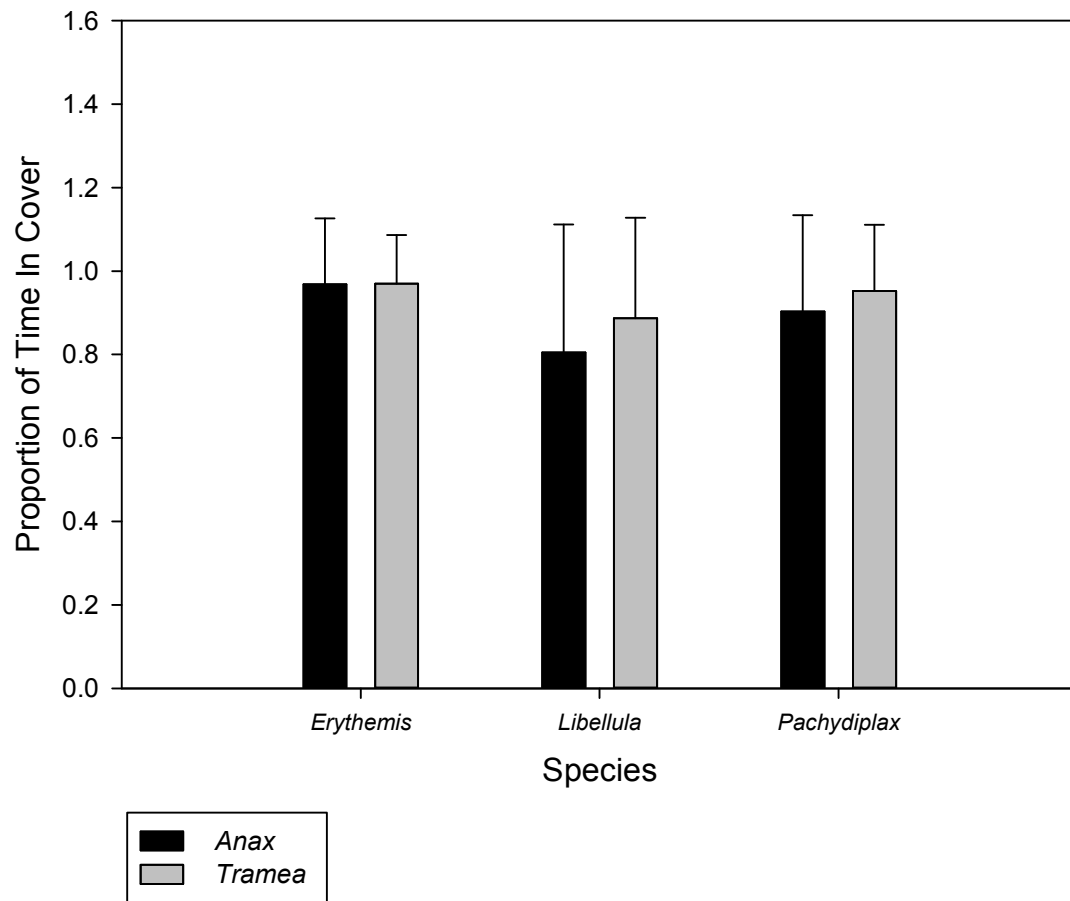


Figure 4-17. IG prey cover use by species and IG predator, negative control excluded. With negative controls excluded and IG predator movement and space use accounted for, cover use by the IG prey nymphs differed between IG prey species and by IG predator identity. While the overall relationships were statistically significant, the amount of explained variation was low, and *Erythemis* did not respond to IG predators. Error bars=1 SD, which pushes the display range above 1.0.

When *Anax* was the only predator considered, logistic regression performed on mortality data indicated that IG predator/IG prey size ratio ($B=0.343$, $B_{exp}=1.409$, $P=0.034$), predator movement ($B=0.870$, $B_{exp}=2.388$, $P=0.084$), and prey movement ($B=0.966$, $B_{exp}=2.628$, $P=0.002$) rates had any significant impact on death probability for IG prey, all positive. Though, predator movement was marginal. Log-likelihood was 260.848. When *Tramea* was the only predator considered IG prey movement ($B=2.277$, $B_{exp}=9.751$, $P=0.002$) increased the probability of death, along with the size ratio ($B=0.845$, $B_{exp}=2.327$, $P=0.008$) Log-likelihood was 94.805.

Discussion

Non-Lethal Tests

Irrespective of how it was measured, most IG prey species either reduced their movement in response to increasing prey density, or did not respond. The one exception was *Erythemis simplicicollis*, which increased its movement rate in response to high prey density.

Climbing propensity varied between IG prey species and was modified by prey density for some IG prey species, with most of them increasing climbing in response to high prey density. *Epitheca princeps*, *Erythemis simplicicollis*, and *Tramea lacerata* showed the largest changes between prey density treatments.

When caged predators were included and higher degrees of habitat heterogeneity were used, dragonfly nymphs moved less as they became larger. However, the prey density relationship reversed relative to the earlier tests. Other than *Libellula*, dragonfly nymphs responded to high prey density by relocating more often and increasing the distance they travel. *Libellula* relocation frequency was unaffected, but the distance decreased. This may be an effect of cover offered by the vegetation to the prey. The cover may make the prey density perceived by the nymphs to be very low, approaching zero in some instances. Under such conditions, a nymph may conserve energy by reducing foraging activity and waiting for conditions to change (Schaffner and Anholt 1998, Hirvonen 1999).

In climbing tests, only *Erythemis* and *Pachydiplax* spent significant amounts of time climbing within the artificial vegetation. *Libellula* only appeared to climb incidentally to movement. This runs somewhat contrary to the appearance of *Erythemis* as a generalist in the first experiment. This species is most commonly found near the surface in mats of floating vegetation (Corbet 1999), often in water that is very shallow, such as at the edge of a pond (Corbet 1999). The structural complexity present in the vegetation is likely important for microhabitat selection in this species (Mcnett and Rypstra 2000, Schofield 2003), and may be a consequence of the artificial *Elodea* used in the second experiment being a more suitable habitat to elicit this behavior compared to the wooden dowels used in the first experiment.

Cover use, in this case spending time on the side of the aquaria that had aquatic plants, differed between IG prey species. When predators were not present, *Libellula* was most likely to spend time outside of this zone, while *Erythemis* and *Pachydiplax* spent most of their time there. *Pachydiplax* did not change this behavior for any predator, while *Tamea* did drive *Erythemis* from the cover region into open space on occasion. *Libellula* by contrast increased its reliance on vegetative cover in the presence of both *Tamea* and *Anax*.

Lethal Tests

In lethal tests (direct exposure to predator), *Pachydiplax* and *Erythemis* increased movement in response to high prey density, while *Erythemis* did not. Climbing propensity was modified by size, with increasing body length leading to an increasing tendency to climb. *Pachydiplax* and *Erythemis* both displayed a strong tendency to climb, while *Libellula* mostly stayed on the substrate. Prey density responses varied between IG prey species. *Libellula* and *Erythemis* did not appreciably change climbing behavior at different prey densities, while *Pachydiplax* increased climbing when density was low. When body length was removed from the analysis, the IG prey species by IG predator interaction became significant. This indicates that at least some of the body size relationship is anti-predator in nature, and that IG prey nymphs

assess their own body size as an element of risk. The smaller they are, the greater the risk they perceive.

For both *Libellula* and *Pachydiplax*, climbing decreased in the presence of IG predators, particularly *Anax*, which is itself a climbing species. Not only is this result different from the non-lethal test, but it appears to increase mortality. When the IG predator was free and able to prey upon the IG prey nymphs, the IG predator's movement provides an additional stimulus that the IG prey can potentially detect (Cooper 1998). When caged, any potential chemical cues passed into the water column—thus alerting IG prey that they were in the vicinity—but the cage prevents them from getting close enough to be a danger, or even be localized due to the movement-sensitive visual systems dragonfly nymphs possess (Land 1997).

When predator movement was taken into account, there were two responses made by IG prey. The first was to spend more time on the substrate when the IG predator was in cover. The second was to climb more as the IG predator climbed into the vegetation.

Anti-predator cover use varied between IG prey species and with IG predator identity, with different strategies utilized by each species. *Erythemis* did not respond to predators at all in this respect, and heavily utilized cover irrespective of predator species or the lack thereof. *Libellula* tended to spend more time in cover when exposed to predators, with a stronger response to *Tramea* than *Anax*. By contrast, *Pachydiplax* moved out of cover in the presence of *Anax*, which closely followed their climbing strategy as well, in which they dropped to the substrate when *Anax* was present.

In the presence of competitors, all IG prey species had different movement responses that interacted with prey density. At low prey density, *Erythemis* reduced movement in response to *Pachydiplax* and other *Erythemis*, but did not respond appreciably to *Libellula*, which competes with it weakly for *Gammarus* prey (Chapters 2, 3). It increased its movement at high prey density in response to *Pachydiplax* competitors, but reduced it in response to *Libellula* and did not respond to *Erythemis*. *Libellula* decreased its movement in response to all other IG prey species as well as conspecifics at low prey density, and increased its movement at high density in

response to all IG prey species. *Pachydiplax* at low density increased its movement in response to *Libellula* and *Erythemis*, but decreased its movement in response to conspecifics. At high density, it only increased movement in response to *Erythemis* only.

Only *Pachydiplax* changed its climbing behavior in response to prey density changes, and no species did so in response to competitors. Cover use was a different matter. It did not vary with prey density, but IG prey species did respond to competitors. *Erythemis* did not respond to any species compared to when no competitors were present. *Libellula* however increased its use of cover slightly in response to competition by conspecifics, and reduced cover use in response to *Erythemis*. *Pachydiplax* responded to competition from *Erythemis* by reducing cover use, and did not respond to competition otherwise.

Predator Responses

Predators adjusted their behavior to fit available prey, for both shared prey and IG prey species. Both IG predator species reduced their movement in response to high shared prey density, and *Anax* was consistently more active than *Tramea*, which is consistent with prior literature that characterizes *Anax* as a sit and pursue forager (Michel and Adams 2009). In trials with only one IG prey species, *Anax* activity was highest when *Erythemis* was present, and was equal between *Libellula* and *Pachydiplax*. This is likely because *Erythemis* is more difficult to find due to its generally cryptic behavior. *Tramea* did less searching overall compared to *Anax*, and displayed patterns of behavior more consistent with a sit and wait forager (Huey and Pianka 1981, Yong 2005).

Just as they did with their own movement, climbing behavior by IG predators was also sensitive to their IG prey, and the density of shared prey. *Anax* climbed much more in response to low prey density, likely as part of search pattern, and incidental to movement. *Tramea* by contrast either did not respond to changes in prey density, or climbed slightly less at low prey density.

In response to IG prey, *Tramea* climbed less overall, both IG predator species responded similarly to each IG prey species. Both of them climbed the least when in the presence of

Libellula, which is a sprawler, and so climbing was not necessary to locate, capture, and consume it. *Anax* maximized its climbing behavior when searching for *Pachydiplax*, while *Tramea* did so when searching for *Erythemis*; both of them primarily climbing species. This search behavior might be the reason why *Pachydiplax* often leaves the vegetation, both based on these data and prior literature (Wellborn and Robinson 1987). When only one IG prey species was present, use of cover by *Anax* was approximately equal for both *Pachydiplax* and *Erythemis* and minimized for *Libellula*. *Tramea* displayed a similar pattern, equaling *Anax* in this regard for both *Pachydiplax* and *Erythemis* IG prey, but with significantly decreased cover use when *Libellula* was present.

In addition to these responses, there were also combined responses to multiple IG prey. Compared to cases wherein *Erythemis* was the only IG prey present, all combinations of *Erythemis* and other species caused a decrease in movement. Additionally, *Pachydiplax* and *Libellula* combinations induce more activity than either of those species by themselves. *Tramea* responds differently. It either keeps its movement response the same as single IG prey trials, or decreases its movement rate, depending on the combination.

Habitat Complexity and Foraging Behavior

Gammarus responds to the presence of predators (Wudkevich et al. 1997, Pennuto and Keppler 2008), and will use aquatic vegetation and detritus as cover against consumption by predators (Holmlund et al. 1990, Åbjörnsson et al. 2004). This likely affects what the dragonfly nymphs perceive as the density of prey. When dowels were used to simulate vegetation, there were fewer hiding places for *Gammarus* and the prey density perceived by nymphs was likely higher under those conditions than it was when vegetation was more structurally complex. Each species likely has different search response curves to different prey densities (Cooper et al. 2005), but these may not necessarily be minimized at high prey densities (Hirvonen 1999). As perceived prey density decreases below a certain point, foragers may decrease their foraging costs by not moving and reverting to an ambush foraging mode (Hirvonen 1999), or relocate to a

different area entirely in accordance with marginal value theorem (Krebs et al. 1974, Charnov 1976, Hassell and Southwood 1978). When predators and competitors are added, prey availability decreases and the risk of predation increases. When this induces a reduction in cover use, it can be interpreted as an attempt to leave the foraging patch (Shrader et al. 2008, Stav et al. 2010).

Movement did not respond directly to the simple presence or absence of an IG predator or its identity. However, when IG predators were taken as a given (always present) and negative controls (with no IG predator) excluded to examine IG prey responses to IG predator movements, IG prey responded to both predator behavior and predator identity. *Anax* was more active than *Tramea*, so the benefit of a movement reduction when *Anax* is present should be lower than it is when *Tramea* is present, and spatial relocation a greater benefit than the risk of detection is a cost (Wohlfahrt et al. 2006). Climbing behavior by the predators also tended to reduce IG prey movements independent of predator identity. An IG predator that is high in the vegetation can ambush IG prey in the substrate from above (Convey 1988, Schultz et al. 2009), and can reach IG prey that are moving at elevation within the vegetation that would otherwise be out of reach.

A similar interaction occurred with IG prey climbing behavior. Initial tests did not reveal any relationship with predator presence or identity, until IG prey size was removed from the equation. Then there was a significant IG predator by IG prey species interaction term that indicated collinearity with IG prey size and that relationship. Size and climbing were directly related. This may indicate that the defensive benefit to climbing into the vegetation is size-dependent. Perhaps for a small individual the stems of the artificial vegetation and their attachment sites provided just as much protection as the leaves. When predator movements were taken into account, much more of these data are explained. Anti-predator behavior became evident in response to predator identity, predator occupancy was negatively related to IG prey climbing, and predator climbing was positively related to IG prey climbing. These may seem contradictory, until one considers that cover use correlates strongly with climbing behavior. Any individual that did not leave the vegetation in response to predation risk may have climbed into

the vegetation because it provides both physical protection and prevents detection (Walls 1995, Janssen et al. 2007). It is also worth noting that individual IG prey species have different responses to IG predators, and the patterns seen in the continuous covariates are in addition to these responses. To illustrate: increasing predator size relative to IG prey size decreases IG prey climbing behavior. This response is layered on top of what might be a tendency to remain on the substrate for smaller individuals that, when negative controls are excluded, swamps the anti-predator response in collinearity.

For all of these IG prey species, the presence of an IG predator in the environment is virtually a given in nature (Corbet 1999, McCauley et al. 2008). Some aspects of their behavior may be fixed rather than being induced by the presence of an IG predator (DeWitt et al. 1998, Hoverman et al. 2005), and the mere presence of an IG predator will not change IG prey behavior. Instead, their behavioral response to predation risk in terms of their movement and climbing behavior may be sensitive to the interaction between predator identity and the actual behavior of that predator, which may be a more reliable indicator of risk (Cooper Jr 1998).

Anti-predator cover-use changes were evident irrespective of whether or not predator movement was accounted for. In response to *Anax*, *Pachydiplax* occasionally left cover, which corresponded to its reduction in climbing behavior in response to this predator. This is fully consistent with prior studies of their anti-predator behavior (Wellborn and Robinson 1987, Hopper 2001) and indicates that they prefer to use spatial avoidance strategies over detection-avoidance strategies. *Erythemis* did not respond one way or the other indicating a preference for detection-avoidance given its other behavior, while *Libellula* increased cover use in the presence of *Tamea*, but not *Anax*. Increased predator size relative to IG prey tended to decrease cover use just as it decreased climbing behavior, indicating that the larger the predator was, the greater the risk, and the more likely the IG prey was to simply leave the area.

Mortality

Selecting the best possible models for both Cox regression and Logistic regression, *Anax* was the more lethal predator, as was seen in previous experiments. It is more aggressive, an active forager and its mouthpart morphology allows it to attack larger prey items (Chapter 2). IG prey movement rate increased mortality, while climbing decreased mortality. Differences in these variables translated to differential mortality between IG prey species that display different behaviors in response to both predators and competition.

An individual does not have to have perfect predation avoidance strategies; they just have to be better at avoiding predators than their competitors in order to avoid being killed. Different species will utilize different strategies in order to accomplish this, trading off other biological imperatives such as foraging in the process, with varying success (McPeck 1990a, Power et al. 1992, Walls 1995). This was seen in these data. *Pachydiplax*, for example, in the presence of heterospecific competitors, tended to increase its movement rate which likely increased its probability of detection (Montgomery and Macdonald 1987, Martel and Dill 1995). It even reduced its climbing and moved out of cover more often in response to *Anax*. However, its movement rate was approximately equal to that of *Libellula*, which spent most of its time on or near the substrate and more time in the open. Even with its behavioral changes *Pachydiplax* still climbed more when under threat of predation and spent more time in cover. As a result, *Libellula* got detected and consumed more often when these two species co-occurred. This translated to increased survivorship relative to when no competitors or a conspecific were present for *Pachydiplax*, even though the strategy it adopted was sub-optimal for predator avoidance. When *Erythemis* was present instead of *Libellula*, *Pachydiplax* survivorship dropped. Its movement increased and was approximately equal to that of *Erythemis* (which itself increased movement in response to *Pachydiplax*), but while *Erythemis* did not move out of cover or alter its climbing patterns, *Pachydiplax* did both. It was thus more likely to be detected first, and was consumed more often.

IGP Stability

There are two ways structural complexity can increase IGP stability in a two-predator system. The first, on a smaller scale, is by providing cover from IG predators (Wellborn and Robinson 1987, Gotceitas and Colgan 1989, Swisher et al. 1998, Michel and Adams 2009). This can reduce the effect of apparent competition in high productivity systems and increase the parameter space in which IGP is stable. The second, when that complexity is patchy, is to provide spatial separation between IG predator and prey (Heithaus 2001, Janssen et al. 2007, Vanak et al. 2013). When two species share different microhabitat preferences, or can shift between multiple microhabitats in response to changes in the biotic environment, then both competitive (Brown 1981, Keen 1982) and predatory (Tarr and Babbitt 2002, Suutari et al. 2004, Van de Meutter et al. 2004) interactions can be moderated.

These data provide some evidence for both of these, though primarily through the anti-predator responses themselves. IG prey species climbed into aquatic vegetation in order to avoid predators and doing so reduced their mortality rate over time, which was expected, as was an increased tendency to climb in response to the interaction of high prey density. At higher prey density, apparent competition predominates in most IGP models (Polis et al. 1989, Holt and Polis 1997). However, that is dependent on the rate at which IG prey are consumed by IG predators (Polis et al. 1989, Sentis et al. 2013). Thus, any response on the part of IG prey that can reduce the rate at which they are consumed by IG predators can increase the stable parameter space of IGP (Kimbrell et al. 2007, Sentis et al. 2013). In tests where the negative control was included and predator movements not examined this pattern still holds true, with increases in climbing in response to predation risk and high prey density, with the exception of *Pachydiplax*, which used a different strategy.

This strategy, particular to *Pachydiplax* in these experiments, was probably an attempt to relocate away from *Anax*. It did not impact their mortality rate, likely because the aquarium was small enough that they could not exit *Anax*'s detection range (Aksnes and Giske 1993, Land 1997, Olberg 2012). If the space available were larger, they could conceivably have moved to

another patch out of the IG predator's reach. This could also improve IGP stability by reducing both the pressure of competition on the IG predator, and by reducing the pressure of predation on IG prey (Wissinger 1992, Bruce 2011, Sentis et al. 2013, Vanak et al. 2013).

Differential vulnerability to predation can also increase IGP stability provided that the vulnerable species is also the competitively superior species in an IG prey pair (Holt et al. 1994, Woodward and Hildrew 2002b). Here, only one shared prey type was used (*Gammarus*); however that will not be the case in nature (Burcher and Smock 2002). High movement rates increase prey encounter rate (Gendron and Staddon 1983, MacKenzie and Kjørboe 1995), while simultaneously making detection by IG predators easier (Montgomery and Macdonald 1987, Koperski 1998). Here, high movement rate affected the probability of death, and this translated to differential mortality between IG prey species when they were placed at risk of predation, with interactions between IG prey species that coincided with their movement rates.

There are several ways in which this work can be improved upon and extended. The first is to extend the spatial scale. By expanding the available space and creating a mosaic of open spaces and vegetated spaces, it may be possible to examine more clearly how species like *Pachydiplax* move between areas to avoid IG predators like *Anax*. Examining the effect of multiple IG predators on behavior and mortality between species might also be useful.

It would be extremely valuable to examine this system with a simulated population. This could be done either through a lab mesocosm with periodic re-stocking, or through field enclosure experiments that incorporate natural reproduction or immigration. The adults are strong flyers with long dispersal distances (Azuma and Watanabe 1988, Michiels and Dhondt 1991, Conrad et al. 1999), and as a result the breeding population can be decoupled from what is going on inside the pond (Conrad et al. 1999, McCauley et al. 2008). Source-sink dynamics can stabilize IGP irrespective of pond conditions (Amarasekare 2006), and accounting for that is important. Different species also reproduce at different times, and develop at different rates, which can lead to priority effects modifying the dynamics of IGP across landscapes (Padeffke and Suhling 2003,

van der Hammen et al. 2010). Lab mesocosms or controlled field enclosures can account for these issues.

Chapter 5

Defensive Morphology

Introduction

Previous chapters have primarily dealt with how behavior affects intraguild predation through the interaction between competitive interactions and predator avoidance mechanisms. This chapter examines vulnerability to intraguild predation through the interruption of the attack sequence by morphological structures. Just as morphology plays a role in prey-capture, it is also used by organisms to avoid being eaten. In systems where intraguild predation exists, morphological traits may affect the strength of predatory interactions (Mikolajewski and Rolff 2004, Kratina et al. 2010, Strobbe et al. 2010, Hopkins et al. 2011), which may influence the stability of intraguild predation directly (Kratina et al. 2010, Nakazawa et al. 2010) and indirectly (Kimbrell et al. 2007).

Differential mortality between IG prey may stabilize IGP in a multi-predator system (Holt et al. 1994, Holt and Polis 1997, Smith 2006, Hawley 2009) when mortality and competitive ability are positively correlated. But defensive morphology alone cannot create that specific type of differential mortality without significant physiological costs that come with developing and maintaining that morphology (DeWitt et al. 1998, Relyea and Auld 2005). There is scant evidence (Flenner et al. 2009a) of direct physiological costs for most types of defensive morphology in the Odonata. Examining these costs is beyond the scope of the current treatment, but defensive morphology has to be examined if for no other reason than to rule out its effect on mortality and ensure that the mortality rates observed in Chapters 3 and 4 are the result of behavior and not morphology. For example, in the experiments described in Chapter 4, *Libellula* was the most vulnerable of all IG prey species to IGP, but that may not have necessarily been due to its behavior, but because it is more vulnerable once attacked.

Many odonates have defensive morphological structures such as lateral and dorsal spines (Arnqvist and Johansson 1998, Mikolajewski et al. 2010). These spines have been shown to defend a nymph from fishes by increasing the probability that it will be rejected (Abrahams

1995, Mikolajewski and Rolff 2004, Lescak and von Hippel 2011). These same spines decrease survivorship for nymphs attacked by aeshnid nymphs (Mikolajewski et al. 2006). Morphological variation in spine length exists between congeners (genus *Leucorrhinia*) that primarily inhabit ponds with fish, and those inhabiting ponds lacking fish, where *Anax* is the top predator. These character states appear to represent specific adaptations to those respective habitats (Mikolajewski et al. 2006). It may be the case that spines provide a “handhold” on the IG prey's abdomen for the palpal lobes of *Anax* (Reimchen 1980), giving them an easy gripping surface, or guiding an attack that otherwise would have glanced off an angled surface into a solid grip. The particular mechanism has not been investigated for this group, but the “hand hold” hypothesis has been proposed to occur in sticklebacks (Reimchen 1980, Reist 1980, Marchinko 2009). Both of these can happen with a flat labial mask. But an IG predator species with a cup-shaped labial mask may be hindered by spines if they ward off the broad surface of the palpal lobes. This difference should not be generalizable to the legs because they are independently mobile and insufficiently close together to provide an effective barrier to a cup-shaped labial mask. There also appears to be a physiological tradeoff with defensive spines. Closely related species that differ in their spine length have differences in the thickness of the cuticle of their exoskeleton (Flenner et al. 2009b), which might impact their defensive ability on locations other than the abdomen.

Another type of defensive morphology is armor, which serves to protect an animal from attack either through its geometry or material properties (DeWitt et al. 2000, Rhee et al. 2009, Song et al. 2011, Yang et al. 2012, Salmon and Scholl 2014), though it is expensive to produce (Palmer 1992, Trussell and Nicklin 2002) and can limit mobility (Bergstrom 2002, Losos et al. 2002). As a result of both of these tradeoffs, the extent and location of armor tends to vary among taxa that possess it (Stayton 2011), and sometimes even within taxa as result of local adaptation (Bergstrom 2002, Rivera 2008, Marchinko 2009) or phenotypic plasticity (Dzialowski et al. 2003).

Dragonfly nymphs are not obviously armored. They do not have plates of dermal bone or thickened skin like many vertebrates (Abrahams 1995, Chen et al. 2011, Yang et al. 2012), and

they do not reinforce their exoskeleton with calcium like many crustaceans (Boßelmann et al. 2007). However, that does not imply that their exoskeletons do not provide some protection against attack. Chitin varies in thickness (Evans and Sanson 2005), and hardness (Hillerton et al. 1982). It can also be shaped in such a way that attacks are less successful (Yao et al. 2010, Yap 2012). So a preliminary investigation of the protective qualities of their exoskeleton can be useful insofar as addressing whether or not mortality differences between species under predation risk stem from their morphology or behavior. In these species, the abdomen is the most likely to be well protected. It contains all of the musculature and nerves required to propel the nymph (Mill 1965, Mill and Pickard 1975, Tanaka and Hisada 1980), and a predatory strike—particularly one that penetrates the exoskeleton—can damage those systems and make escape impossible. Even if the nymph does escape after that, it will be severely injured and unlikely to survive subsequent attacks or even be able to feed itself.

In addition to modulating the risk of predation, morphology may interact with defensive behavior. Morphological defenses may decrease the relative importance of behavioral defenses, a phenomenon called trait compensation (Abrahams 1995, Mikolajewski and Johansson 2004, Relyea and Auld 2004) wherein defensive morphology and behavior are negatively correlated. Alternatively, they may also invest more heavily in behavioral defenses (Mikolajewski and Johansson 2004, Mikolajewski et al. 2010). This is trait co-specialization, and it can run in both directions. Behavioral and morphological defenses are positively correlated, and can either both be reduced leading to a species with very little in the way of defenses against predation, or both heavily invested in, leading to a species with very strong over-all defenses against predation. This is usually studied between closely related species that occupy different habitats (Cotton et al. 2004, Mikolajewski and Johansson 2004). Odonates have been shown to vary in patterns of allocation to morphological versus behavioral defenses (Cordoba-Aguilar 2008). Additionally, it may be possible that investment in one form of morpho-physiological defense against predation may positively or negatively correlate with other forms. This leads to the following hypotheses:

- 1) Defensive spines should increase predation risk from intraguild predators with a flat labial mask, and decrease predation risk by those intraguild predators with a cup-shaped labial mask. This is due to a handhold effect that should exist for the former, but not for the latter due to the geometry of the palpal lobes.
- 2) Attacks made to the abdomens of dragonfly nymphs should be the least successful.
- 3) It should be possible to detect covariation between defensive morphology and the defensive behavior observed in Chapter 4, in the form of movement and space use patterns. If the least armored species also displays the least effective defensive behavior, it should have the highest mortality.

Methods and Results

Testing these hypotheses required a single stand-alone experiment, and also incorporates some of the data from Chapters 3 and 4. The stand-alone experiment tested the efficacy of defensive spines. Two spined species, *Tramea lacerata*; which has long spines on the 8th and 9th abdominal segment, and *Pachydiplax longipennis*; which has shorter spines on the 9th abdominal segment, were used in a 2x2 complete block design. One factor was the state of defensive spines. Individuals were randomly assigned to one of two groups: one with abdominal spines intact, the other with spines removed. The second factor was predator, as each trial used either a large *Anax junius*, or a large *Tramea lacerata*. Large, in this case was defined as having a head at least 50% larger than the head of prey heterospecifics. Individuals in the spine-removal treatment had abdominal spines removed using a set of microscissors to the margin of their abdominal segments. Pairs of focal specimens were then placed in a 90 mm petri dish container filled with treated tap water at 25° C. A 1 cm grid was affixed to the bottom of each dish for measurement calibration. Then, after a 5 minute acclimation period, a predator was added to the container. All movement and predation attempts were filmed for a period of 20 minutes. This was replicated 12 times per treatment block, for a total of 24 nymphs of each IG prey species per block. Pairs were used to maximize the number of attacks observed.

Attack sequences were scored by their locations for initial contact, initial capture success or grabs, and total success which was indicated by the IG prey species being eaten. Initial contact was defined as an attack that makes contact with but does not necessarily result in the capture of a focal nymph. These data were analyzed using a battery of statistical tests. The first was Cox regression, which used the number of attacks and their success rates to generate a hazard function, with IG prey species, IG predator species, and body length to predator head width ratios as predictors. Two forms of logistic regression were also used: standard binary logistic regression for every attack, and a generalized estimating equation that utilizes a binary logistic function within SPSS, which serves as a repeated measures procedure for each individual IG prey nymph.

Initially, the data used in logistic regression were restricted to include only those attacks that contacted the abdomen so that spine status could be used as a predictor variable. Cox regression included spine status, but it could not be restricted to include only abdominal attacks.

The second analysis utilized data taken from Chapter 3. In these experiments, attacks were made by *Anax junius* and *Tramea lacerata* upon *Pachydiplax longipennis*, *Libellula lydia*, and *Erythemis simplicicollis* under conditions identical to those observed here in the experiments described in this chapter, with the exception of shared prey being present (See physical methods described in Chapter 3). Locations of attacks and their results were recorded identically. As a result, the same battery of statistical tests can be performed.

A third analysis used the predicted probability of death per attack for a given IG prey species of a given size as a proxy for morphological defenses as a predictor of movement and space use data collected from the experiments described in Chapter 4. Analyses were done using logistic regression to obtain the probability of death per strike, and linear regression was used to test for behavioral trait compensation.

Defensive Spines

Examining the effect of defensive spines against predation by *Anax*, there was no relationship found in logistic regression for either *Pachydiplax* or *Tramea*. Spines had no effect, irrespective of other factors, whether or not strike location was inclusive or restricted to the abdomen. Strike location (df=4, Chi Square=18.358, $P<0.001$) was significant in logistic regression for initial capture success with a -2LL statistic of 102.994 (Figure 5-1, Table 5-1). The same pattern was seen in the repeated measures generalized estimating equations, with strike location (df=4, Chi Square=22.458, $P<0.001$) being the only statistically significant variable. For this, the Adjusted Quasi-Likelihood statistic (a measure of model-fit in bigger-is-better form) was 222.282.

When total attack success, and thus death for the IG prey, was examined in the same way, IG predator head to IG prey body length ratio (df=1, Chi Square=9.991, $P=0.002$, $B=6.613$, $B_{exp}=744.895$) increased the probability of IG prey death. Strike location was also significant (df=4, Chi Square=14.095, $P=0.007$). In terms of model fit, -2LL was 91.384 (Figure 5-2). Using the generalized estimating equation, the results are the same, though parameters are sign reversed in that procedure. The Adjusted Quasi-Likelihood statistic was 247.001 (Table 5-2). When logistic regression was done using only those attacks that resulted in initial capture, only the predator/prey size ratio was significant, though IG prey species was marginal. The -2LL statistic was 20.247 (Table 5-3).

Table 5-1. Logistic regression results for initial grabs against *Pachydiplax* and *Tramea* by *Anax*.

This shows the result of a logistic regression used to calculate the probability that an *Anax* will succeed at initial capture of *Pachydiplax* and *Tramea* on the basis of what body region it attacks. The thorax is the reference category.

	B	S.E.	Wald	df	Sig.	Exp(B)
Thorax (reference)			18.358	4	0.001	
Head	0.105	1.030	0.010	1	0.919	1.111
Leg	0.693	0.816	0.721	1	0.396	2.000
Lateral Abdomen	-1.910	0.792	5.808	1	0.016	0.148
Posterior Abdomen	-1.558	0.724	4.626	1	0.031	0.211

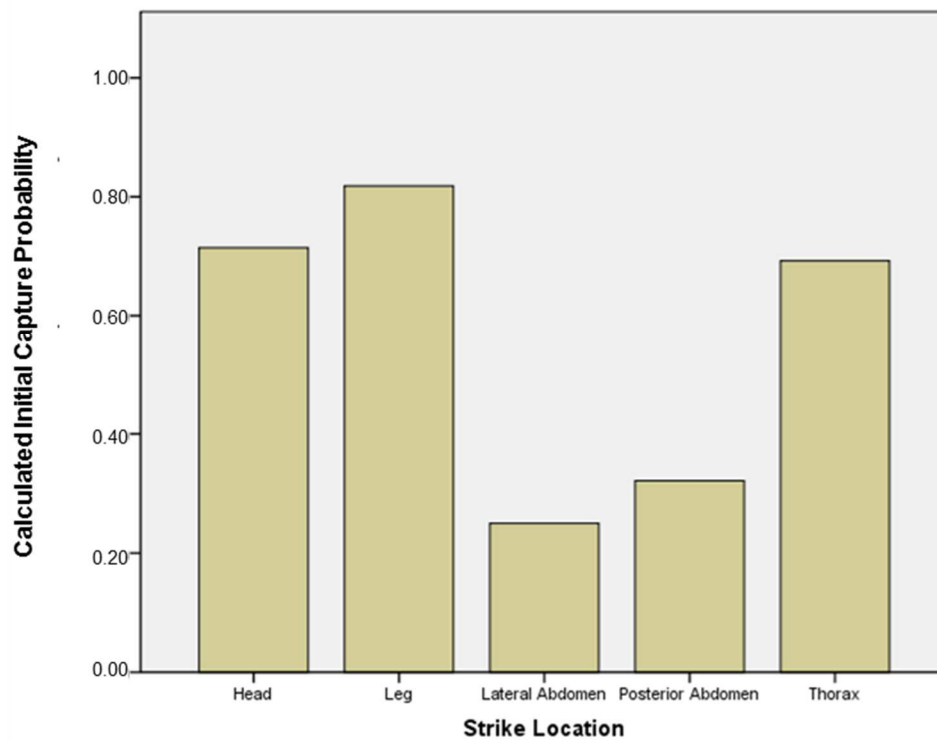


Figure 5-1 Initial capture varies with strike location.

This is the visualization of a logistic regression used to calculate the probability that an *Anax* will succeed at initial capture of *Pachydiplax* and *Tramea* on the basis of what body region it attacks.

Table 5-2. Total attack success against *Pachydiplax* and *Tramea* by strike location.

This shows the result of a generalized estimating equation (similar to a logistic regression, but with repeated-measures capability) used to calculate the probability that *Anax* will succeed at killing *Pachydiplax* and *Tramea* on the basis of what body region it attacks. The thorax is the reference category. These data are inclusive of attacks that missed and did not lead to initial capture.

Parameter	B	Std. Error	Hypothesis Test		
			Wald Chi-Square	df	Sig.
(Intercept)	1.696	1.0384	2.668	1	0.102
Head	0.595	1.2011	0.245	1	0.621
Leg	0.676	0.6275	1.160	1	0.281
Lateral Abdomen	2.211	0.7136	9.602	1	0.002
Posterior Abdomen	2.637	0.8562	9.487	1	0.002
Thorax (reference)	0.000
Size Ratio	-4.395	1.7352	6.414	1	0.011
(Scale)	1.000				

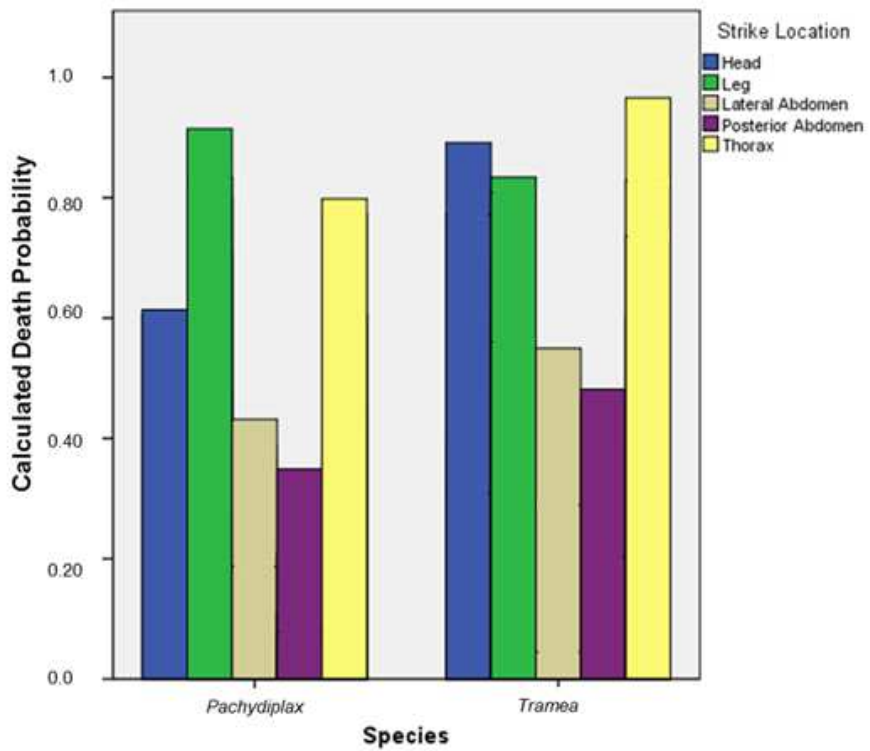


Figure 5-2 Probability of death varies by species and strike location with *Anax* predators. This is based on the same generalized estimating equation as Table 5-2. It was used to calculate the probability that an *Anax* will succeed at killing *Pachydiplax* and *Tramea* on the basis of what body region it attacks. The thorax is the reference category, and the values seen are calculated from the model and are inclusive of attacks that missed and did not lead to initial capture.

Armor and Strike Location

Preliminary analysis using Cox regression to determine the number of predatory strikes until death indicated no differences between IG prey species when subjected to predatory strikes by *Anax*. Logistic regression found that maximum burst swimming speed slightly decreased the probability of death for IG prey nymphs ($B=-0.007$, $B_{exp}=0.993$, $P=0.022$), with a $-2LL$ statistic of 200.119. When a more detailed analysis was conducted that explicitly included strike location per attack, there were significant effects of both IG prey species ($df=2$, Chi Square=6.271, $P=0.043$) and strike location ($df=4$, Chi Square=6.533, $P<0.001$). There was no effect of size, or any significant interaction terms. Adjusted Quasi-Likelihood was 1225.56 (Figure 5-3). When this same procedure was done with the probability of death per attack both IG prey species ($df=2$, Chi Square=28.268, $P<0.001$) and strike location ($df=4$, Chi Square=186.046, $P<0.001$) were significant, with an adjusted Quasi-Likelihood statistic of 1640.728 (Figure 5-4).

Using the same procedure, this analysis was re-run including only strikes that resulted in initial capture. Here, IG prey species ($df=2$, Chi Square=154.822, $P<0.001$) and strike location ($df=4$, Chi Square=1993.968, $P<0.001$) were both significant, as was the ratio between IG predator head and IG prey body length. There was also a significant IG prey species by strike location interaction ($df=6$, Chi Square=1219.34, $P<0.001$). Adjusted Quasi-Likelihood statistic was 662.837 (Figure 5-5).

When this was done for total probability of death with the head and thorax recoded into one variable due to a singular Hessian Matrix, the Hessian Matrix was no longer singular and the model was able to converge properly. Strike location was the only significant variable ($df=3$, Chi Square=32.58, $P<0.001$). The Adjusted Quasi Likelihood statistic was 1521.154, which indicates a superior model to the first in this set (Figure 5-6). When this procedure was also performed for attacks that had already resulted in a successful initial capture, the Hessian Matrix was still singular due to the low probability that strikes to the lateral abdomen would result in initial capture. Data were recoded into abdomen along with strikes to the posterior abdomen. When this was done, only the IG predator head size to IG prey body length ratio was significant ($B=5.446$,

BexP=0.007, df=1, Chi Square=7.249, P=0.007) with an Adjusted Quasi-Likelihood statistic of 384.257 (Figure 5-7).

Table 5-3. Capture success against *Pachydiplax* and *Tramea* from resulting in initial capture.

This shows the result of a logistic regression used to calculate the probability that an *Anax* will succeed at killing *Pachydiplax* and *Tramea* on the basis of what body region it attacks. The thorax is the reference category. These data exclude attacks that missed and did not lead to initial capture.

	B	S.E.	Wald	df	Sig.	Exp(B)
PredRatio	34.882	12.438	7.865	1	0.005	1.409E15
IG prey species	3.914	2.060	3.611	1	0.057	50.106
Thorax (reference)			5.326	4	0.255	
Head	-2.457	2.477	.984	1	0.321	0.086
Leg	-3.973	2.136	3.461	1	0.063	0.019
Lateral Abdomen	-3.831	2.652	2.086	1	0.149	0.022
Posterior Abdomen	-5.610	2.516	4.972	1	0.026	0.004
Swim Speed (mm/sec)	-0.024	0.014	2.762	1	0.097	0.977
Constant	-9.631	5.408	3.172	1	0.075	0.000

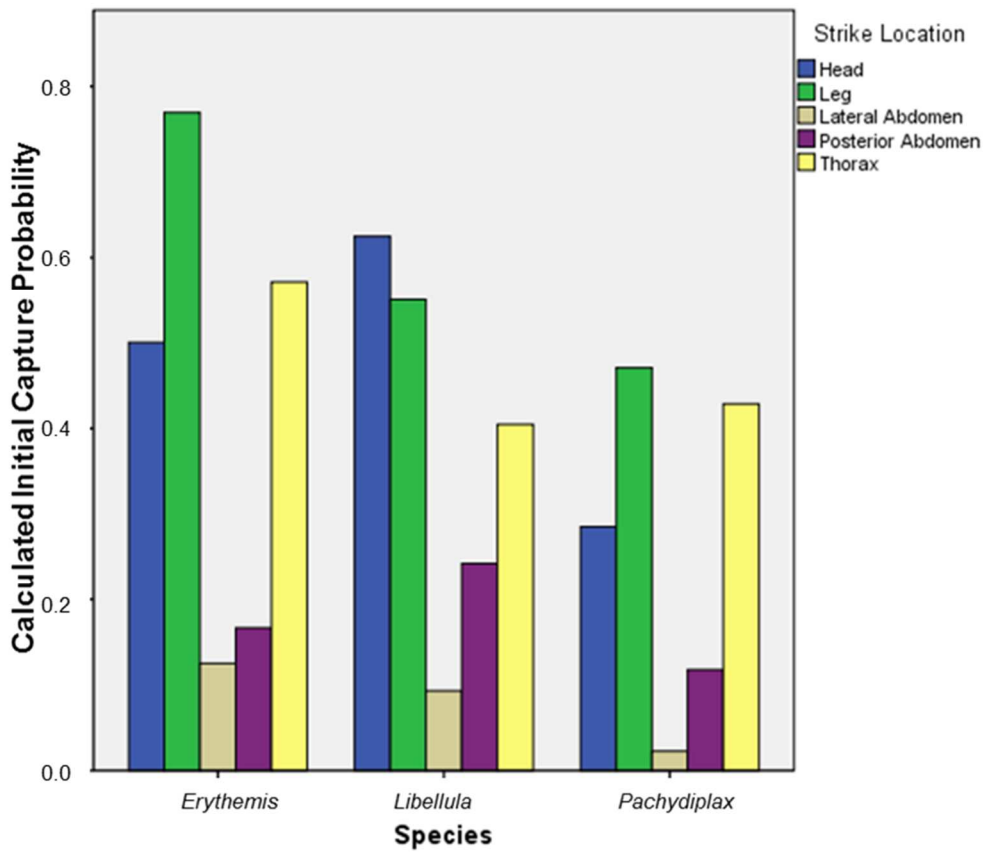


Figure 5-3. Initial capture varies by IG prey species and strike location.

This reflects a logistic regression used to calculate the probability that an *Anax* will succeed at grabbing hold of *Pachydiplax*, *Libellula*, and *Erythemis* on the basis of what body region it attacks. The thorax is the reference category.

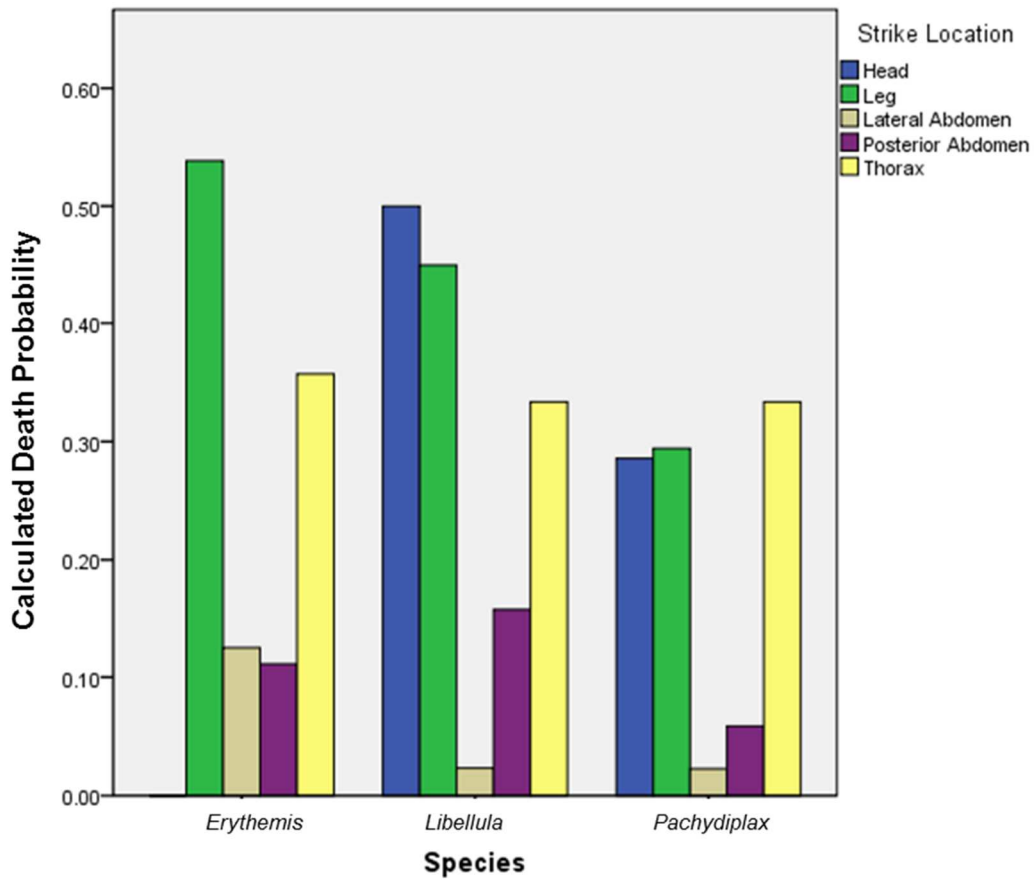


Figure 5-4. Probability of death varies by species and strike location.

This reflects a generalized estimating equation used to calculate the probability that an *Anax* will succeed at killing *Pachydiplax*, *Libellula*, and *Erythemis* on the basis of what body region it attacks. The thorax is the reference category. These data include attacks that missed or otherwise failed in the initial capture stage.

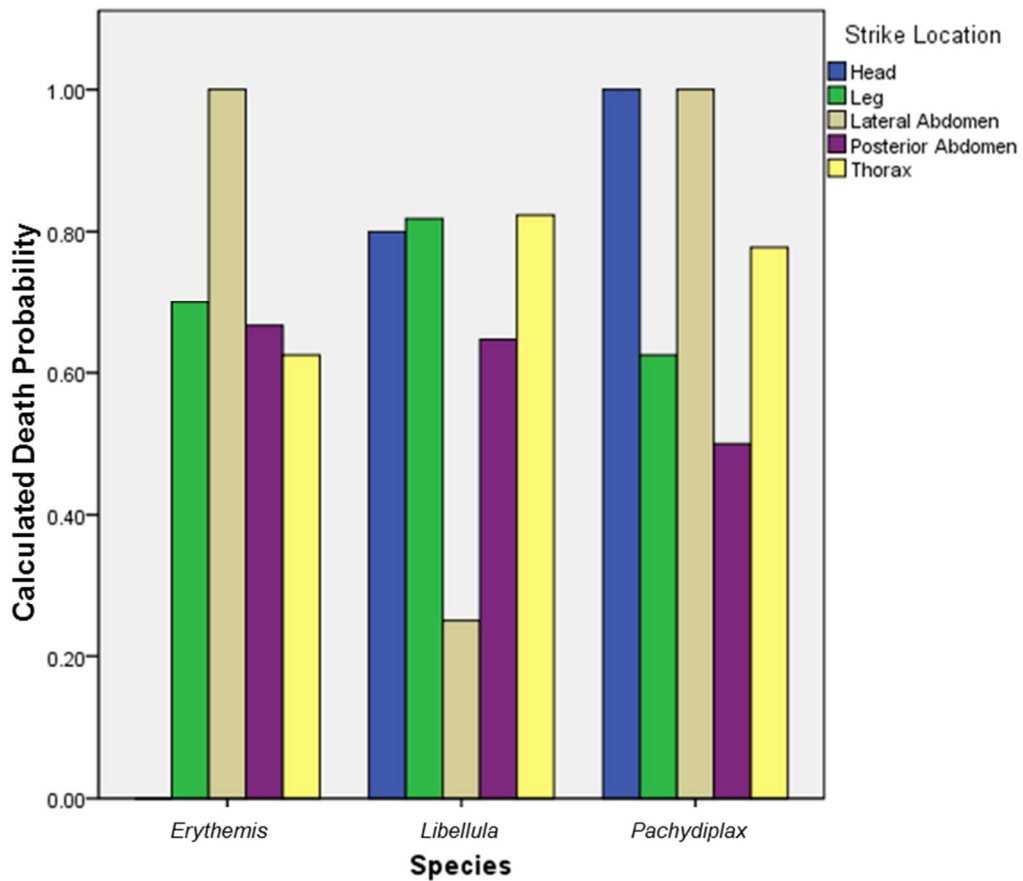


Figure 5-5. Probability of death after initial capture varies by species and strike location.

This reflects a logistic regression used to calculate the probability that an *Anax* will succeed at killing *Pachydiplax*, *Libellula*, and *Erythemis* on the basis of what body region it attacks. The thorax is the reference category. These data exclude attacks that missed or where initial capture failed.

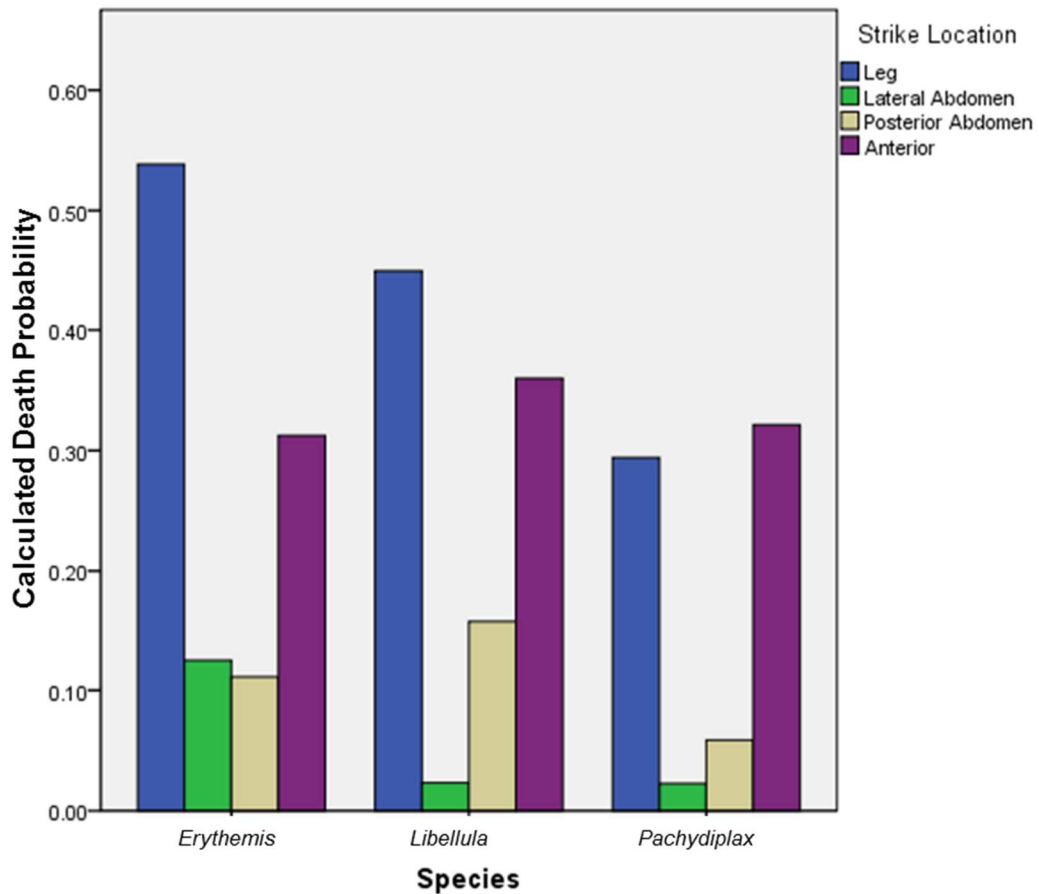


Figure 5-6. Probability of death from all strikes with head and thorax pooled.

This visualizes a generalized estimating equation used to calculate the probability that an *Anax* will succeed at killing *Pachydiplax*, *Libellula*, and *Erythemis* on the basis of what body region it attacked. The head and thorax are pooled as “Anterior”. These data exclude attacks that missed or where initial capture failed.

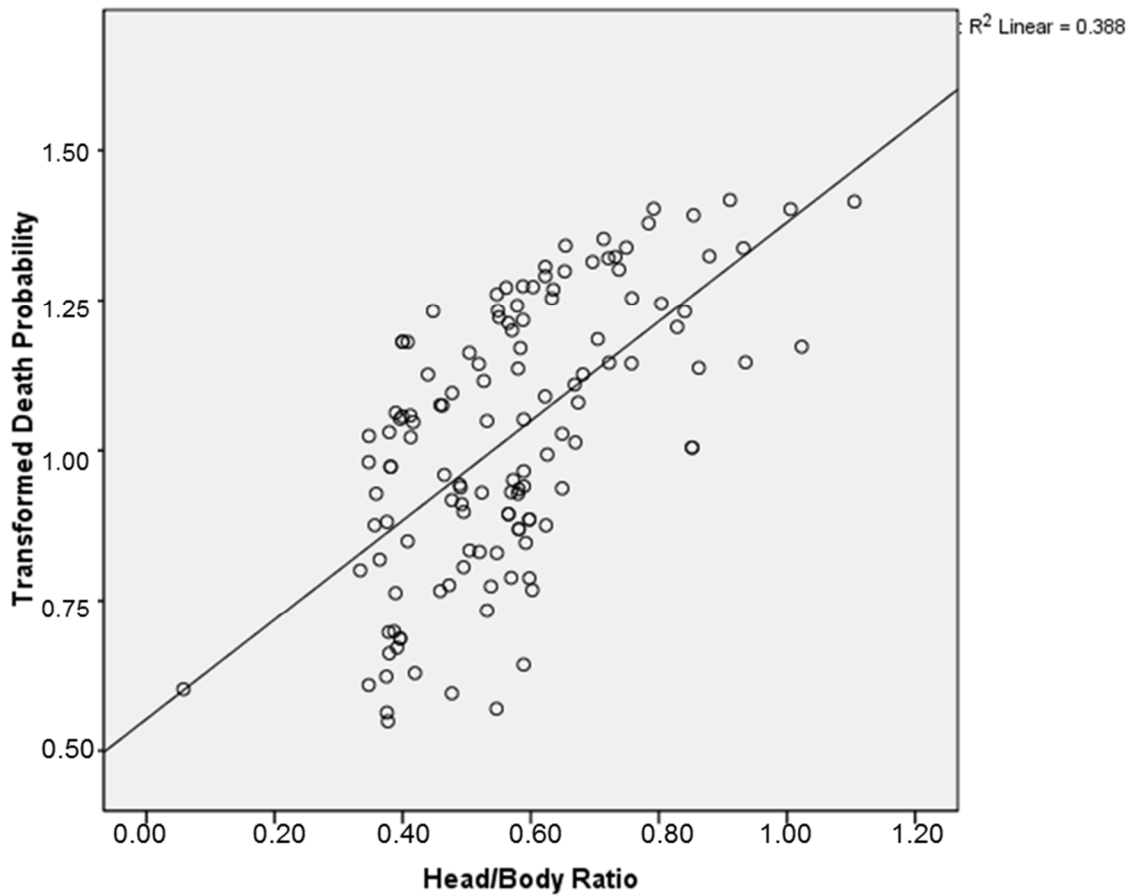


Figure 5-7. IG predator head/IG prey body length ratios positively affects mortality. IG predators like *Anax* are gape-limited. In this case, the best fit line indicates that the larger *Anax* became relative to an IG prey nymph like *Libellula*, the more lethal it was irrespective of strike location on the IG prey nymph's body.

Armor, *Tramea* Inclusive

Because defensive spines did nothing to prevent predation by *Anax*, all *Tramea* were pooled and included with *Erythemis*, *Pachydiplax*, and *Libellula* in a repeated measures generalized estimating equation otherwise identical to the first analysis in this section. It found a significant effect of IG prey species (df=3, Chi Square=14.020, P=0.003) and strike location (df=4, Chi Square=97.304, P<0.001) on initial capture success, with an Adjusted Quasi-Likelihood statistic of 1249.676 (Figure 5-8). Total attack success was affected by both IG prey species (df=3, Chi Square=8.797, P=0.032), and IG predator strike location (df=4, Chi Square=51.201, P<0.001). The adjusted Quasi-Likelihood statistic was 1519.238 (Figure 5-9).

When data were restricted purely to attacks that resulted in initial capture, only the Predator/Prey size ratio was significant (df=1, Chi Square=9.894, B=3.892, Bexp=48.998) in quadratic regression (Figure 5-10). The -2LL statistic for model fit was 173.254. When *Tramea* was used as the IG predator to test the efficacy of defensive spines, initial capture success was unaffected by any variable in the repeated measures generalized estimating equation, though the Predator/Prey size ratio was marginally significant (df=1, Chi Square=3.521, P=0.061), with an Adjusted Quasi-Likelihood statistic of 61.706. Nothing was significant in logistic regression, or even marginal. Tests that used end capture success as a response variable had no significant predictors either, for any logistic regression or a generalized estimating equation.

A multinomial logistic regression was performed to determine the effect of IG prey species and size ratio on body-part specific targeting by *Anax*. Both IG prey species (df=12, Chi Square=24.441, P=0.024) and the ratio of IG predator head width to IG prey body length (df=4, Chi Square=11.056, P=0.026) were significant. The -2LL statistic for model fit came to 900.399 (Table 5-4, Figure 5-11).

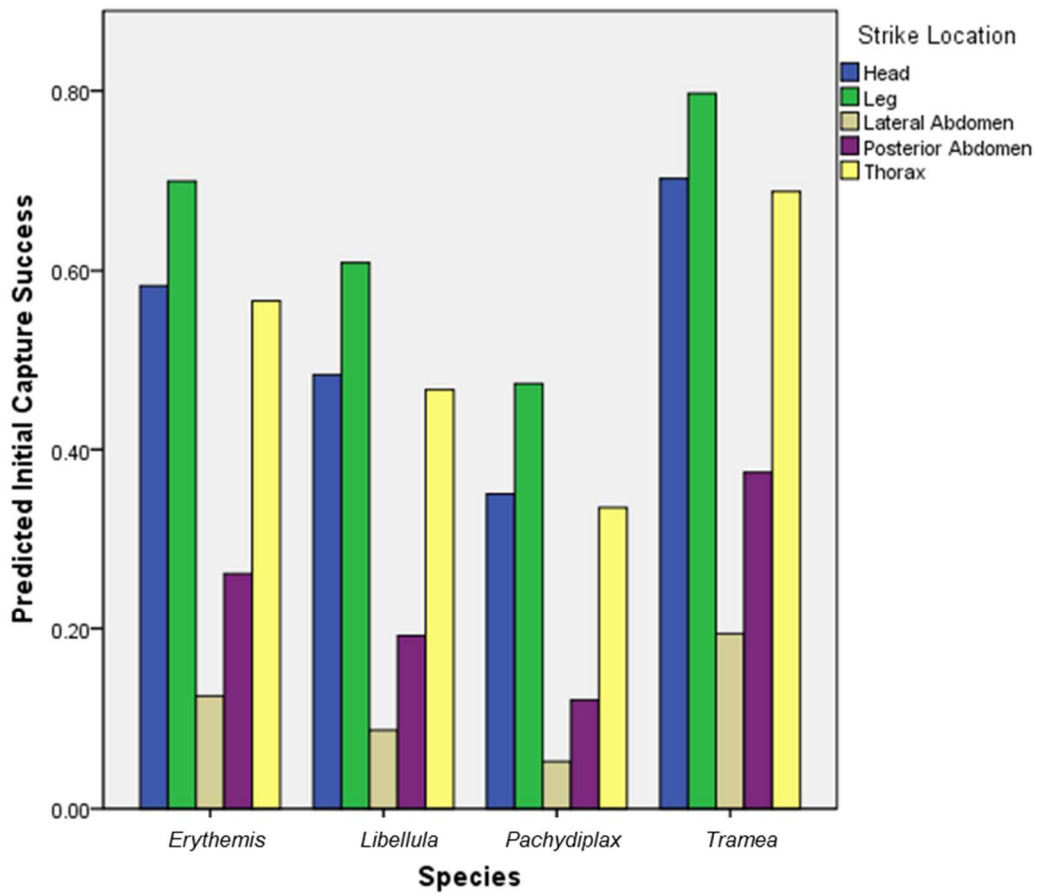


Figure 5-8. Initial capture success by species and strike location with *Anax* predators.

This reflects a logistic regression showing that initial capture success by *Anax* against IG prey nymphs including *Tramea* varied due to the combination of IG prey species and strike location. Predicted values are calculated from the regression.

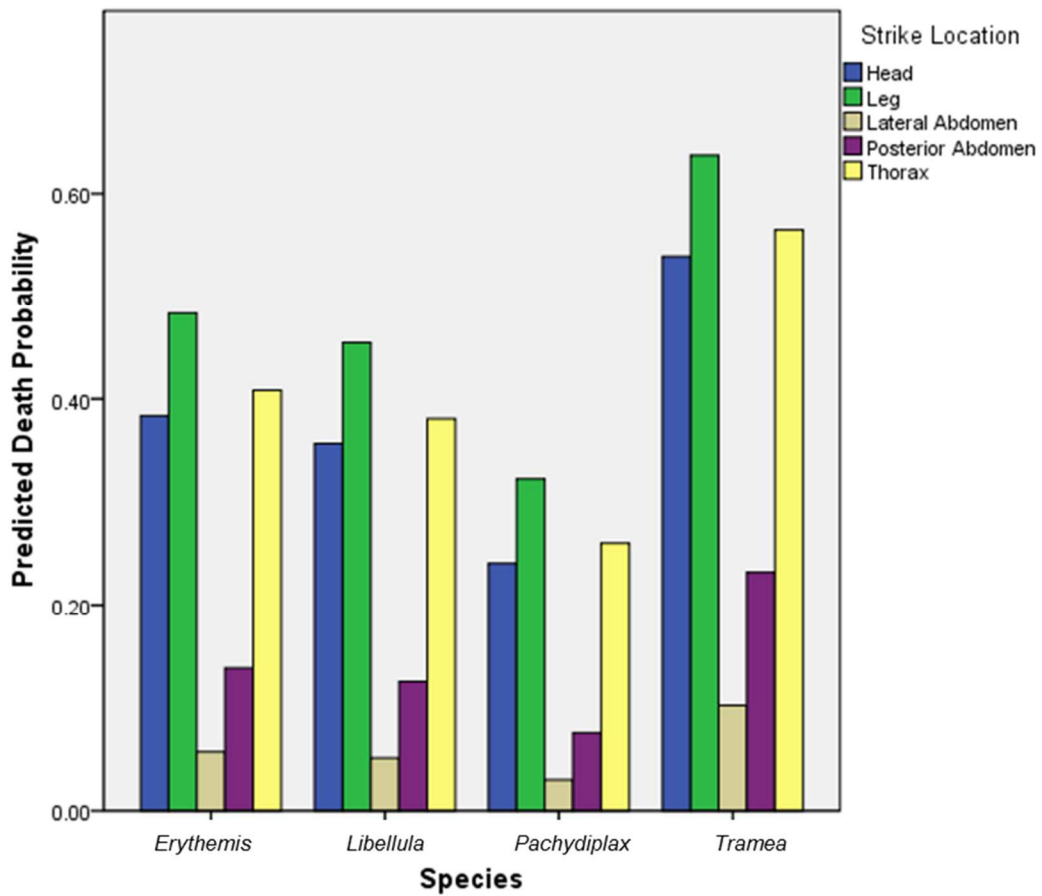


Figure 5-9. The probability of death for all attacks varies by species and strike location.

This reflects of a generalized estimating equation shows that the probability of death—inclusive of attacks that miss or fail to make initial captures—varies by IG prey species and strike location. Values are the predicted values of the statistical test

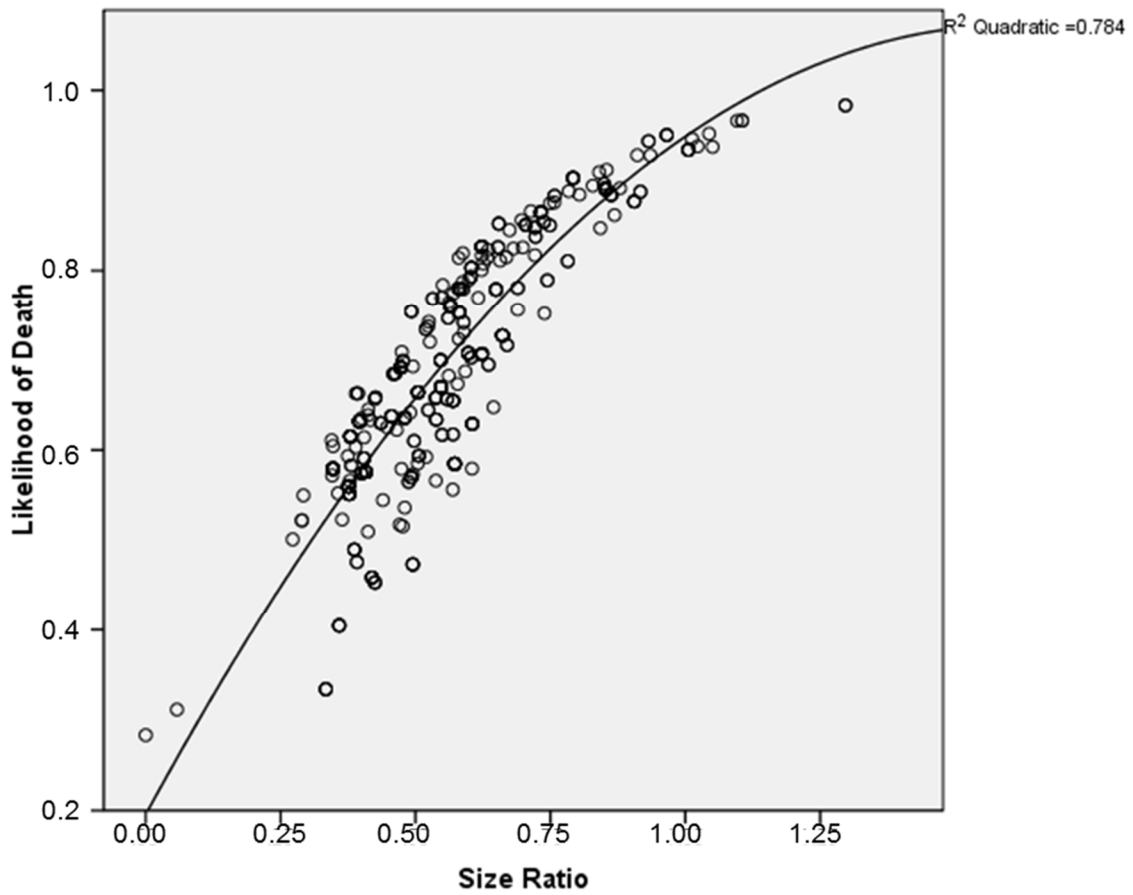


Figure 5-10. Probability of death by predator/prey size ratio as a quadratic function. In a quadratic regression, the chance that an initial capture will result in successful kill by an IG predator approaches 100% as the ratio between IG predator head width and IG prey body length increases. The curve denotes a best fit.

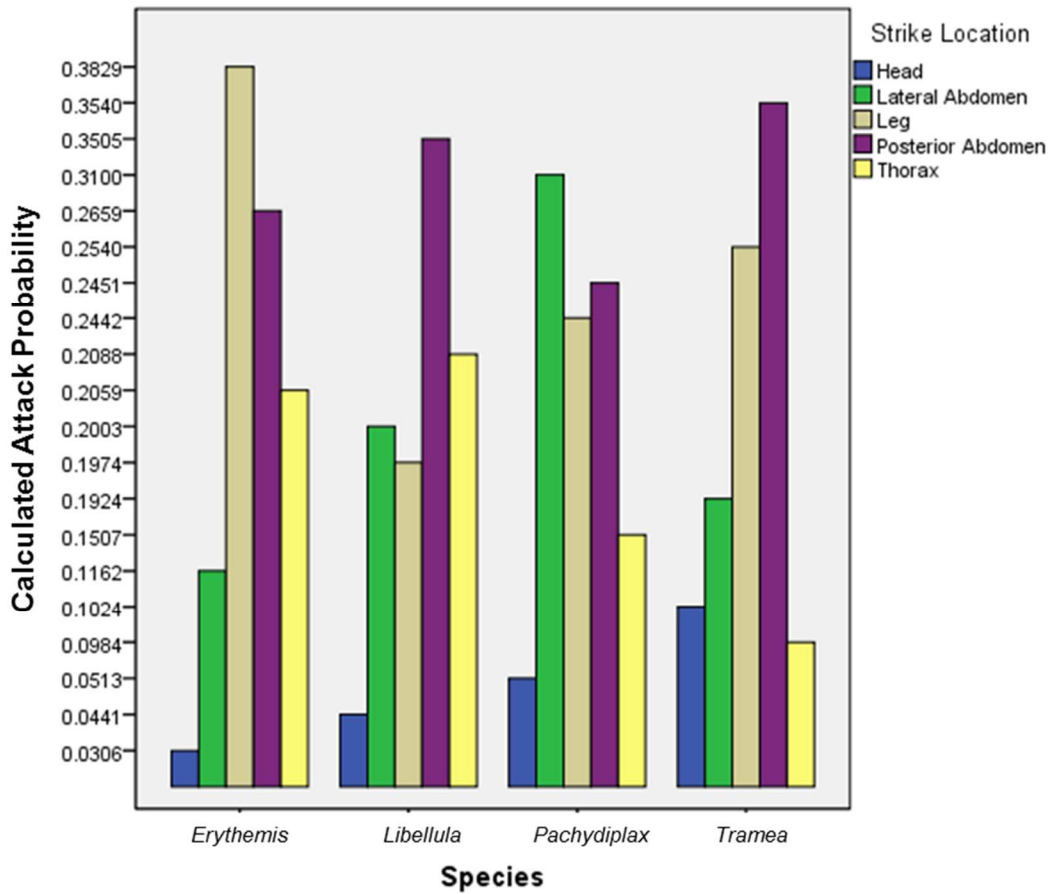


Figure 5-11. IG predators target particular body locations that vary by IG prey species. A multinomial logistic regression was used to determine whether or not an IG predator species like *Anax* targets particular locations on an IG prey nymph. The head was the least likely to be targeted, while the legs or abdomen were most likely to be targeted.

The estimated probabilities of *Anax* striking at a given location on an IG prey species and predator/prey size ratio were arcsine square root transformed to meet normality assumptions, as were the estimated probabilities of initial capture, and death, by strike location and predator/prey size ratio. These were used in a series of linear regressions to determine if the location of any given strike was affected by the probability that those strikes would be successful either in the initial capture phase, or the prey killing phase. The probability of success in the initial capture phase had no effect on the probability of *Anax* attacking the head of another nymph. There was a positive effect of the probability of killing that nymph with a head strike on whether or not a strike to the head occurred ($Y=0.416x-0.016$, $df=1$, $F=14.349$, $P=0.001$, $R^2=0.398$). The same was true of strikes to the thorax, with no relationship seen with initial capture, but a positive one between a thorax-kill and a thorax-strike ($Y=0.110x+0.372$, $df=1$, $F=5.822$, $P=0.018$, $R^2=0.056$). There was a positive relationship between the probability successfully seizing an IG prey nymph by the legs, and *Anax* attacking the legs of that same nymph ($Y=0.295x+0.277$, $df=1$, $F=21.944$, $P<0.001$, $R^2=0.128$), but no relationship between a leg-strike resulting in a kill, and actually striking the legs. *Anax* was more likely to strike the lateral abdomen of another nymph as the probability of successfully grabbing the abdomen decreased ($Y=-0.924x+0.796$, $df=1$, $F=72.639$, $P<0.001$, $R^2=0.408$), with the same being true of a successful kill ($Y=1.621x+0.876$, $df=1$, $F=261.493$, $P<0.001$, $R^2=0.715$). Strikes against the posterior abdomen become more frequent as they become more likely to result in initial prey capture ($Y=0.292x+0.455$, $df=1$, $F=38.824$, $P<0.001$, $R^2=0.214$), and as they become more likely to result in a successful kill ($Y=0.539x+0.403$, $df=1$, $F=166.186$, $P<0.001$, $R^2=0.543$).

Table 5-4. Multinomial regression of strike locations by species and predator/prey size ratio.

A multinomial logistic regression was used to determine whether or not an IG predator species like *Anax* targets particular locations on an IG prey nymph. IG prey species did not appear to directly affect targeting.

Location		B	Std. Error	Wald	df	Sig.	Exp(B)
Head	Intercept	-2.696	0.988	7.449	1	0.006	
	Prementum ratio	2.028	1.192	2.894	1	0.089	7.598
	SpeciesA= <i>Erythemis</i>	-0.930	0.904	1.058	1	0.304	0.395
	SpeciesA= <i>Libellula</i>	-0.629	0.644	0.953	1	0.329	0.533
	SpeciesA= <i>Pachydiplax</i>	-0.038	0.673	0.003	1	0.955	0.963
	SpeciesA= <i>Tamea</i>	0.000	.	.	0	.	.
Thorax	Intercept	-1.150	0.749	2.359	1	0.125	
	Prementum ratio	-0.194	0.820	0.056	1	0.813	0.824
	SpeciesA= <i>Erythemis</i>	1.028	0.619	2.761	1	0.097	2.795
	SpeciesA= <i>Libellula</i>	0.741	0.556	1.779	1	0.182	2.098
	SpeciesA= <i>Pachydiplax</i>	0.773	0.587	1.735	1	0.188	2.167
	SpeciesA= <i>Tamea</i>	0.000	.	.	0	.	.
Leg	Intercept	0.008	0.635	0.000	1	0.990	
	Prementum ratio	-0.496	0.775	0.409	1	0.522	0.609
	SpeciesA= <i>Erythemis</i>	0.688	0.476	2.086	1	0.149	1.989
	SpeciesA= <i>Libellula</i>	-0.309	0.431	0.515	1	0.473	0.734
	SpeciesA= <i>Pachydiplax</i>	0.259	0.450	0.332	1	0.564	1.296
	SpeciesA= <i>Tamea</i>	0.000	.	.	0	.	.
Lateral Abdomen	Intercept	0.774	0.699	1.229	1	0.268	
	Prementum ratio	-2.072	0.883	5.503	1	0.019	0.126
	SpeciesA= <i>Erythemis</i>	-0.261	0.583	0.200	1	0.654	0.770
	SpeciesA= <i>Libellula</i>	-0.231	0.465	0.248	1	0.619	0.794
	SpeciesA= <i>Pachydiplax</i>	0.569	0.472	1.453	1	0.228	1.767
	SpeciesA= <i>Tamea</i>	0.000	.	.	0	.	.

Because the limited resolution of a dragonfly's visual system may prevent the fine-scale recognition assumed in the above tests, strike location was recoded. The head was kept the same, while the legs and thorax were collapsed into one variable, as were both orientations of abdominal strikes. Logistic regression was performed with initial capture success as a response variable; IG prey species (df=3, Chi Square=18.546, $P<0.001$) and strike location (df=2, Chi Square=12.264, $P<0.001$) were statistically significant. Model fit in the form of the -2LL statistic was 491.164.

When strike success was used as the response variable, the size ratio was significant ($B=1.705$, df=1, Chi Square=5.829, $P=0.015$), as was strike location (df=2, Chi Square=53.090, $P<0.001$). IG prey species was marginally significant (df=3, Chi Square=7.218, $P=0.065$). The -2LL statistic for model fit came to 424.558.

When the probabilities of strike locations are regressed against the likelihood of death for the IG prey, using the recodes and recalculated death probabilities as before, the likelihood of a strike to the head increased as the lethality of those strikes (Figure 5-12) increased ($Y=0.404x-0.009$, df=1, $F=15.983$, $P=0.001$, $R^2=0.416$), the same was true of the thorax ($Y=0.126x+0.632$, df=1, $F=6.155$, $P=0.014$, $R^2=0.028$). Abdominal strikes by contrast decreased (Figure 5-13) in likelihood as their success rate increased ($Y=-0.387x+0.939$, df=1, $F=65.165$, $P<0.001$, $R^2=0.208$).

Morphology-Behavior Covariation

Determining whether or not trait compensation or co-specialization occurred required the inclusion of data from Chapter 4. Logistic regression was used to calculate per-strike probabilities of death by *Anax junius* for *Erythemis*, *Libellula*, and *Pachydiplax*, using head width as a covariate. The arcsine square root transformed predicted values from these were used as a predictor in a series of linear regressions for each IG prey species, using movement and space use data from Chapter 4, restricted to include only those individuals subjected to predation risk by *Anax*. Predictor variables were predator head width, and transformed per-strike risk of death.

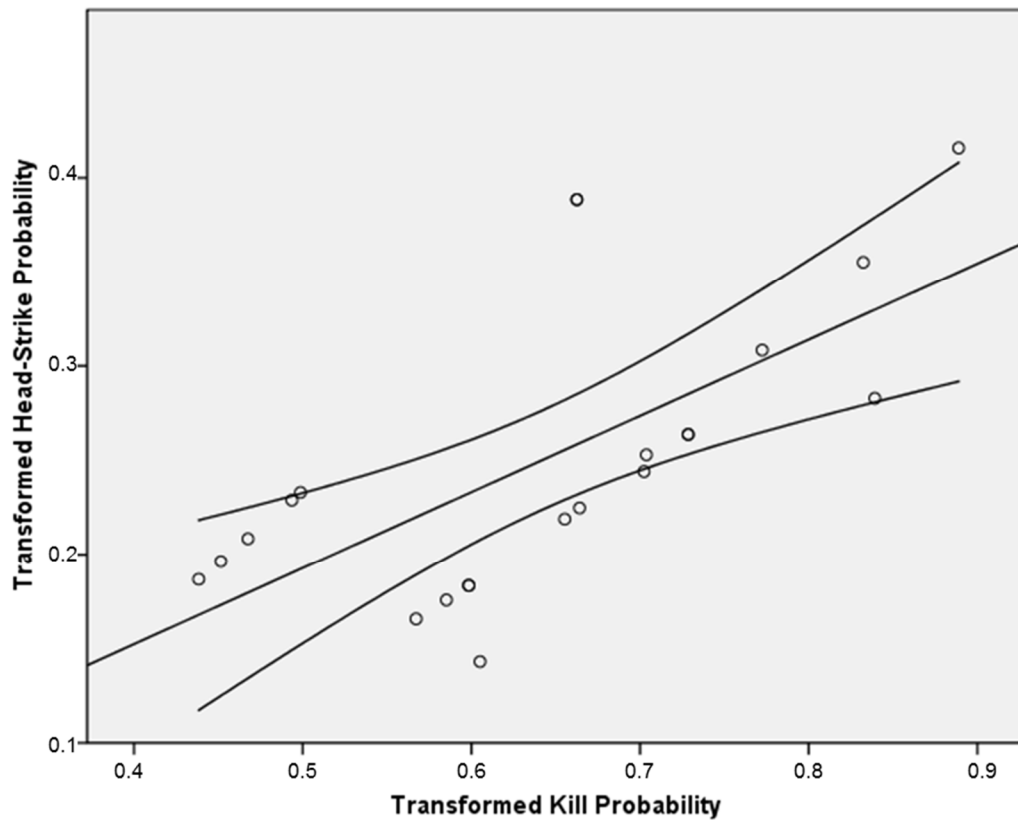


Figure 5-12 *Anax* is more likely to strike the head when a successful kill is more likely. As the probability of a kill from a head strike increased, the higher the probability that *Anax* would attack the head of an IG prey nymph. Curves denote 95% confidence interval around the best fit line.

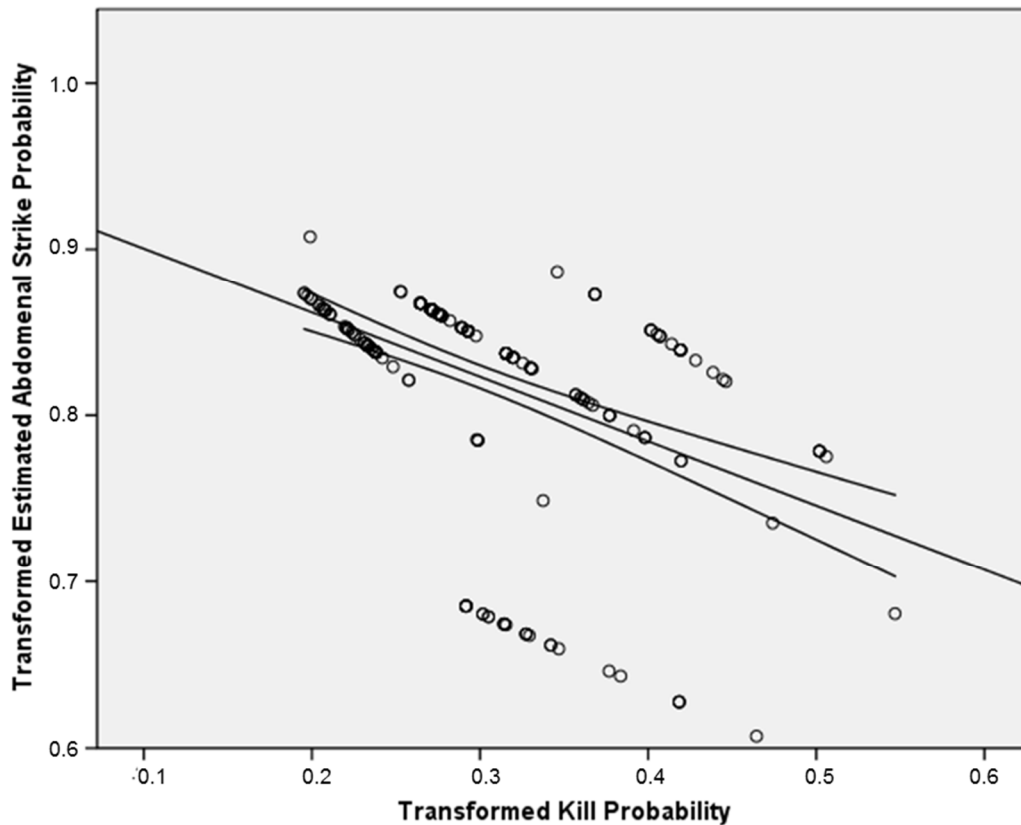


Figure 5-13 Strikes to the abdomen become less likely as the kill probability increases.

As the probability of a strike to the abdomen resulting in a kill increased, the probability that *Anax* would attack the abdomen of an IG prey nymph decreased.

Curves denote 95% confidence interval around the best fit line.

In *Pachydiplax*, the per-strike risk of death affected climbing propensity ($Y = -1.657x + 2.823$, $P = 0.003$) as did the size of *Anax* ($Y = -0.101x + 2.823$, $P = 0.014$). R^2 was 0.14. The use of cover was affected by *Anax* head width ($Y = -0.055x + 1.515$, $P = 0.029$). R^2 was 0.047. Movement was unaffected by predictors. A relationship between *Libellula* cover use and per-strike death risk was nearly significant and negative ($Y = -1.2122x + 2.079$, $P = 0.055$, $R^2 = 0.033$). Movement was marginally negatively affected by *Anax* head width ($Y = -0.071x + 1.170$, $P = 0.056$, $R^2 = 0.022$). With *Erythemis*, no correlations were significant.

Discussion

Spines are a defensive adaptation (Mikolajewski and Rolff 2004, Lescak and von Hippel 2011), but their efficacy depends largely on the behavior and morphology of the IG predator species (Mikolajewski et al. 2006). Against predators that engulf a prey item, defensive spines can cause pain or become lodged in the buccal cavity (Lescak and von Hippel 2011), or they can be used more aggressively to stab a predator during the attack sequence (Hopkins et al. 2011). Against predators with other prey-capture methods such as piercing mouthparts, or gripping claws, spines are likely less useful (Reimchen 1980, Mikolajewski et al. 2006). There is some indication from other studies that they are actually a detriment (Mikolajewski and Rolff 2004, Mikolajewski et al. 2006), but no evidence was found for that in this set of spine removal experiments.

Defensive spines were not a factor in defense against *Anax*. Spine removal had no effect at any stage of predation. In predatory encounters, *Tramea* was not very likely to make predatory attacks against other odonates, and so there were simply not enough such attacks in the spine removal experiments to test their efficacy at all.

This non-replication of prior experimental results using *Anax* could be due to a low sample size like the *Tramea* results. Alternatively, the spines are irrelevant to predation by *Anax*, and the results observed in prior studies are due to confounding behavioral or morphological variables (Mikolajewski et al. 2006). The researchers in question were primarily interested in selection on morphological traits and not the mechanism by which those traits operate, and thus did not record each attack in detail, so there might be something missed. One way to resolve this might be to control the location of strikes by restraining focal specimens using a linear test apparatus and wax, using an increased sample size. This would control for movement and strike orientation. One question that arises from the need for this degree of control is how relevant spines might be, one way or the other. If they are only relevant in attacks directed from a narrow range of directions, and for attacks where the initial strike might be of marginal efficacy were it not for the presence of spines, then it is possible that even if there is an effect of spines it might not

be relevant in nature. Field relevant results could be obtained by using a set of mesocosms with small populations and observing mortality rates over time of spine-manipulated individuals, including artificial spine addition.

Dragonfly nymphs do appear to have effective armor. There are two ways in which a predator like a dragonfly nymph can capture a large prey item. That prey item can have its body pierced by the labial palps (Corbet 1999), or some part of its body can be grabbed by the palpal lobes. Any morphological trait that reduces either of these can be an effective anti-predator trait. Preventing body-puncture can be done by way of armor that, by nature of its thickness and material properties, directly prevents penetration (Connors 2014), or that has an incident angle to an incoming attack such that the attack is likely to be deflected away and fail to penetrate (Hurlich 1951). Angled armor has the secondary benefit of increasing the effective thickness of armor due to the cosine rule (Hurlich 1951, Yap 2012). Preventing seizure by the mouthparts can be accomplished if the surface attacked is sufficiently large that the predator cannot attain a grip (Salmon and Scholl 2014).

From these data it appears that the chitinous cuticle they possess may serve a defensive function (Gross 1993, Flenner et al. 2009a). The Vickers hardness of sclerotized cuticle in the Orthoptera can range from 25 to 80 kgf mm⁻² with a Young's Modulus of 1-20 Gpa (Hillerton et al. 1982, Vincent and Wegst 2004). For comparison, that puts resistance to elastic deformation somewhere between that of the polyethylene terephthalate used in plastic bottles (Cambridge 2003) and that of human bone (Rho et al. 1993), with a resistance to plastic deformation roughly equivalent to that of soft brass (Diehl 2015). Albeit the layers are very thin. If dragonfly nymphs are in any way similar, then some IG prey species might have sufficient cuticle hardness that it serves as armor against puncture (Song et al. 2011) by the sharp palpal lobes of *Anax*, which do not generate very much force. The hardness does vary based on how close to molting any individual happens to be, as the cuticle becomes more sclerotized the closer they get to ecdysis (Hillerton et al. 1982).

When strike locations and the probability of being captured or killed are examined in light of this, certain patterns emerge. The abdomen of dragonfly nymphs was the structure most likely to be attacked by other nymphs, and also the least likely to result in a successful attack. With the exception of *Libellula*, the abdomen of dragonfly nymphs used as IG prey are flattened and angled on both lateral and posterior aspects. *Libellula* has a rounded abdomen, which accomplishes the same function. Almost all attacks made physical contact, but the overwhelming majority of attacks made to the abdomen were deflected, usually up and over the abdomen. This structure was most likely to be attacked primarily because *Anax* most often approached behind, likely to avoid detection by the IG prey nymphs (Krause and Godin 1996, Kaby and Lind 2003). The dragonfly species most likely to be successfully attacked from this direction was *Tramea*, which at smaller instars has a soft cuticle relative to the other species in these experiments.

The structures most likely to result in a successful attack were the legs, thorax, and head, in that order. The legs are small in size and easily grabbed. Combined with a lack of observed leg autotomy (Stoks 1999), attacks to the leg resulted in a high probability of death for the attacked insect. The head and thorax both feature surfaces that make an attack more likely to succeed, such as the wing buds, leg attachment points, and mouthparts. These structures are either soft, or provide a gripping point. The mandibles of the attacking nymph can chew through any armor another nymph might have (Pritchard 1964, Witzig et al. 1986), so whatever the hardness of these structures happens to be, it is no defense if the IG prey nymph is successfully grabbed and the grip maintained. Any defensive value of the cuticle is likely restricted to preventing puncture, and attack deflection.

IG predators did not strike their IG prey in a random location either. They were more likely to attack the head and thorax (including the legs) as their chance of successful predation from those strikes increased (Rowe 1987). They likely do not have the resolving power in their visual system (Frye and Olberg 1995, Land 1997, Sharkey et al. 2012) to differentiate the legs and thorax, but they do not require it. A strike to the thorax is likely to hit the legs simply due to their spatial arrangement. *Anax* also did not simply strike toward the center of mass, because

they were more likely to strike the head as their probability of a successful strike to that location increased. The abdomen is another matter. There, repeated unsuccessful strikes to the abdomen were common. If *Anax* failed the first time, they tried again, chased if their prey moved, and try again; striking toward the abdomen each time as an artifact of their original position and chasing their prey. They often approach from behind. This could be because doing so allows them to avoid detection (Krause and Godin 1996), which in turn depends heavily on the field of view possessed by their prey (Pritchard 1966). An alternative possibility is a lab artifact; given that these experiments took place in large petri dishes and a large amount of time is spent along the edges, it is possible that this restricts approach angles.

Once an IG prey nymph was successfully grabbed, the body region that was grabbed ceased to matter. At that point, whether or not the IG prey nymph managed to escape was affected only by its size relative to the IG predator nymph. The larger it was, the more likely it was to be able to pull away before it suffered sufficient damage to kill or cripple it. Maximum escape speed (as a proxy for maximum thrust) did not appear to affect predation either. It was strongly determined by both size and IG prey species, and its effect likely washed out in collinearity. Non-maximum speed was irrelevant to capture by IG predators, because in this experiment set, IG predators almost always made initial contact with IG prey, there was too little variation to even analyze in that respect.

Tradeoffs between defensive morphology (in this case armor) and foraging behavior responses can operate between species; with some species specializing in defense or competition through positive correlations between morphology and behavior (trait cospecialization), and others compensating for poor morphological defenses with behavior (Figure 5-14) or vice versa (Relyea 2000, Cotton et al. 2004, Kuo et al. 2014). Alternatively (Figure 5-15), and often at the same time, behavior (Van de Meutter et al. 2004, Hoverman et al. 2005) and morphology (Kolar and Wahl 1998, Relyea and Auld 2005, McCoy 2007) can be induced by site-specific conditions such as competition (Relyea and Hoverman 2003, Relyea and Auld 2004) and predation risk (Eklov 2000, Van Buskirk 2001, Schoeppner and Relyea 2009).

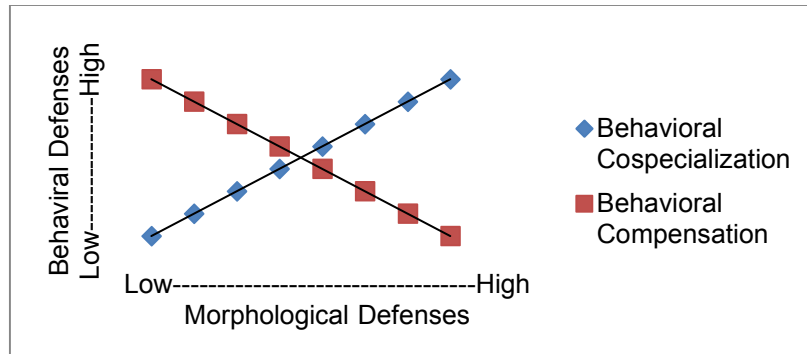


Figure 5-14. Trait compensation (hypothetical).

In trait compensation, behavioral and morphological defenses are negatively correlated. In cospecialization, behavioral and morphological defenses are positively correlated.

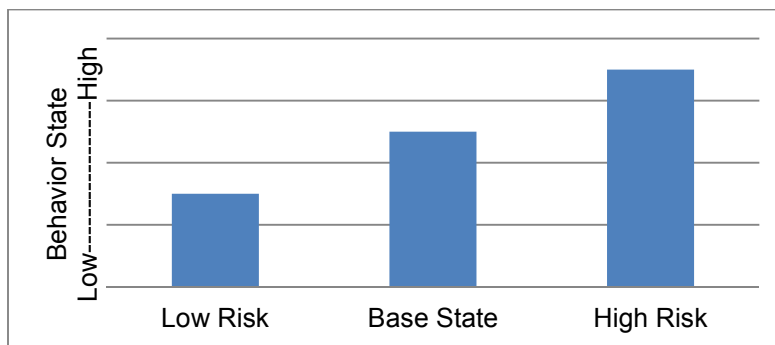


Figure 5-15. Hypothetical induced anti-predator behavior state.

Anti-predator behaviors can be induced. At low risk (when no predators are present, for example), a prey species might forage or move more, while this behavior changes if predators are present in the same region, or very nearby.

Pachydiplax showed the clearest trait-compensation response. As its morphological defenses became less effective as a function of the difference in size between it and an IG predator, it became more likely to attempt a spatial relocation by dropping to the substrate and leaving cover in an attempt to find another habitat patch (Wellborn and Robinson 1987). *Libellula* responses were marginally significant, but indicated a similar pattern with respect to cover use. This indicates for these species (and *Pachydiplax* in particular) a behavioral response that operates on a sliding-scale as trait compensation. *Erythemis* did not change its behavior at all, which, given its lack of behavioral response to predation risk generally, would indicate that its movement and microhabitat preferences are fixed, but that it compensates for a lack of investment in morphological defenses with crypsis.

There is always the possibility that the differences in vulnerability to IGP seen in Chapter 4 were not grounded in behavior, but in morphology. The present results show that this to be unlikely. The least vulnerable IG prey species in the movement and space use trials where morphology could not be examined is the most vulnerable morphologically, with the opposite being true of the most vulnerable species in those same earlier tests. It is the behavioral differences, not the morphological differences between IG prey species, that are ultimately responsible for differential mortality among IG prey.

Chapter 6

Conclusion and Prospectus

Several things are very clear: morphology affects prey capture in ways that are likely more complicated than originally thought, as are the factors that affect prey choice and movement in dragonfly nymphs. Defensive morphology is also far more interesting and complex than the simple presence or absence of spines.

Dragonfly nymphs have highly varied diets that range from small fish and tadpoles to *Daphnia* and other aquatic insects like *Notonecta*, various worms, and larger crustaceans such as crayfish and fairy shrimp, depending on the pond and season (Pritchard 1964, Corbet 1999). The data presented in this work indicate that there is the possibility for prey specialization that is mediated by morphological differences between species, as well as size. The range of prey that is available for one species might be unavailable to a species of similar size simply because the morphology of the mouthparts differs between them. This can mean that direct competition between species can be moderated, and permit two species to coexist (Koss and Snyder 2005, Holt and Huxel 2007, Svanback and Bolnick 2007). The same can occur due to microhabitat selection. The range of prey available to a bottom-dwelling sprawler like *Libellula* can be very different from the prey that is available to a climber like *Pachydiplax* (Harris 1986, McIvor and Odum 1988, Corbet 1999, Verberk et al. 2005).

As a result, one thing I would like to do in the future is expand the range of prey under examination, and more systematically determine at what size-class (if any) a given species can begin consuming a particular prey species, and determine what morphological traits mediate this interaction. Given the lack of intraspecific variation in morphology, it may be necessary to use closely related species that vary in particular morphological traits (such as the density of setae), or find a way to manipulate morphology without killing or otherwise hampering the individual. This would be coupled with microhabitat manipulation to determine how diet composition changes in different environments. Beyond that, I would also like to examine further how changes to diet

composition affect the tradeoff between foraging and predation risk, and how this interacts more directly with respect to microhabitat use patterns.

It is worth mentioning as well that there is the possibility that in this system and more generally in IGP that there may be no local equilibrium, but instead a regional or global equilibrium due to metapopulation dynamics (Harrison 1991, Amarasekare 2007a, Su et al. 2008). Dragonfly reproduction is pulsed (Corbet et al. 2006) and the adults disperse far from their natal ponds (Michiels and Dhondt 1991, Conrad et al. 1999, Purse et al. 2003, Dijkstra 2007). If there is a tradeoff between foraging and predation risk in these organisms as there appears to be, and if this is sensitive to locally available prey due to morphological prey specialization, any given pond may serve as a source or a sink for different species (Harrison 1991, Dias 1996), and this can change from year to year for any given pond as location conditions change (Bazzanti et al. 1996). As a result it is possible that no one pond will ever reach a stable equilibrium. Investigating this might not actually be feasible because it would require excluding migrants over large areas of otherwise identical ponds. It may be possible with artificial ponds if migration and reproduction can be replicated using controlled releases of individuals into a field enclosure or lab mesocosm.

While defensive spines do not appear to have a defensive function against other dragonfly nymphs, armor does. Moreover, the behavior of the nymphs appears to be influenced by how much armor protects them from attack, perhaps suggesting that on some level dragonfly nymphs may be able to assess the degree to which they are at risk. The armor itself is interesting because the armor is inconspicuous, and like spines (Arnqvist and Johansson 1998) the degree to which it is effective as a defense probably depends on the attack mode of a particular predator (West and Cohen 1994, Smith and Jennings 2000). A tough cuticle may have evolved as a defense against piercing mouthparts in much the same way that spines likely evolved as a defense against being swallowed (Swaffar and O'Brien 1996). Not only should the material properties of the cuticle of dragonfly nymphs be studied further, but its efficacy against various other predators like water bugs needs to be investigated as well, either on its own, or in an ecosystem context. For example, do species that sacrifice armor to produce spines as a defense

against fish (Flenner et al. 2009b) suffer higher predation from insect predators as a result, and does this affect patterns of site occupancy?

IGP is one of the more poorly understood sets of interactions in nature, largely because they are complex enough that modeling and prediction is difficult. Even if equilibrium states are possible, that stability is likely rooted in the biology of a given system (Arim and Marquet 2004), and while the principles involved may be generalizable, they are sufficiently complex that parameterization is difficult, and there is the possibility that equilibrium effectively do not exist, but that IGP is maintained by constant changes in system productivity, habitat change, and migration.

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Biographical Information

Benjamin Thomas Allen received a B.S. in Biology from Arizona State University in 2008. While there he worked on a number of projects. These included iridescence and sexual selection in the hummingbird *Calyptra anna* as a spring volunteer in the McGraw lab. As a long-term tech in the Gadau lab he worked on inter-queen conflict in pleometrotic *Pogonomyrmex californicus* colonies, facultative diapause in *Nasonia vitripennis* and the annotation of the *Nasonia vitripennis* genome.

In 2015 he finished his PhD at the University of Texas at Arlington. His primary research interests are multi-faceted. Benjamin studies the functional morphology of prey capture and defense in aquatic insects, as well as competitive and anti-predator behavior in these organisms. He is also interested in the morphological and behavioral mechanisms that underpin population and community level processes in ecology. He also has an interest in the practical applications of this knowledge to conservation and maintenance of ecosystem services, particularly in agriculture and infectious disease prevention.