Density dependence and fighting in species with indeterminate growth: a test in a fiddler crab

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Many forms of selection are density dependent. It is often assumed that all individuals of a given sex compete for the same resources, but in many species different types of individuals (e.g. morphs or body sizes) compete for different resources. Selection on competitive traits should be examined relative to the density of the relevant competitors (and contested resources) rather than total population density. Crucially, a predictable decline in effective competitor density with size might affect selection on fighting behaviour in species with indeterminate growth. We investigated whether male fighting behaviour over burrows in the fiddler crab *Uca annulipes* is consistent with size-dependent burrow usage that affects the density of relevant competitors and contested resources (burrow availability is limited). We show that larger males occupied larger burrows and occurred at lower densities, so they must travel further to locate new, suitably sized burrows. This should favour larger males investing more in each fight that they initiate. Indeed, larger males fought for significantly longer than smaller males, which increased their likelihood of winning a burrow. The observed increase in fight duration is not readily explained by ontogenetic changes in fighting costs (i.e. 'giving up' thresholds). It is worth testing whether increased fight duration with size/age occurs in the innumerable other species with indeterminate growth that compete for refugia (e.g. hermit crabs, reef fish) because a decline in density with body size is inevitable owing to cumulative mortality, and a physical constraint on the minimum-sized refugia that can be entered is commonplace.

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If all individuals compete for the same resources, then density-dependent selection depends on the total population density. Sometimes, however, individuals compete nonrandomly with each other for specific resources (e.g. one sex competes for access to the other). Here it is the density of relevant competitors relative to contested resources, rather than the total population density, that determines the selection that an individual will experience. Measuring the relevant density often requires detailed knowledge of the species' biology. For example, in Eurasian oystercatchers, *Haematopus ostralegus*, males and females subtly partition food resources and do not compete for every food item (van de Pol et al. 2009). The use of different resources by different types of individuals based on age or life history stage (Mouquet et al. 2005; Einum et al. 2006), sex (van de Pol et al. 2009), body condition (Curtis et al. 1995), morph type (reviewed in Smith & Skúlason 1996) and body size (Shine et al. 2001) is widespread in many taxa. If the ratio of the density of competitors to contested

resources shifts, then selection for competitive traits might vary among classes (but see Kokko et al. 2012). If there are consistent, predictable differences in competitor and/or resource density with age, size or sex, this should select for the evolution of levels of competitive behaviour that vary among different classes of individuals.

Sexual selection studies have long focused on how males and females compete for different resources (i.e. the opposite sex), and when this might lead to density-dependent selection (Kokko & Rankin 2006). For example, a higher density of males increases male–male encounter rate, which might select for greater investment in weaponry (Weir et al. 2011). By contrast, far fewer behavioural studies have investigated whether density-dependent selection varies among different types of individuals of the same sex. Ecological studies of within-class density-dependent selection are usually restricted to species with distinct cohorts that are at spatially segregated stages in the life cycle. For example, in the butterfly *Maculinea arion*, first-stage larvae live on host plants, where they show strong contest competition, whereas second-stage larvae occupy ant nests and experience severe scramble competition (Mouquet et al. 2005; see Einum et al. 2006 for another example).

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We suggest that the phenomenon of different classes of individuals experiencing different densities of competitors is not confined to species with distinct life history stages, and is actually widespread. It can arise even in continuously distributed populations of interacting individuals. Specifically, in species with indeterminate growth, cumulative mortality with age means that larger individuals are less common and occur at a lower density. This implies that competition will decline with size (i.e. fewer competitors) if fighting is size assortative. However, some of the resources that individuals require might also depend on their body size. For example, in fiddler crabs there is indeterminate growth and males compete for burrows. Fights between males are often size assortative, probably because larger males are physically incapable of entering smaller burrows (e.g. Jennions & Backwell 1996). There is also evidence that mating is size assortative, partly because a large female cannot enter a small male's burrow. This suggests that each male only competes with similar-sized males for access to burrows and females.

We investigated whether a size-based difference in competitor numbers and resource availability affects density-dependent selection on males in the fiddler crab, Uca annulipes. Male–male fights over burrows are strongly size assortative (Jennions & Backwell 1996). Males are unable to dig new burrows within the population, as there is no unchallenged surface space (territories abut each other and residents fight off a male that attempts to dig a new burrow between existing territories). In addition, smaller intruders struggle to defeat a larger resident (Callander et al. 2012). Uca annulipes exhibits indeterminate growth, so larger males should be less common as a result of cumulative mortality. Given the body–burrow size correlation and the destruction of unoccupied burrows by tidal action (Hemmi & Zeil 2003), there should be a corresponding decline in the availability of larger burrows. Whether this leads to a lower density of suitable burrows for larger males depends on whether or not similar sized burrows are spatially clumped. If not, large males must travel greater distances to acquire a new burrow, which elevates their exposure to predators (Koga et al. 1998) and travel costs. Based on our previous work on U. annulipes we therefore predicted that larger males would value burrow ownership more highly. All else being equal, this should generate a positive correlation between male size and fight intensity/duration, because individuals are more persistent when fighting for a more valuable resource (Enquist & Leimar 1987).

Mutual Assessment

In order to use fight duration of size-matched fights to determine whether perceived resource value increases with male size, you need to test whether fights are resolved by mutual assessment or individual cost thresholds. Males may be more persistent because they have higher cost thresholds (Payne & Pagel 1996) rather than because of the effect of resource value on fight duration. Higher cost thresholds, however, are not expected to affect the relationship between fight duration and the mean size (i.e. strength) of size-matched rivals if fights are resolved by mutual assessment of strength.

How fight duration changes with the size of two competitors depends on how they determine whether to continue or abandon a fight. There are two main categories of fighting models: 'mutual assessment' and 'individual cost threshold' (or self-assessment) models. The best-known mutual assessment models are 'asymmetric war of attrition' (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and 'sequential assessment' models (Enquist & Leimar 1983). Here, individuals assess their own and their rival's resource-holding potential (RHP; sensu Parker 1974) to decide whether to escalate, prolong or abandon a contest. The greater the similarity in RHP, the more

difficult it is for each contestant to assess who is the weaker individual. It is assumed that contestants continue to fight and escalate the fight's intensity to gain additional information about their rival's RHP. The best-known 'individual cost threshold' models are the 'war of attrition without assessment' (Mesterton-Gibbons et al. 1996), the 'energetic war of attrition' (Payne & Pagel 1996, 1997) and the 'cumulative assessment' models (CAM; Payne 1998). Here, there is no assessment of a rival's RHP. Instead, a fight ends when the cost threshold of the weaker individual (lower RHP) is reached. Costs accumulate as the fight continues and increase with the intensity of the fighting and/or the opponent's RHP.

Mutual assessment and individual cost threshold models are distinguished by investigating natural fights between males that differ in size. If fight duration is determined by an individual's cost threshold, only the weaker rival's RHP will positively correlate with contest duration in a multiple regression (Taylor & Elwood 2003). Although there may be a weak relationship between the winner's RHP and contest duration (Gammell & Hardy 2003; Briffa & Elwood 2009), the fight is thought to end once the weaker rival's cost threshold is reached. If, however, there is a positive effect of the weaker contestant's RHP and a negative effect of similar magnitude for the stronger contestant's RHP, then fight duration is determined by the contestants' relative RHP. This suggests there is mutual assessment of RHP. An effect of relative male size is, however, also possible for one individual cost threshold model: the CAM model of Payne (1998). Here, fight duration is determined by the weaker individual's cost threshold, but rivals impose costs on each other that are proportional to their RHP. Consequently, the greater the RHP of the stronger contestant, the sooner the weaker contestant will abandon the fight. Distinguishing between CAM and mutual assessment models is, however, still possible if we have direct information about how costs are imposed (i.e. are the models' assumptions upheld?).

Assuming size is indicative of RHP, the 'mutual assessment' and 'individual cost threshold' models make different predictions about the relationship between fight duration and the mean size of males in size-matched fights. If fight termination depends on the weaker male's individual cost threshold there should be a positive correlation between mean male size and duration (i.e. because the weaker male's size and the mean size are synonymous). If mutual assessment occurs, however, fight duration should be independent of mean size because the relative size difference is unchanged (Enquist & Leimar 1983). Two small males should take as long as two large males to determine the inferior competitor. If, however, larger males place greater value on gaining a burrow, then fight duration should increase with mean size in size-matched fights, even with mutual assessment (Fig. 1).

We used fight duration in size-matched fights to determine whether perceived resource value increases with male size. We therefore tested whether fights are resolved based on mutual assessment or individual cost thresholds (see Morrell et al. 2005). Specifically, if mutual assessment occurs, then a positive relationship can plausibly be attributed to selection for greater investment in fighting by larger males (although, of course, as in any observational study additional unknown variables might also be responsible). Alternatively, if males simply fight until the weaker one reaches his individual cost threshold, then a positive relationship is predicted given an increase in the cost threshold with size. It is then difficult to 'remove' this underlying relationship to test for a residual positive correlation between mean size and fight duration owing to an increase in resource value (Fig. 1).

Testing the Predictions

To test our prediction, we documented the size distributions of burrow owners and burrow-seeking males that fight residents for