Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level

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Abstract: Animals often compete directly with conspecifics for food resources, and fighting success can be positively related to relative resource-holding power (RHP) and relative resource value (i.e., motivation to fight). Despite the ease of manipulating resource value during fights over food (by manipulating hunger levels), most studies have focused on male fighting in relation to gaining access to mates. In this study, pairwise contests over single food items were used to examine the effects of being the first to acquire a resource, relative body mass, relative body size (femur length), and relative level of food deprivation (i.e., hunger) on competitive feeding ability in male and female house crickets, *Acheta domesticus*. Only when the food pellet was movable did acquiring the resource first improve fighting success. When the pellet was fastened to the test arena, increased relative hunger level and high relative body mass both increased the likelihood of a takeover. However, the effects of body mass disappeared when scaled to body size. When the attacker and defender were equally hungry, larger relative body size increased takeover success but, when the attacker was either more or less hungry, body size had little effect on the likelihood of a takeover. Thus fight outcomes were dependent on an interaction between RHP and motivational asymmetries and on whether the resource was movable or stationary. Contest duration was not related to the magnitude of morphological differences between opponents, suggesting that assessment of fighting ability may be brief or nonexistent during time-limited animal contests over food items.

Résumé : Les animaux d'une même espèce se font souvent une compétition directe pour les ressources alimentaires et le succès des combats peut être en corrélation positive avec leur pouvoir de rétention relatif de la ressource (RHP) et la valeur relative de la ressource (i.e. motivation à se battre). En dépit de la facilité de manipulation de la valeur de la ressource pendant les combats pour la nourriture (en manipulant la faim), la plupart des études se sont attardées aux combats de mâles pour obtenir l'accès à des partenaires. Dans cette étude, nous avons observé les combats entre deux individus pour l'obtention de certains aliments afin de déterminer les effets sur la capacité de compétition pour des aliments, de la masse corporelle relative de femelles du grillon *Acheta domesticus*, de leur taille relative (longueur du fémur) et de l'importance relative de la privation de nourriture (i.e., faim). Il n'y a que dans les cas où la boulette de nourriture est déplaçable que le fait de prendre la ressource avant l'adversaire favorise le succès au combat. Quand la boulette est fixée dans l'arène d'observation, un accroissement de la faim et une masse relative élevée augmentent la probabilité de s'approprier la ressource. Cependant, l'effet de la masse disparaît quand celle-ci est évaluée par rapport à la taille. Lorsque l'attaquant et le défenseur ont tout aussi faim, la taille relative plus élevée de l'un augmente ses chances de succès, mais, lorsque les animaux ont plus ou moins faim, la taille influence peu les chances de succès. L'issue des combats dépend de l'interaction entre le pouvoir de rétention de la ressource et les asymétries dans la motivation ainsi que de la mobilité de la ressource. La durée des combats n'est pas reliée à l'importance des différences morphologiques entre les protagonistes, ce qui semble indiquer que l'évaluation de la capacité de l'adversaire est brève ou inexistante au cours des combats de durée limitée d'animaux pour des aliments.

[Traduit par la Rédaction]

Introduction

Animals often compete directly with conspecifics for resources such as mates, space, and food. The fighting success of an individual can be increased by high resource-holding power (RHP sensu Maynard Smith and Parker 1976) and elevated motivation to fight (Enquist and Leimar 1987 for review; Elwood et al. 1998). RHP is composed of both intrinsic and extrinsic components of fighting ability. Intrinsic fighting ability is often influenced by factors such as body size (Crespi 1986*a*, 1986*b*, 1988; Huntingford and Turner 1987 for review; Alcock 1996), fat reserves (Marden and Waage 1990; Plaistow and Siva-Jothy 1996; but see Cristol 1992), and aggressiveness (Barlow et al. 1986). Extrinsic aspects of fighting ability, such as prior ownership of a resource, can provide a strategic or positional fighting advantage in some cases (Crespi 1986*b*; Alcock and Bailey 1997; Hack et al. 1997; Cutts et al. 1999). The motivation of an animal to fight depends on its willingness to expend energy or to risk injury; elevated value of a resource should increase the motivation of an animal to fight (Enquist and Leimar 1987; Cristol 1992; Rodríguez-Gironés et al. 1996). Overall fighting success is determined by the joint effects of RHP, ownership, and resource value (e.g., Hansen 1986; Simmons 1986; Edsman and Jonsson 1996; Cutts et al. 1999).

Competition for food represents an important ecological process in animal populations, and the ability to gain access

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to food resources can influence lifetime fitness through its effects on survival and reproductive success (Marden and Waage 1990; Plaistow and Siva-Jothy 1996; Nosil and Reimchen 2001). Despite the potential influence of competitive feeding ability on fitness, most studies of fighting ability have focused on the relative ability of males to compete for mates or access to them (e.g., Crespi 1986*a*, 1986*b*, 1988; Alcock 1996; Plaistow and Siva-Jothy 1996; Enders et al. 1998; Tachon et al. 1999; but see Hansen 1986; Cristol 1992; Rodríguez-Gironés et al. 1996; Cutts et al. 1999).

Being the first to acquire a resource, relative body size, and hunger level (i.e., motivation) could all potentially influence fighting success in contests over food resources (Hansen 1986; Cutts et al. 1999). Acquiring a resource before an opponent may confer an advantage that is due to a more complete knowledge of the resource value or, for defenders versus attackers, a positional advantage (Alcock and Bailey 1997; Hack et al. 1997; Cutts et al. 1999). Larger individuals can usually overpower smaller opponents and may be less likely to incur injury (Huntingford and Turner 1987; Crespi 1988; Alcock 1996; Enders et al. 1998; but see McLachlan and Cant 1995; Hernandez and Benson 1998). Finally, increased hunger may elevate the motivation of an animal to fight for a food item (i.e., increase the value of the resource for the hungrier animal only) and thus improve fighting success (Hansen 1986; Enquist and Leimar 1987; Cristol 1992; Rodríguez-Gironés et al. 1996). At some point, however, food deprivation will deplete energy reserves to the point where competitive ability is reduced.

Field crickets (Orthoptera: Gryllidae) frequently exhibit agonistic behaviour and thus can provide an opportunity to examine the influence of various factors on relative fighting success. Indeed, field and laboratory studies of male gryllids have revealed that large body size (Dixon and Cade 1986; Simmons 1986; Souroukis and Cade 1993), prior burrow residency (Burk 1983; Simmons 1986), and a successful fighting history (Simmons 1986; Adamo and Hoy 1995) all improve fighting success. In house crickets, *Acheta domesticus*, male fighting ability has been positively related to body mass and to prior burrow residency (Hack 1997*a*). Furthermore, the energetic costs of fighting are well known (Hack 1997*a*, 1997*b*), and contests follow a pattern consistent with sequential assessment models of fighting behaviour (cf. Enquist and Leimar 1983). However, these studies generally examined the ability of males to gain dominance or access to females. In this study, I examined the effects of being the first to acquire a resource, relative body size (dry mass and hindleg femur length), and relative hunger level (assessed by level of food deprivation) on competitive feeding ability using male and female *A. domesticus*. I predicted that initial ownership of the resource, greater body size, and greater food deprivation (i.e., increased motivation due to increased value of the resource) would all increase fighting success during pairwise contests over food pellets.

Materials and methods

House crickets, *A. domesticus*, were reared from hatching to maturity in Plexiglas containers (50 × 50 × 75 cm) at densities of 150–200 individuals per cage. Crickets were provided with unlimited food (guinea pig chow, carrot and apple slices) and water and kept at 28°C with a 8 h light : 16 h dark photoperiod. For this study, adults were used in pairwise contests over single food items (pellets of cichlid fish food). To erase the effects of previous agonistic encounters, each test animal was kept in a separate 10-cm petri dish for 1 week prior to testing (after male field crickets lose a fight, they display no further agonistic behavior for 10 min but then gradually regain their agonistic behaviour within 1 h; an entire week of isolation is conservative; Adamo and Hoy 1995). Initially, trials were run with crickets that had not been food-deprived. In very few of these trials did either of the crickets feed on the pellet within 20 min (3 of 20 trials), and physical contact between crickets was never observed; thus the decision was made to compare the fighting success of crickets that had both been food-deprived (either equally deprived or deprived to different degrees).

For the trials reported herein, animals were provided with unlimited food (guinea pig chow) and water until either 48 or 72 h prior to the experiments, at which point only water was provided (via a moistened paper towel). All fights were between two crickets deprived of food for 48 h or between a cricket deprived of food for 48 h and a cricket deprived of food for 72 h (field crickets can withstand 1 week of food deprivation without an increase in mortality; Adamo and Hoy 1995). All contests were between members of the same sex, and no individuals were used twice. Differences in relative body mass and body size (femur length) were determined after the contests. I used two types of food resources: a movable food pellet and a stationary food pellet (the same type of pellet as the movable one but glued to the test arena). In a few cases ($n = 7$), the crickets ignored the food item or avoided fighting (pairs observed for 15 min) or a cricket managed to dislodge a glued pellet. These trials were discarded and are not included in the analysis of the 128 trials in which fights over food were observed.

I minimized age differences between pairs of cricket using two methods: for all fighting trials, (1) only adult crickets were used and (2) crickets of similar age were paired (this was accomplished by monitoring immature crickets and separating them from immature conspecifics once they reached adulthood). Thus adults that had matured within several days of each other were paired in all fighting trials. There were clear size and colour-pattern differences between opponents, allowing individual crickets to be distinguished during fighting trials without the use of marking.

Experiment 1: movable food resource

Two crickets were placed within a 10-cm petri dish and given 3 min to acclimate prior to the commencement of a fighting bout. The crickets within each petri dish were separated from each other and from the pellet by cardboard dividers. The cardboard partitions were removed as simultaneously as possible, the dish was covered with a lid, and observations commenced ($n = 27$ pairwise bouts between females, 24 bouts between males). I noted which cricket picked up and defended the pellet first and observed the crickets until the food pellet was entirely consumed (about 3–5 min; see Table 1). I recorded whether the cricket initially holding the pellet was attacked and whether the attacker successfully appropriated the pellet from the defender. The trial was scored as a successful takeover if the attacker gained possession of

Table 1. Mean time required for the defender to be attacked (fight initiation, designated by stridulation or any form of physical contact) and mean fight duration, in pairwise bouts between house crickets, *Acheta domesticus*, over single food items.

	Mean (s)	SD	*N*
Expt. 1: movable resource			
Fight initiation (attackers win)	29	49	13
Fight initiation (defenders win)	17	38	38
Fight duration (attackers win)	94	130	13
Fight duration (defenders win)	293	111	38
Expt. 2: stationary resource			
Fight initiation (attackers win)	11	14	33
Fight initiation (defenders win)	32	52	44
Fight duration (attackers win)	77	82	33
Fight duration (defenders win)	345	121	44

Note: For bouts in which the defender successfully defended the pellet, fight duration was measured as time between fight initiation and consumption of the entire pellet. For bouts in which the attacker usurped the pellet, fight duration was measured as the time between fight initiation and the successful takeover.

the pellet and the defender did not regain control of it. Otherwise, the trial was scored as a victory for the defender.

I noted whether aggressive stridulation and (or) more aggressive behaviours, such as kicking, biting (mandible lunge), head charges, and wrestling, occurred (see Hack (1997*a*, 1997*b*) for agonistic behaviour in house crickets). I also recorded the time required for the defender to be attacked (fight initiation—designated by any form of agonistic behaviour) and the duration of the fight. For bouts in which the defender successfully defended the pellet, fight duration was measured as the time between fight initiation and consumption of the entire pellet. For the bouts in which the attacker appropriated the pellet, fight duration was measured as the time between fight initiation and the successful takeover. Fight duration was measured in this manner, because fighting was continual as long as the pellet was present.

After each fighting bout, the crickets were fixed in 80% ethanol and dried to constant mass in a drying oven at 24°C. Each specimen was then weighed to the nearest 0.01 mg, using an electronic balance, and the length of its left hindleg femur measured with a digital micrometer under a light microscope (×65; 50 specimens were measured twice, to assess repeatability). This linear measurement was found to be highly repeatable in both sexes (ANOVA: males, $R = 99.7$, $F_{[27,55]} = 698.49$, $p < 0.001$; females, $R = 99.9$, $F_{[24,47]} = 1792.67$, $p < 0.001$) and was used as a measure of body size (mm) in all further analyses (in a previous study using crickets, leg length was correlated with body length, indicating that it constitutes a reasonable measure of body size; Simmons 1986). Furthermore, body mass was highly correlated with femur length in the crickets examined in this study ($r = 0.75$, $p < 0.001$). However, the slopes of this regression differed between the sexes ($B = 2.22$ and 4.41 for males and females, respectively; ANCOVA, test of parallelism, $F_{[1,256]} = 24.52$, $p < 0.001$) and, consequently, I calculated "condition" as the residuals of the regressions of body mass versus femur length (using separate regressions for each sex). Notably, dry mass was highly correlated with wet mass (bivariate correlation, $r = 0.74$, $p < 0.001$, $n = 50$).

Experiment 2: stationary food resource

The setup for this experiment was similar to that for experiment 1, except that the food pellet was fastened to the test arena (near the edge of the petri dish) using Elmer's white glue. After the cardboard partitions were removed, I noted which cricket initially found and defended the pellet ($n = 20$ pairwise bouts between females, 57 bouts between males). I recorded the time at which the initial defender was first attacked and, if a successful takeover did not occur within 5 min (or by the time the pellet was entirely consumed), terminated the trial. If a takeover did occur, I recorded it as successful providing the attacker retained control of the pellet for 5 min (or until the pellet was entirely consumed), at which point, I terminated the trial. If the original defender regained control of the pellet within 5 min, I recorded the trial as a victory for the defender (i.e., not a successful takeover). Aggressive stridulation, time until fight initiation, and fight duration (for fights where a successful takeover occurred) were recorded. Crickets were preserved, dried, weighed, and measured as described above.

Statistical analyses

Analyses were conducted separately for experiments 1 and 2. I evaluated whether acquiring the pellet first influenced fighting success by testing whether defenders won significantly more than half the trials (binomial tests). I then tested whether the effects of acquiring the pellet first were dependent on sex (χ^2 test) and whether the effects of initial ownership of the pellet were influenced by consistent mass, size, condition (Wilcoxon's signed rank (WSR) test), or food-deprivation differences between defenders and attackers (sign test, using only trials where combatants differed in the level of food deprivation).

I used logistic regression to examine the dependence of a successful takeover (0 = no, 1 = yes) on morphological and food-deprivation differences between attackers and defenders. I conducted three separate analyses (with mass differences, size differences, or both mass and size differences as covariates). Analysis 1 examined whether the likelihood of a successful takeover was influenced by mass differences between paired crickets (attacker mass – defender mass), food-deprivation differences between paired crickets (0, equally deprived; 1, attacker was food-deprived for a longer period than the defender; –1, attacker was food-deprived for a shorter period than the defender), the sex of paired crickets, and all two- and three-way interactions between these three factors. Mass difference was a continuous variable, while the other factors were designated categorical variables. In analysis 2, I substituted body-size difference (femur length) for body-mass difference and, in analysis 3, I included both mass and size as covariates. Likelihood-ratio (LR) tests were used to determine the significance level of each main effect and interaction term. Backward elimination was employed to derive a reduced model, and removed all terms for which the significance of –2(log LR) was >0.10 (Norusis 1993). I report significant ($p < 0.05$) results from the initial model (full model (FM)) and the reduced model (RM).

I used ANCOVA to determine whether time until fight initiation and fighting duration (covariates) were correlated with the absolute magnitude of mass, size, or condition differences between combatants (dependent variables) and to

test whether such associations differed between relative food-deprivation categories and between the sexes (i.e., test for homogeneity of slopes). Separate analyses were run for each experiment, for each of the three morphological traits, and for bouts resulting in a victory by the attacker versus the defender. Significance was set at $p < 0.05$ and all tests were two-tailed. Statistical analyses were done using SPSS v. 10.

Results

Fight outcomes

Experiment 1: movable food resource

In the movable food resource trials ($n = 51$), being first to acquire the resource increased fighting success, and larger relative body size increased fighting success in males when the attacker and defender were equally hungry. The first cricket to gain ownership of the pellet successfully defended it in 75% of the fighting bouts (binomial test, $p < 0.01$). This priority effect was independent of sex (Fig. 1; $\chi^2_{[1]} = 0.52$, $p = 0.47$) and was not due to consistent differences between attackers and defenders in body mass, body size, condition, or level of food deprivation (WSR test: defenders heavier in 24 trials, $Z = -0.76$, $p = 0.45$; defenders larger in 27 trials, $Z = -0.03$, $p = 0.98$; defenders in better condition in 21 trials, $Z = -0.61$, $p = 0.54$; sign test: defenders food-deprived for a longer period in 14 of 25 trials, $p = 0.69$).

I conducted three analyses to determine whether the likelihood of a successful takeover was dependent on morphological and (or) food-deprivation differences between paired combatants (analysis 1, mass differences as covariate; analysis 2, size differences as covariate; analysis 3, both mass and size differences as covariates; see Statistical analyses). For analysis 1, the probability of a successful takeover was not dependent on mass or food-deprivation differences between paired combatants (all main-effect and interaction terms not significant). For analysis 2, I detected an effect of body size on takeover success but this effect was dependent on food-deprivation differences between the attacker and defender and on sex (femur-length difference × food-deprivation difference × sex, LR = 9.67 for RM, df = 2, $p < 0.01$). In males, increased relative femur length increased the likelihood of a takeover only when the attacker and defender were equally food-deprived ($B = 2.48$, LR = 4.23, df = 1, $p < 0.05$; other comparisons not significant). In females, relative femur length did not have an effect on fighting success in any case (all comparisons not significant). A similar result was observed in analysis 3, in which both femur length and body size were included as variables (femur-length difference × food-deprivation difference, LR = 6.68 for RM, df = 2, $p < 0.05$; all other main effects and interactions not significant).

Experiment 2: stationary food resource

In the stationary food resource trials ($n = 77$), increased food deprivation improved fighting success, and large relative body size increased fighting success when the attacker and defender were equally food-deprived. In contrast with experiment 1, there was no effect of being first to acquire the resource on fighting success (binomial test: 57% of the fighting bouts won by defender, $p = 0.25$). As in experiment

Fig. 1. Proportion of pairwise contests between house crickets over a movable food resource (pellet) in which the defender successfully defended the pellet against the attacker and thus won the fight. This positive effect of prior ownership was significant (binomial test, $p < 0.01$) and independent of sex.
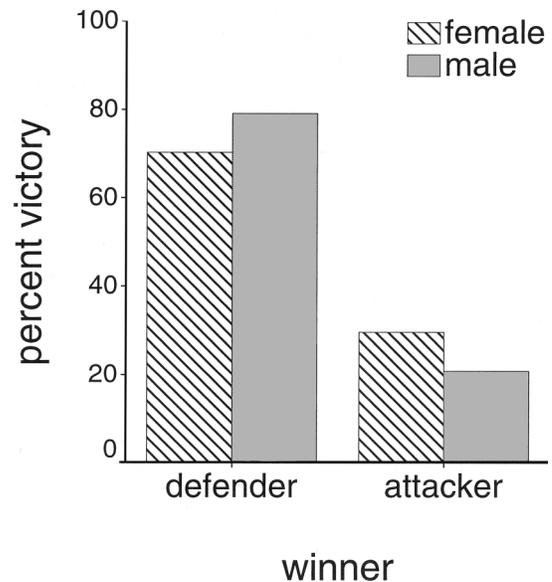
1, there was no tendency for defenders to be heavier, larger, in better condition, or hungrier than attackers (WSR test: defenders heavier in 32 trials, $Z = -1.77$, $p = 0.08$; defenders larger in 33 trials, $Z = -1.48$, $p = 0.14$; defenders in better condition in 47 trials, $Z = -1.15$, $p = 0.25$; sign test: defenders hungrier in 22 of 39 trials, $p = 0.32$). Thus a positive effect of being first to acquire the resource on fighting success was observed only in experiment 1, indicating the probability of the defender winning the bout was dependent on the type of resource (i.e., movable versus stationary; $\chi^2_{[1]} = 4.02$, $p < 0.05$).

Body-mass, body-size, and food-deprivation differences between the attacker and the defender all influenced the probability of successful takeover. In the analysis using body mass, elevated body mass of the attacker relative to the defender increased the probability of a successful takeover (Fig. 2a; LR = 10.73 for RM, df = 1, $p < 0.01$) and this association was independent of sex and of differences in the level of food deprivation (all interactions not significant). Increased food deprivation of the attacker relative to the defender also increased the probability of a successful takeover (Fig. 3; LR = 16.96 and 26.71 for FM and RM, respectively, df = 2, both $p < 0.001$).

In the analysis using body size (femur length), the effect of relative body size on takeover success was dependent on differences in the level of food deprivation (femur-length difference × food-deprivation difference, LR = 12.36 for RM, df = 2, $p < 0.01$; food-deprivation difference, LR = 17.56 and 17.03 for FM and RM, respectively, df = 2, both $p < 0.001$). Increased relative body size increased the likelihood of a successful takeover when combatants were equally hungry, but had no effect on fighting success when the attacker was less or more hungry than the defender (Fig. 2b). This interaction was independent of sex (LR = 4.08 and 5.20 for FM and RM, respectively, df = 2, $p = 0.13$ and 0.08,

Fig. 2. The relationship between mass (mg) and size (femur length, mm) differences between paired combatant house crickets (attacker and defender) and the likelihood of a successful takeover of a stationary food pellet (predicted probabilities derived from logistic regression models). Mass difference was included in analysis 1, whereas both mass and size differences were included in analysis 3. (A) Analysis 1. The likelihood of a successful takeover increased with increased mass of the attacker relative to the defender ($p < 0.01$) and this relationship held for all three categories of food-deprivation difference. (B) Analysis 3. The likelihood of a successful takeover was influenced by an interaction between size and food-deprivation differences ($p < 0.01$). Increased size increased fighting success only when combatants were equally food-deprived. Mass difference no longer had an effect.
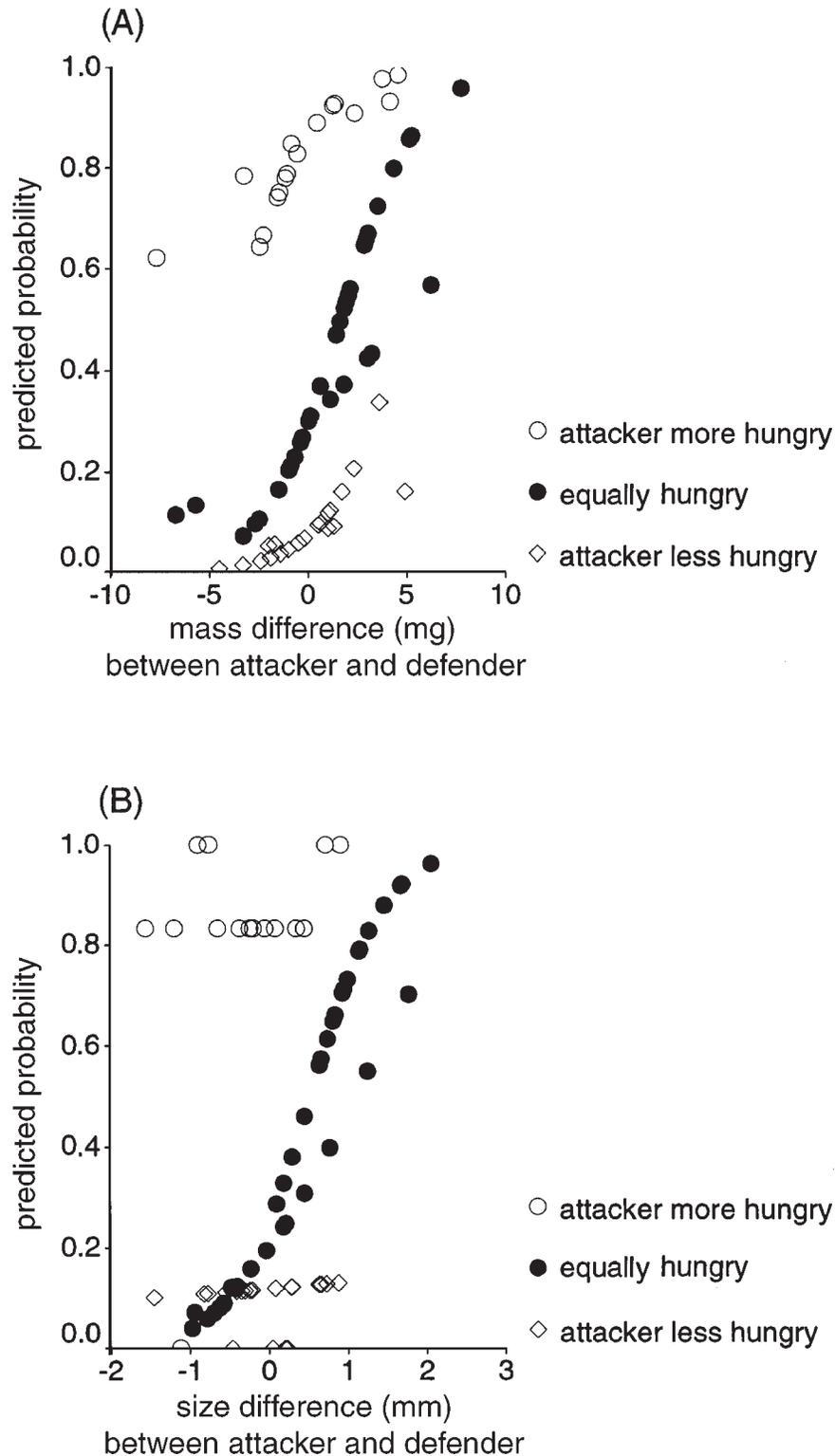
Fig. 3. The mean (±95% confidence interval) proportion of successful takeovers of stationary food pellets by attackers in pairwise contests between house crickets for three categories of relative food deprivation: less, the attacker was food-deprived for a shorter period than the defender; equal, attacker and defender were equally food-deprived; more, the attacker was food-deprived for a longer period than the defender. Crickets were deprived of food for either 48 or 72 h. The probability of a takeover was greatest when attackers were hungrier (i.e., more food-deprived) than defenders and least when attackers were less hungry (i.e., less food-deprived) than their opponents ($p < 0.001$).
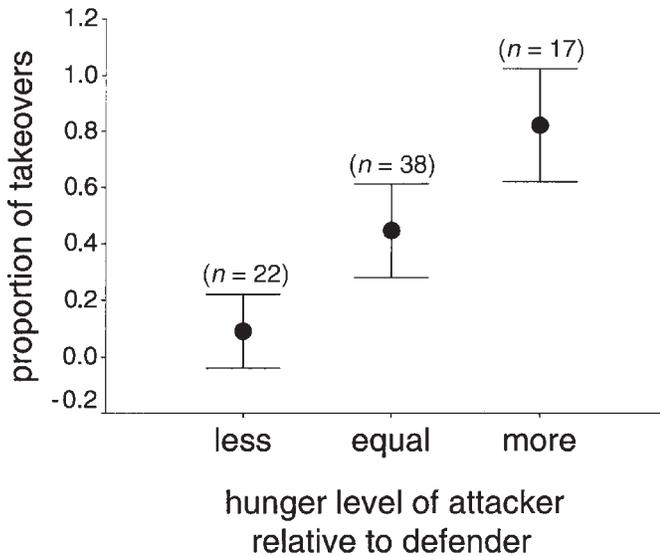
respectively). A similar effect was observed in analysis 3, in which both mass and size differences between the attacker and defender were included (for RM: food-deprivation difference, LR = 17.03, df = 2, $p < 0.001$; femur-length difference × food-deprivation difference, LR = 12.36, df = 2, $p < 0.01$; femur-length difference × food-deprivation difference × sex, LR = 5.20, df = 2, $p = 0.07$). Relative body mass had no effect on the likelihood of a takeover once size differences between attackers and defenders were statistically accounted for (main effect and interactions with mass difference were all not significant).

Thus increased food deprivation (i.e., hunger) increased fighting success, as did large relative body size when combatants were equally food-deprived. Notably, two subgroups within the "equally hungry" group are evident in Figs. 2*a* and 2*b* and this variability may represent variation in other intrinsic determinants of fighting ability (e.g., aggressiveness, endurance).

Contest durations and agonistic behaviour

The relationship between the time until fight initiation and the magnitude of morphological differences between paired combatants (absolute mass difference, absolute size difference, absolute condition difference) was not significant in any case and was not dependent on sex or relative level of food deprivation (interaction and main effects of ANCOVA all not significant; see Table 1 for fight initiation and contest durations). Similarly, there was no relationship between fighting duration and the degree of morphological difference between opponents in any case, and this result was not dependent on

sex or relative level of food deprivation (main effect and interaction terms of ANCOVA all not significant). In experiment 1, stridulation was common during fighting bouts (47% of all males tested were observed stridulating) but was never observed before physical contact. Thus behaviours such as antennal lashes and kicks, which involve physical contact, always preceded stridulation. In experiment 2, stridulation did not occur. During both experiments, one or more high injury risk behaviours, such as head charges, kicks, mandible lunges, bites, and wrestling, were observed (50 and 65% of trials in experiments 1 and 2, respectively; see Hack (1997*a*, 1997*b*) for a complete description of these behaviours and their energetic costs).

Discussion

When animals compete directly over resources, fighting success is often determined by RHP and motivational asymmetries among individuals (Maynard Smith and Parker 1976; Enquist and Leimar 1987; Elwood et al. 1998). Most studies of fighting success have focused on males competing for mates or mating territories (e.g., Crespi 1986*a*, 1986*b*, 1988; Alcock 1996; Plaistow and Siva-Jothy 1996; Enders et al. 1998; Tachon et al. 1999; but see Adamo and Hoy 1995; Cutts et al. 1999; Shelly 1999). In male house crickets, both high relative body mass and prior burrow residency have been shown to increase success during fights over dominance status or burrow ownership (Hack 1997*a*, 1997*b*). In this study, I examined the dependence of competitive feeding ability of male and female house crickets on three factors: being first to acquire the resource, relative body size, and relative level of food deprivation (i.e., a measure of hunger). Consistent with general predictions, prior ownership, large relative body size, and increased food deprivation (i.e., motivation) all increased fighting success, but such effects were often interactive and dependent on the nature of the resource being defended.

A number of studies have documented a positive effect of prior ownership on fighting success, primarily in the context of territorial defence (Crespi 1986*b*; Alcock and Bailey 1997; Hack et al. 1997; Cutts et al. 1999; but see Goldsmith et al. 1996). Several studies have shown that prior burrow residency increases fighting success in crickets (field crickets, Burk 1983; Simmons 1986; the house cricket, Hack 1997*a*). Often, this is attributed to the fact that defenders have better knowledge of the value of the resource than attackers (e.g., Hack et al. 1997). Alternatively, there may be a tendency for defenders (i.e., holders of a territory) to win fights or to have acquired the resource first owing to increased intrinsic RHP; for instance, if they are larger or more fit than attackers (Crespi 1986*b*; Alcock and Bailey 1997). It is unlikely that defenders had an intrinsic advantage in the present study, as defenders were not heavier, larger, or in better condition than attackers. Also, it may be generally easier to defend than usurp a resource (e.g., defence offers a positional advantage). In this study, acquiring the food pellet first increased fighting success when the resource was movable but not when it was stationary, suggesting that the influence of acquiring a food resource first on fighting success was dependent on the nature, or defensibility, of the contested resource.

In stationary food resource trials, the relative level of food deprivation had a large positive effect on fighting success. The likelihood of a successful takeover was greatest when the attacker was hungrier than the defender and least when the attacker was less hungry than the defender. Presumably, this was because hunger asymmetries increased the value of the resource, and thus the motivation to fight, for the hungrier animal (Enquist and Leimar 1987; Cutts et al. 1999). Similar results have been reported for bald eagles where small individuals with low RHP could appropriate food (salmon) from larger opponents as the larger birds became satiated (Hansen 1986), in dark-eyed juncos (*Junco hyemalis*) where food-deprived birds were dominant over normally fed birds (Cristol 1992), and in the blue footed-booby (*Sula nebouxii*) where small chicks could dominate larger siblings only when hungrier than the larger siblings (Rodríguez-Gironés et al. 1996).

Large body size is predicted to increase RHP, and numerous studies in crickets (field crickets, Dixon and Cade 1986; Simmons 1986; Souroukis and Cade 1993; the house cricket, Hack 1997*a*) and other taxa (Crespi 1986*a*, 1986*b*, 1988; Alcock 1996; Edsman and Jonsson 1996; Enders et al. 1998; Cutts et al. 1999) have documented positive associations between body size and fighting success. In this study, both high relative body mass and large relative body size increased fighting success, but the effects of body mass disappeared when scaled to differences in size. Although previous studies have found abundant energy reserves and good body condition (e.g., residual mass) to be important predictors of high competitive ability (Marden and Waage 1990; Plaistow and Siva-Jothy 1996; Nosil and Reimchen 2001), the results of this study indicate that size per se rather than condition influenced fight outcome (see Cristol 1992).

The effects of body size were, however, highly dependent on hunger level. When the attacker and defender were equally hungry, the larger opponent had greater fighting success but, when the attacker was either more or less hungry than the defender, body size had little effect on the outcome of the contest. Thus the results indicate that fighting success in house crickets is likely to depend on interactions between a number of competitive asymmetries, as has been reported for a species of field cricket (*Gryllus bimaculatus*, Simmons 1986), as well as for fish (Hansen 1986; Cutts et al. 1999), birds (Rodríguez-Gironés et al. 1996), crustaceans (Edsman and Jonsson 1996; Jennions and Backwell 1996), and other arthropods (Goldsmith et al. 1996; Hack et al. 1997).

Studies examining fighting and competitive ability in the context of feeding success, as opposed to competition over mates, are relatively rare (but see Cristol 1992; Rodríguez-Gironés et al. 1996; Cutts et al. 1999). In this regard, it is interesting to contrast the results of the present study with those reported for animal contests dealing with access to mating opportunities, which are often ritualized events involving sequential assessment of an opponent's ability and which often result in escalation of fighting behaviour when opponents exhibit similar RHP and motivational level (Enquist and Leimar 1983; Neat et al. 1998). Assessment models of fighting behaviour predict that contest duration will be inversely related to the magnitude of competitive asymmetry between opponents, and there is empirical support for this prediction (e.g., Crespi 1986*a*; Hack et al. 1997; Molina-

Borja et al. 1998; the house cricket, Hack 1997*a*). However, I did not detect such an association in this study, indicating that detailed assessment may not be occurring during fights over food items.

It should be noted that previous authors have suggested that a correlation between competitive asymmetry and fight duration does not necessarily provide support for sequential assessment (Jennions and Backwell 1996 for review). For example, "all-out" fights not involving assessment would generate the same pattern (i.e., fights with large differences in fighting ability between combatants will be settled more quickly than fights in which opponents are evenly matched). The best support for sequential assessment is provided by demonstrations that fights escalate towards the use of more costly tactics and that rates of aggressive behaviour are highest in contests between animals of similar fighting ability and motivational state (e.g., Crespi 1986*a*, 1986*b*, 1988; Molina-Borja et al. 1998). In house crickets, fights between males for dominance and burrow ownership appear to involve assessment and escalation, with winners eventually expending more energy than losers (Hack 1997*a*, 1997*b*).

Although my data do not allow me to test explicitly for such escalation during fights over food, I note that stridulation, an energetically low-cost behaviour that does not result in injury, was never used by males when fighting over a stationary food resource and was never observed prior to physical contact during fights over a movable food resource. This observation is more consistent with an "all-out" fight than with a sequential-assessment model of fighting behaviour (see Jennions and Backwell 1996). Indeed, the brief amount of time required to completely consume a food pellet (about 3–5 min) places a limit on the duration of a contest and may favour brief or no assessment of an opponent's ability. If so, "all-out" fighting ability and the motivation to fight may directly determine the outcome of contests over food, with assessment playing, at most, a minor role. Further work could be directed toward determining the role played by assessment of fighting ability in time-limited animal contests (i.e., most contests over food; but see Hansen 1986).

Another interesting consideration is the difference in lifetime fitness provided by winning a fight over a food item versus winning a fight over a mate. In a number of studies of fighting over mates, it has been demonstrated that increased fighting success in males leads to a mating advantage (Crespi 1986*a*, 1988; Alcock 1996; Luiselli 1996; Bondurianski and Brooks 1999; but see Goldsmith et al. 1996; the house cricket, Nelson and Nolen 1997). As higher rates of food intake can improve survival and mating success (e.g., by increasing body size or energy reserves; see Marden and Waage 1990; Plaistow and Siva-Jothy 1996; Nosil and Reimchen 2001), it is likely that winning fights over food items translates into increased fitness. In both male and female field crickets (*G. bimaculatus*), kicking, biting, and lunging were more common during fights over food than during agonistic encounters without food (Adamo and Hoy 1995). Further work is required to determine the magnitude of these fitness gains and to determine the relative costs and benefits of winning fights over food versus winning fights over mates.

In conclusion, being first to acquire the resource, relative body size, relative hunger level (i.e., motivation, which was assessed by differences in level of food deprivation), and

resource type (movable or not movable) all influenced the outcome of contests between house crickets over single food items. This is one of the few studies examining the influence of multiple factors on fighting success during contests over food items rather than during contests over mates, and the results suggest that fighting success is likely to be determined by interactions between RHP asymmetries, motivational asymmetries, and the nature of the resource being defended.

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