

What factors contribute to an ownership advantage?

S. A. Fayed, M. D. Jennions*
and P. R. Y. Backwell

School of Botany and Zoology, Australian National University,
Canberra, Australian Capital Territory 0200, Australia

*Author for correspondence (michael.jennions@anu.edu.au).

In most taxa, owners win fights when defending a territory against intruders. We calculated effect sizes for four factors that potentially contribute to an ‘owner advantage’. We studied male fiddler crabs *Uca mjoebergi*, where owners won 92% of natural fights. Owners were not more successful because they were inherently better fighters ($r=0.02$). There was a small effect ($r=0.18$) of the owner’s knowledge of territory quality (food availability) and a medium effect ($r=0.29$) of his having established relations with neighbours (duration of active tenure), but neither was statistically significant. There was, however, a significant effect due to the mechanical advantage the owner gained through access to the burrow during fights ($r=0.48$, $p<0.005$).

Keywords: fighting; ownership; territoriality

1. INTRODUCTION

In most taxa, an owner is more likely to win a fight with an intruder for a resource. Retaining ownership of a territory has major effects on evolutionary fitness, but recent models confirm that this ‘ownership advantage’ or ‘prior residency effect’ could arise due to a simple rule of ‘respect for ownership’ (Kokko *et al.* 2006). There are, however, other factors that can increase the ownership advantage. First, in territorial species, stronger individuals could accumulate as owners so that non-resident intruders are inherently weaker fighters (Whiting *et al.* 2006). Second, residency might increase the relative value of a territory for the owner (Parker 1974). For example, if there are offspring on the territory, the owner has more incentive to retain it than a rival that only gains a territory. Third, owners can acquire personal information that increases only the territory’s value to them (e.g. learning food or refugia locations or establishing relations with neighbours). Greater resource value increases the motivation to win a fight (i.e. investment in costly fighting; review: Arnott & Elwood 2007). Fourth, the defended resource might offer a mechanical advantage to owners (e.g. the ability to retreat into a refuge could provide greater leverage during contests of strength; Funakoshi 2005).

Here, we document an ownership advantage in male crabs. We then use experimental manipulations to examine four factors that are potentially responsible and quantify their relative importance. These factors are owner–intruder differences in fighting

ability, two measures of territory value and access to a central burrow.

2. MATERIAL AND METHODS

Uca mjoebergi was studied in Darwin, Australia from September to December 2006. This species breeds year round. Each male defends a 10–25 cm diameter territory centred on a burrow against burrowless males (hereafter ‘floaters’). The burrow is used for mating and predator evasion, and the surrounding sediment for feeding and courtship. Males use their enlarged claw to attract females and to fight males. Male territory owners repel floaters that try to usurp their territory. Floaters are males that have recently lost their territory to another male, relinquished it to a mate or spontaneously abandoned it. The male with the larger claw is more likely to win a fight (Morrell *et al.* 2005). Owners sometimes retreat into the burrow during a fight, either blocking the entrance with their claw or wedging into it while claw grappling with their opponent.

For each owner–floater fight, we noted male claw length and which male won the encounter. We excluded fights if males had a regenerated claw (Backwell *et al.* 2000) or if a neighbour intervened (Backwell & Jennions 2004). The floater always initiated the fight. Before starting our experiments, we documented naturally initiated owner–floater fights. There is an ownership advantage as the owner won 92% of fights (binomial test, $p<0.001$, $n=37$).

- (i) To determine whether floater males are inherently poorer fighters, we documented fights between an owner and either a natural or experimentally created floater male ($n=40$, 40). The latter were former territory owners that we had just captured. In each trial, the focal floater was captured, measured, marked and released at a distance more than 2 m from his site of capture. If natural floaters are weaker fighters than owners, they should win fewer fights than are won by the experimentally created floaters.
- (ii) To alter the relative value of a territory to owners and floaters, we manipulated food availability. Information about territory quality is available only to owners, so food addition can affect only their motivation to retain a territory. To test whether food availability affects owners’ fighting success, we added either food (4 g fish flakes/70 ml of water) or water to 0.25 m² plots (demarcated with string) for 3 days ($n=25$, 25). On day 4, we captured a floater male, released him onto a plot that was temporally enclosed, and documented the first fight with an owner. We recorded one fight/plot and used 50 different floater males. Given the strong ownership advantage (92%), it is hard to detect an increase in owner success. We therefore released larger males as floaters to decrease the fighting success of owners. This increases the likelihood of detecting a difference between treatments if food addition increases owner success.
- (iii) We attempted to alter territory value for owners by experimentally manipulating their territory tenure. We assume that increased tenure is beneficial because boundary disputes between neighbours decrease over time, and established neighbours sometimes form coalitions to repel intruders (Backwell & Jennions 2004). We therefore predict that the ownership advantage increases with territory tenure owing to a greater motivational asymmetry between owners and floaters. To test whether longer tenure increases the ownership advantage, we documented fights for owners that varied in their duration of residency on a territory. We erected 11 circular cages (0.23 m²) by embedding plastic meshing into the mudflat sediment. Cages had a solid rim to prevent crabs from exiting or entering. We then captured, marked and individually released territory owners into a cage. Once they had acquired a territory, we removed the defeated male. Each burrow was marked with a numbered flag to monitor occupancy. We introduced males over several days until each cage contained several males that varied in their tenure of ownership. To estimate how often each owner interacted with his new neighbours, we made daily spot samples every 30 min and noted surface activity. Our measure of effective ‘active tenure’ was the total number of samples in which the male was surface active prior to the focal fight. To measure the ownership advantage, we introduced a floater male into a cage. We then noted the outcome when he fought with a marked male that was still in the burrow he originally acquired. We documented one fight per owner and each floater was removed from the cage after one fight.
- (iv) To test for a mechanical advantage, we captured, released and tracked 35 males until they fought a territory owner. At the

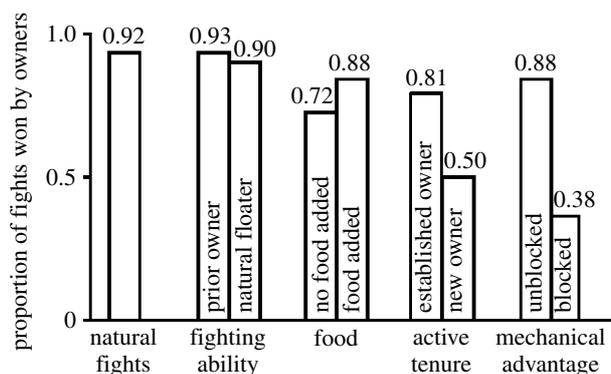


Figure 1. The proportion of fights won by owners (see text for sample sizes). For illustrative purposes, for tenure, we define males as a 'new owner' if they spent less than 1 h surface active ($n=9$) or 'established owner' if they spent 1 h or more than that surface active ($n=21$).

start of 18 fights, we blocked the burrow using a flat blade attached to a 2 m long rod. Once a fight had started, we slowly slid the blade across the burrow entrance at a distance less than 1 cm below the sediment surface to prevent the owner from using the burrow. For the 17 control fights, we slid the blade up to the burrow but did not block the shaft. We then noted which male won the fight.

For each of the four datasets, we ran a binary logistic regression to test whether the likelihood that an owner won depended on his class/treatment (categorical) and included the difference in opponents' claw size as a continuous covariate. There were no significant interactions between experimental treatment/class and claw size difference, so they were removed from final models. Claw size difference was retained, even if it did not attain statistical significance, because previous studies show that it has a small but biologically significant effect on fight outcome. For the tenure study, there was no categorical variable as active tenure is a continuous variable. Summary statistics are presented as mean \pm s.e. and we set $\alpha=0.05$.

Finally, we calculated effect sizes for each experiment to compare directly the relative importance of the four explanatory factors on fight outcome (owner-floater fighting ability, owner information on food availability, active tenure on a territory and mechanical effect). We converted the χ^2_1 statistic for the main treatment/class effect to Pearson's r using $r = \sqrt{\chi^2/N}$, then calculated the 95% CI using Fisher's Z -transformation of r , to calculate $Z_r \pm 1.96$ s.e., where s.e. = $1/\sqrt{N-3}$ and finally back-transforming the interval to r (Cooper & Hedges 1994).

3. RESULTS

The proportion of fights won by owners in each experiment is shown in figure 1.

- (i) We found no evidence that floaters lose fights because they are intrinsically poorer competitors. The fighting success of natural floaters and prior owners that were forced to float was indistinguishable ($\chi^2_1=0.03$, $p=0.86$), even after the significant effect of a size difference between opponents was taken into account ($\chi^2_1=4.42$, $p=0.04$; $n=40, 40$).
- (ii) Greater food availability on a territory did not increase the owner's fighting success ($\chi^2_1=1.60$, $p=0.21$), and the size difference between opponents did not have a significant effect ($\chi^2_1=0.27$, $p=0.60$; $n=25, 25$).
- (iii) Established owners were slightly better than new owners at defending their territory ($\chi^2_1=2.05$, $p=0.15$; figure 1). The size difference between opponents had no significant effect ($\chi^2_1=0.19$, $p=0.66$; $n=30$).

- (iv) Territory owners gained a clear advantage when they had access to their burrow during fights. They won significantly more contests if the entrance remained open ($\chi^2_1=7.89$, $p=0.005$). The size difference between opponents did not have a significant effect ($\chi^2_1=0.68$, $p=0.41$; $n=17, 18$).

4. DISCUSSION

There is a strong territory ownership advantage in *U. mjoebergi*. Owners won 92% of fights when floaters attempted to usurp their territory. Estimating effect sizes allows us to directly compare the importance of the four factors we examined. A mechanical advantage due to access to a burrow while fighting had the strongest influence on the proportion of fights the owner won ($r=0.47$; 95% CI: 0.18–0.69). The period of active residency on the territory also appeared to have an effect ($r=0.26$; 95% CI: -0.09 to 0.56), albeit a marginally non-significant one. Information about greater food availability had only a small effect ($r=0.18$; 95% CI: -0.10 to 0.43), and there was no evidence that a difference in the intrinsic fighting ability of floaters and owners contributes to the ownership advantage ($r=0.02$; 95% CI: -0.20 to 0.23).

It is initially surprising that floaters were not detectably weaker than owners, because at least some floaters are males that have recently lost their own territory. One explanation is that fight outcome is size related and floaters can choose to fight slightly smaller opponents that they have some chance of defeating (Jennions & Backwell 1996). The low fighting success of floaters suggests, however, that they trade off the likelihood of winning against the reduced value of obtaining a territory from a much smaller male. If a male wins a burrow from a smaller male, he then has to spend time enlarging it which reduces its value.

We manipulated two variables that should increase only the value of a territory for the owner, namely food availability and the owner's tenure of residency. Longer residency reduces one cost of territory ownership because boundaries with neighbours become established so that neighbour-neighbour fighting decreases. If owners value a territory more highly, they should invest additional energy into fights (i.e. show greater motivation), increasing their fighting success. However, food manipulation failed to increase fighting success. One explanation is that we did not change the owner's evaluation of his territory. For example, natural food supplies might be temporally stochastic so that past food availability rarely predicts future availability on a territory. In contrast, there was a weak trend ($r=0.26$, $p_1=0.15$) for residency duration to effect fight outcome. Although logistically we made a sizable effort to obtain data, our sample size was modest, so residency effects will be the focus of a future study with greater statistical power.

Finally, owners gained a clear mechanical advantage when they used their burrow during fights. They won 88% of fights when they could enter their burrow, and 38% if prevented from so doing. Interestingly, Morrell *et al.* (2005) reported that owners

won 67% of fights against experimentally created floaters, as opposed to the 93% reported here. However, they specifically excluded fights where the owner partly entered his burrow. This emphasizes the benefit of access to the burrow during fights, although the proximate mechanism by which burrow access increases fighting success remains to be determined.

Although a mechanical advantage offers a readily testable explanation for a prior residency effect, it has been neglected in favour of theoretically richer explanations based on owner–intruder differences in resource evaluation or motivation. This is unfortunate, as preliminary evidence suggests that it is an important factor in several species (e.g. Takahashi *et al.* 2001; Funakoshi 2005; this study). Even more compelling is the evidence that animals possess morphological adaptations that increase their mechanical advantage when defending a resource (Lee 2001; Navas & James 2007). Future studies, especially of burrow, shell or cavity dwellers and males that hold females in amplexus, should pay greater attention to testing whether owners have a mechanical advantage during fights.

This study conformed to Australian and university animal ethics requirements.

We thank Lindsey McFarlane for assistance, and the ARC and Ecological Society of Australia for funding.

Arnott, G. & Elwood, R. W. 2007 Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. *Proc. R. Soc. B* **274**, 3011–3017. (doi:10.1098/rspb.2007.1196)

Backwell, P. R. Y. & Jennions, M. D. 2004 Coalition among male fiddler crabs. *Nature* **430**, 417. (doi:10.1038/430417a)

Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D. & Passmore, N. I. 2000 Dishonest signalling in a fiddler crab. *Proc. R. Soc. B* **267**, 719–724. (doi:10.1098/rspb.2000.1062)

Cooper, H. & Hedges, L. V. (eds) 1994 *The handbook of research synthesis*. New York, NY: Russel Sage Foundation.

Funakoshi, S. 2005 Intraspecific and interspecific competition for larval nests of the caddisflies *Stenopsyche marmorata* and *Stenopsyche sauteri*. *Entomol. Sci.* **8**, 339–345. (doi:10.1111/j.1479-8298.2005.00133.x)

Jennions, M. D. & Backwell, P. R. Y. 1996 Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* **57**, 293–306. (doi:10.1006/bjil.1996.0017)

Kokko, H., Lopez-Sepulcre, A. & Morrell, L. J. 2006 From hawks and doves to self-consistent games of territorial behavior. *Am. Nat.* **167**, 901–912. (doi:10.1086/504604)

Lee, J. C. 2001 Evolution of a secondary sexual dimorphism in the toad, *Bufo marinus*. *Copeia* **4**, 928–935. (doi:10.1643/0045-8511(2001)001[0928:EOASSD]2.0.CO;2)

Morrell, L. J., Backwell, P. R. Y. & Metcalfe, N. B. 2005 Fighting in fiddler crabs *Uca mjoebergi*: what determines duration? *Anim. Behav.* **70**, 653–662. (doi:10.1016/j.anbehav.2004.11.014)

Navas, C. A. & James, R. S. 2007 Sexual dimorphism of extensor carpi radialis muscle size, isometric force, relaxation rate and stamina during the breeding season of the frog *Rana temporaria* Linnaeus 1758. *J. Exp. Biol.* **210**, 715–721. (doi:10.1242/jeb.000646)

Parker, G. A. 1974 Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47**, 223–243. (doi:10.1016/0022-5193(74)90111-8)

Takahashi, M., Suzuki, N. & Koga, T. 2001 Burrow defense behaviors in a sand-bubbler crab: *Scopimera globosa*, in relation to body size and prior residence. *J. Ethol.* **19**, 93–96. (doi:10.1007/s101640170004)

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C. & Blomberg, S. P. 2006 Ultraviolet signals ultra-aggression in a lizard. *Anim. Behav.* **72**, 353–363. (doi:10.1016/j.anbehav.2005.10.018)