



Male-biased predation of a fiddler crab

TSUNENORI KOGA*, PATRICIA R. Y. BACKWELL†, JOHN H. CHRISTY‡, MINORU MURAI‡ & EIITI KASUYA§

*National Institute for Environmental Studies

†Smithsonian Tropical Research Institute

‡Tropical Biosphere Research Center, Sesoko Station, University of the Ryukyus

§Department of Biology, Faculty of Science, Kyushu University

(Received 3 November 2000; initial acceptance 20 December 2000;

final acceptance 8 March 2001; MS. number: 6742)

Great-tailed grackles, *Quiscalus mexicanus*, prey on fiddler crabs, *Uca beebei*, either by running straight at them or by running past them then angling sharply back to strike. Grackles that used angled runs caught only males and were twice as successful as birds that used straight runs and caught equal numbers of males and females. Why do grackles that use angled runs catch only males? Males were not differentially available, nor did grackles prefer them to females in choice tests. Fewer crabs entered their burrows when we moved a model predator past them than when we moved it directly towards them and crabs allowed the model to get closer when it passed then returned to strike. Although crabs may take more risks when birds use angled runs, the sexes did not differ in their escape responses. Hence, differential risk taking cannot explain male-biased predation by birds using angled runs. We suggest that males, with their large claws and lighter colours, are more conspicuous than cryptic females. When a bird runs past then turns to dash back at a crab it may be able to keep track of a male much better than a female. Indeed, grackles missed all females they struck at using angled runs. Hence, males may be conspicuous and preferred prey to birds using angled runs. Males' enlarged claws, bright colours and other sexually selected traits may increase male predation rate in this context.

© 2001 The Association for the Study of Animal Behaviour

Sexually selected male traits enhance male fighting ability and attractiveness to females, but often at the expense of reduced survival (Darwin 1871). Males are usually more active than females in mate acquisition, and their courtship signals, displays and signalling behaviour may make them more conspicuous to predators and impede escape (Magnhagen 1991). Males may partially compensate for their greater vulnerability to predation by being more vigilant and by initiating escape responses earlier than females (Martin & Lopez 1999). However, both heightened vigilance and early and frequent escape are often incompatible with male mate seeking and courtship and may cost males missed mating opportunities. Hence, levels of vigilance and escape decisions are likely to represent a fine balance between their survival benefits and reproductive costs.

Fiddler crabs (genus *Uca*) provide an excellent opportunity to study the naturally selected costs of sexually selected male traits. Males have one small claw that they use for feeding and grooming and one greatly enlarged claw that can be up to 50% of an adult male's body weight. Males wave their large claw to attract females for mating and use it to threaten and fight other males. Male performance in both courtship and aggressive contests increases with the size of the claw (Christy 1983; Jennions & Backwell 1995; Backwell & Passmore 1996). Males are also typically brightly coloured and conspicuous against the generally dark intertidal sediments where they live. In contrast, females lack the large claw and usually have a generally dark and mottled colour pattern that makes them cryptic compared with males.

It is not yet clear whether the sexually selected traits of male fiddler crabs increase their vulnerability to predation. In some species, the enlarged male claw may inhibit rapid escape from predators (Montague 1980) and the added nutritional content of the claw muscle may make males more profitable and hence preferred prey (see Zwarts & Blomert 1990). However, males may be more difficult for some predators to catch (Wolf et al. 1975), and Bildstein et al. (1989) found that the claw offers some protection as a potentially dangerous weapon that some

Correspondence and present address: T. Koga, Faculty of Education, Wakayama University, Wakayama 640-8510, Japan (email: tkoga@center.wakayama-u.ac.jp). P. R. Y. Backwell and J. H. Christy are at the Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A. M. Murai is at the Tropical Biosphere Research Center, Sesoko Station, University of the Ryukyus, Okinawa 905-0227, Japan. E. Kasuya is at the Department of Biology, Faculty of Science, Kyushu University, Hukuoka 812-8581, Japan.

avian predators avoid. Here we show that great-tailed grackles, *Quiscalus mexicanus*, prey exclusively on male *Uca beebei* when using one of their common hunting techniques and we present the results of field experiments to determine the cause of this pattern, particularly the possible effects of sexual dimorphism on predation rates.

Uca beebei (≤ 1 cm carapace width) lives in mixed-sex colonies on intertidal mudflats on the Pacific coast of tropical Central and South America (Crane 1975). Both sexes defend burrows and are active on the surface during diurnal low tides. Female and immature grackles are common and persistent predators of *U. beebei* (Koga et al. 1998). Grackles most often hunt by running in a low posture across the mudflat and lunging to catch a crab, typically at a burrow entrance. They run in either a nearly straight or a sharply angled path and a given bird will use both kinds of runs. In a straight run, the bird lunges at a crab positioned along its path. In an angled run, the bird first runs straight but then veers sharply, often opening its wings briefly as it turns, and lunges at a crab it has passed. Preliminary observations indicated that birds caught both sexes of crab when they used straight runs, but predominantly males when they used angled runs. Why are males more vulnerable to predation by birds that pass them and then angle back to strike?

METHODS

We studied grackle predation on *U. beebei* on a mudflat on the west bank of the Pacific entrance to the Panama Canal (see Christy 1988; Koga et al. 1998). We collected data during 6-h periods centred on the times of the diurnal low tides in December 1998 and January, February and April 2000. A permit from the Marine Authority of the Republic of Panama authorized this research and collection of crabs (see below).

Foraging Tactics and Success Rates

We placed small stakes 2 m apart on the mudflat and watched and videotaped hunting grackles. We used the grid of stakes to estimate the distances (and, with time measurements from the tapes, velocities) that hunting birds ran along the single leg of straight paths and both legs of angled paths.

We recorded the success rate and the sex of the crabs captured in 94 straight and 153 angled runs by noting the presence (male) or absence (female) of an enlarged claw on the crab in the bird's beak. We determined the sex of the crabs that birds struck at but missed in an additional 20 straight and 50 angled runs. To do this, when we saw birds miss, we located the burrows at which they struck crabs by the distinctive beak marks they left in the mud. We dug the crabs out of these burrows and determined their sex.

Predation of Burrow Resident and Wandering Crabs

In *U. beebei*, and most other fiddler crabs, burrow residents and nonresident wandering crabs (both sexes) are

usually on the surface. Crabs become wanderers when they leave or are aggressively displaced from their burrows. When predators approach, wanderers usually run to and attempt to enter nearby burrows but residents often block them, leaving the wanderer partially exposed at the burrow entrance where it is presumably easily seen and reached by the predator. This interaction might explain differential predation on males by birds using angled runs. If resident crabs are less likely to descend into their burrows fully when a predator runs past them than when it approaches directly, and if male residents are more likely to block wandering males than wandering females, then male wanderers might more often be forced to remain on the surface during the passing leg of angled runs making them conspicuous and especially vulnerable to predation. If true, then wandering males should be the predominant prey of grackles that use angled runs.

To determine whether grackles using straight and angled runs hunted and caught both residents and wanderers, we dug up the burrows at which birds made successful and unsuccessful strikes. We judged that the bird hunted a resident when the strike was successful and the burrow was empty, and when the bird missed and the burrow had one crab. Conversely, we judged that a wanderer was the target when the strike was successful but there was a crab in the burrow and when the bird missed and there were two crabs in the burrow. In the latter case we assumed that the crab nearest the surface when we dug it up was the intruding wanderer. We dug up burrows at 30 successful and 50 unsuccessful strikes after angled runs, and 19 successful and 20 unsuccessful strikes after straight runs.

Sex Ratio and Sex-based Prey Preferences

If males are more abundant than females, then this might explain, in part, why they are more often caught by grackles. We therefore determined the sex ratio of both wandering and resident crabs. Crabs that have their own burrows are residents. We counted the number of resident males and females that were active on the surface in 51 nonoverlapping plots of 50 × 50 cm placed to sample the entire flat. To determine if there was a sex bias in wanderers, we walked along transects 32 m long and counted and sexed all crabs in burrow entrances that we could touch with the tip of a pencil. This method takes advantage of the fact that wanderers are burrowless individuals that attempt to enter residents' burrows. The residents prevent them from entering the burrow, forcing them to stay at the very top of the burrow shaft, close to the entrance. We walked 42 transects at 15-min intervals on 3 days.

All else being equal, grackles may prefer to eat males. We tested this by presenting birds with a simultaneous choice of dead size-matched (≤ 1 mm difference in carapace width) males and females on white plastic plates on the mudflat. We killed 40 crabs (20 size-matched pairs) by immersing them in ice water. Within seconds they folded and relaxed their appendages indicating that the cold had an anaesthetizing effect. We presented the crabs to the birds soon after they died, while they still had their

natural colours. Two pairs were presented simultaneously to five or six birds that were foraging at the same time on the flat. After all the crabs were consumed another set of pairs was presented until 20 trials were completed. We found it impossible to recognize predators individually so we do not know how many birds ate crabs from the plates. However, many grackles entered and left the flat during this experiment and it is unlikely any given bird ate more than a few crabs.

Responses to Directly and Indirectly Approaching Birds

When a predator approaches, crabs run to their burrows and either immediately descend into them or stay partly exposed and vigilant at their entrances. We determined whether males and females differed in their tendency to descend into their burrows when a model of a predator approached them directly, as in a straight run, or indirectly, as in the passing leg of an angled run. If males descend into their burrows less often than females in response to a passing predator, then this would bias their availability as prey (Backwell et al. 1998) and perhaps explain their differential predation by birds using angled runs.

We placed a 1-m² wire frame divided into four squares of 50 × 50 cm on the mudflat and set up a guideline so that we could move a model of a grackle to one corner of the frame. When the crabs resumed full surface activity, we counted the number of males and females in the two squares on the diagonal that did not include the corner where the model would stop. We then moved a model of a grackle up to the frame and counted the number of males and females on the surface immediately after the model stopped. The model stopped equidistant (50 cm) from the two diagonally opposed squares, one on the axis and one off the axis of the model's path (Fig. 1a). We considered crabs in the on- and off-axis squares to be potential prey of birds making straight and angled runs, respectively.

The bird model, carved from foam, was the size and shape of a female grackle and was painted to resemble one. It was suspended with a wire hook on a taut 2-m-long, clear monofilament guideline fixed to two wooden poles set in the mud. The model was weighted and hung so that it cleared the sediment by about 5 cm. It was moved by hand with a monofilament control line at about 1.5 m/s, a velocity typical of a running grackle (see Results). Fiddler crabs use movement-sensitive vision to detect predators (Land & Layne 1995), so the lack of odour, vibration and other cues produced by real running birds was unlikely to reduce the efficiency of the model. We used each frame location for one trial, then moved the frame ($N=30$ locations and trials). We did not reuse locations on subsequent days and it is highly unlikely that we recorded more than one response per crab.

Timing of Descent During Straight and Angled Runs

Crabs that have detected a predator and run to their burrows but stopped at the entrances descend into their

burrows if the predator continues to approach them. Males and females may time their descent differently and move at different speeds. If males begin their descent later (predator closer) and they move more slowly than females when a predator dashes towards them on the second leg of an angled run, then this could explain male-biased predation by grackles that use this hunting tactic.

Using a frame of 50 × 50 cm and a grackle model, we simulated straight runs by pulling the model from 2 m away across the diagonal to the opposite corner and beyond (Fig. 1b). The crabs descended into their burrows when the model passed over them. We videotaped the scene from above. From the tapes we measured when each crab began its descent and disappeared from view and when the model passed over the two diagonal corners of the frame. Crabs disappeared when they were 1–2 cm down their burrow shafts, a depth probably sufficient to escape the low-angled strike of a grackle. We assumed that the velocity of the model was constant and used the time measurements to calculate crab-to-model distances at the beginning and end of each crab's burrow descent. We conducted 18 independent trials.

Using the same 50 × 50-cm frame, we simulated angled runs with two grackle models, one for the passing leg and the other for the final redirected approach. The guideline for the passing leg was positioned so that the model passed 50 cm to one side of the frame and ended 50 cm beyond the back corner of the frame. When the first model reached that point, we immediately moved the second model along a second guideline that angled back to and crossed the frame diagonally (Fig. 1c). We videotaped the scene and made the measurements described above from the tape. We conducted 19 independent trials.

Statistics

For data analysis, we used nonparametric tests because at least one sample from each experiment was non-normally distributed or the samples were heteroscedastic, even after transformations (StatView 5.0). For this reason we were unable to use multivariate statistics. All tests were two tailed.

RESULTS

Running Distance and Speed

Grackles walked on the mudflat in an erect posture, then extended their necks, lowered their heads and ran straight for 0.9 ± 0.4 m ($\bar{X} \pm \text{SD}$; range 0.3–1.5, $N=15$) before they struck at a crab in their path or for 0.8 ± 0.4 m (0.5–1.7, $N=16$) before turning sharply and running another 0.8 ± 0.4 m (0.4–1.6, $N=16$) before striking at the end of an angled run. Birds ran the final legs of angled runs significantly faster than the initial legs (final: 2.5 ± 1.7 m/s, $N=16$; initial: 1.0 ± 0.3 m/s, $N=16$; Wilcoxon: $T=0$, $P<0.001$). There was no difference in velocity between straight runs and the final legs of angled

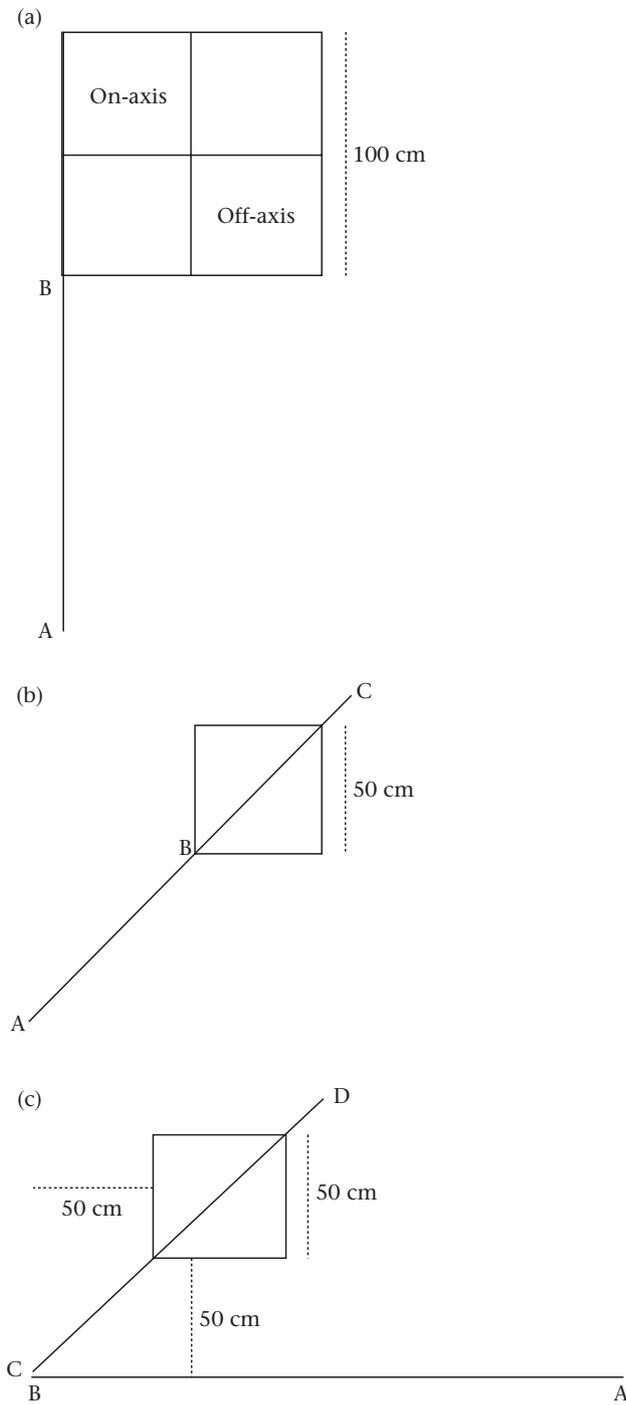


Figure 1. Designs of experiments to investigate the responses of crabs to directly and indirectly approaching birds (a), and the timing of burrow descent by male and female crabs in response to birds using straight (b) and angled runs (c). In (a), a single model bird started from A when male and female crabs in the 1-m² frame were active on the surface and stopped at B. In (b), the single model started from A when crabs in the frame were active on the surface, passed through B and the frame and stopped at C. In (c), the first model started from A when the crabs in a frame were active on the surface and stopped at B, and then the second one started from C and stopped at D. See text for details.

runs (straight: 1.6 ± 0.6 m/s, $N=15$; Mann–Whitney: $U=152.5$, $P=0.199$).

Success Rates

Grackles were more than twice as successful when they used angled runs (83/153, 54%) as when they used

straight runs (23/94, 25%; Fisher's exact probability test: $P<0.001$; Fig. 2). Grackles caught both sexes in equal numbers with straight runs (11 males, 10 females, 2 unidentified) but only males with angled runs (74 males, 9 unidentified; Fisher's exact probability test for number of males and females: $P<0.001$; Fig. 2). Approximately

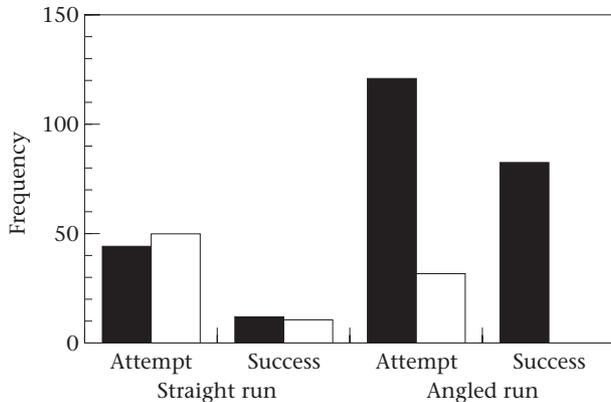


Figure 2. Estimated number of successful and unsuccessful predation attempts on males (■) and females (□) by birds using straight and angled runs. These estimates are based on attempted predation in 94 straight and 153 angled runs and the observed proportions of each sex that were caught and missed by birds using the two foraging modes (see text).

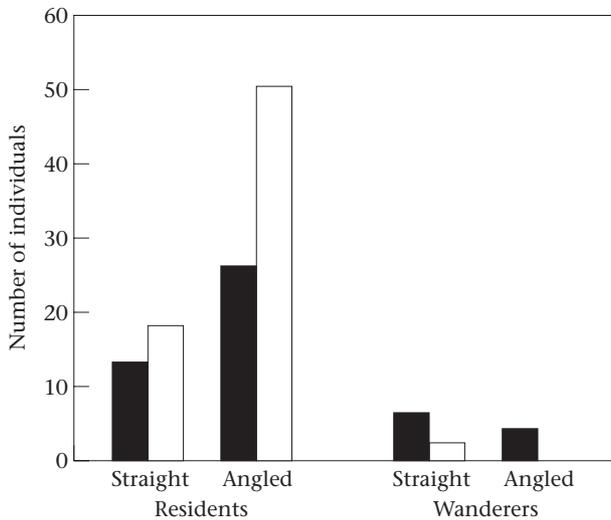


Figure 3. Predation of burrow resident and wandering crabs by birds using straight and angled runs. ■: Crabs that were caught; □: crabs that escaped.

equal numbers of males and females escaped strikes in both straight and angled runs (straight: 9 males, 11 females; angled: 27 males, 23 females). Birds therefore struck at equal numbers of males and females in straight runs (proportionately: males 44; females 50) but they struck at more males than females in angled runs (proportionately: males 121; females 32; binomial test: $P=0.00029$; Fig. 2).

Grackles hunted primarily resident crabs (binomial test: $P<0.001$ for both straight and angled runs; Fig. 3). Clearly, they did not target wandering males when they used angled runs.

Sex Ratio and Sex-based Predator Preferences

The sex ratio of both active burrow residents and wanderers was about 1:1. In 51, 0.25-m² plots we found 343 males and 354 females (males: $\bar{X} \pm \text{SD}=6.73 \pm 3.38$;

Table 1. Number of males and females above ground in on- and off-axis plots before and after the model predator approached, and ratio of the crabs remaining above ground after the model approached ($N=30$)

	Before	After	Ratio
On axis			
Males	3.53±2.22	0.83±1.29	0.17±0.24
Females	2.80±1.03	0.43±0.57	0.16±0.24
Off axis			
Males	2.80±1.58	1.33±1.09	0.50±0.38
Females	2.53±1.17	1.20±0.85	0.51±0.34

Means are given \pm SD. See Fig. 1a for location of on- and off-axis plots.

females: 6.94 ± 3.36 ; Wilcoxon signed-ranks test: $Z=0.02$, $N=51$, $P=0.98$). When we walked 42 transects we found 56 male ($\bar{X} \pm \text{SD}=1.33 \pm 1.36$ per transect) and 48 female (1.14 ± 0.87 per transect; $Z=-0.89$, $N=42$, $P=0.37$) wanderers at the entrances to resident's burrows.

When given a choice between size-matched dead crabs of each sex, grackles did not prefer to eat either sex first (11 males and 9 females eaten first; binomial test: $P>0.25$).

Responses to Directly and Indirectly Approaching Birds

Before we moved the model grackle, there were equal numbers of males and females within and between the on-axis and off-axis plots (Friedman's test: $\chi^2_3=2.33$, $N=30$ frames, 60 plots, $P=0.51$). After we moved the model, there was a significant difference in the number of crabs that remained on the surface ($\chi^2_3=13.71$, $N=30$, $P=0.003$; Table 1). There was no difference between the ratios of males and females that remained above ground in either the on-axis (Wilcoxon signed-ranks test: $Z=-0.07$, $N=30$, $P=0.943$) or off-axis plots ($Z=-0.11$, $N=30$, $P=0.914$). However, both sexes were much more likely to remain above ground in the off-axis than the on-axis plots (male: $Z=-3.50$, $N=30$, $P<0.001$; female: $Z=-3.78$, $N=30$, $P<0.001$; both significant at 1% level after Bonferroni correction; Table 1). Hence, the sexes did not differ in their responses to approaching predators and both males and females were more likely to take refuge inside their burrows when predators ran straight at them.

Timing of Descent During Straight and Angled Runs

Males and females were equally responsive to the model predator during both straight and angled approaches; they started and ended their burrow descent at comparable times and crab-to-predator distances (Table 2). However, both sexes allowed the model to come significantly closer before they escaped into their burrows during the last leg of simulated angled runs than on the single leg of simulated straight runs (Mann-Whitney test: males: $U=282.0$, $N_1=18$, $N_2=19$, $P=0.001$; females:

Table 2. Responsiveness of males and females to approaching model predators moved to simulate straight ($N=18$) and angled runs ($N=19$)

Response	Type of run	Crab-model distance		Wilcoxon Z	P
		Males	Females		
Start burrow descent	Angled	57.0±16.8	52.9±12.0	-0.89	0.38
	Straight	93.2±33.6	83.5±45.8	-1.37	0.17
Disappear from view	Angled	31.3±9.8	27.1±6.6	-1.33	0.18
	Straight	47.02±33.4	36.3±32.1	-1.07	0.29

Responsiveness was measured as crab-to-model distances ($\bar{X}\pm SD$ cm) when the crabs started to enter their burrows and when they disappeared from view.

$U=258.0$, $N_1=18$, $N_2=19$, $P=0.008$; both significant at 5% level after Bonferroni correction).

DISCUSSION

We found no evidence that male crabs were more abundant than females. Birds caught primarily burrow residents and the sex ratios of both residents and wanderers were about 1:1. We also found no evidence of selective foraging based on prey profitability (see Bildstein et al. 1989) as grackles did not prefer males when given a simultaneous choice between size-matched dead males and females.

Differences in risk taking may in part explain why grackles were more successful when they hunted with angled runs. More crabs stayed on the surface at their burrow entrances when the model predator passed them, as in the first leg of an angled run, than when the model approached directly, as in a straight run. Crabs also entered and descended into their burrows later and allowed the model to get closer during simulated angled runs. Hence, response time may contribute relatively more to crab vulnerability in angled than in straight runs. Any slight pause may be fatal because the approaching predator is so near. By contrast, since crabs began their descent much earlier when the predator approached directly, small, inadvertent delays are unlikely to be fatal during straight runs. Clearly, the crabs could detect a bird's approach direction and took more risks when it moved past them; fewer descended into their burrows immediately and those that waited at their entrances allowed the returning predator to get within about 30 cm (roughly within lunge and strike range) before they disappeared from view. This difference in risk taking may explain, in part, why grackles were more than twice as successful when they used angled runs. Why do crabs take more risks when a grackle runs near but past them?

Upon detecting a predator, crabs run back to their burrows and either enter it immediately or wait at the entrance. Burrow entry limits the amount of time crabs have for other activities, time that is already limited by the tidal cycle. Grackles are nearly always present on the mudflat (Koga et al. 1998) so crabs could not afford to descend into their burrows in response to each potential

danger. It is more likely that they assess the level of danger posed by a particular bird, as well as the potential payoffs of not responding, and adjust their risk taking accordingly. Behaviour consistent with such decision making has been shown in fiddler crabs: males take more risks when their chances of mating are greatest (Backwell et al. 1998). The balance an individual strikes between the costs and benefits of retreating when it detects a potential predator determines its availability as prey (Ens et al. 1993).

Although crabs took more risks when the model predator was moved to simulate angled runs, males did not take more risks than females. Indeed they disappeared from view slightly sooner and at greater crab-to-predator distances. Hence, greater risk taking by males cannot explain why grackles caught only males when they hunted with angled runs.

The last possible explanation for the strongly male-biased predation by grackles that use angled runs is that males are more conspicuous than females to passing grackles. During straight runs, birds strike at crabs in their path and they probably use binocular vision to select their prey. During angled runs, birds evidently select a crab as they run past it and must therefore detect their prey using peripheral monocular vision. Straight-running grackles strike and catch equal numbers of males and females (which are equally available as residents and wanderers) suggesting that neither sex is more conspicuous. However, males, with their large claws and generally lighter body colour, may be more conspicuous to fast-moving birds that use peripheral, monocular vision. Indeed grackles struck at significantly more males than females when they passed them then angled back to strike, even though the escape responses of the two sexes were comparable and they were equally available as prey. Grackles sometimes struck at females but always missed. Perhaps as birds turn and dash back they are less able to keep track of and accurately strike cryptic females than conspicuous males. Finally, birds may learn that males are easier to catch using angled runs and they therefore may specifically target off-axis males.

The enlarged claws and bright colours of male fiddler crabs may offer mating and fighting advantages (Christy & Salmon 1984; Jennions & Backwell 1995; Backwell & Passmore 1996), but in *U. beebei*, they appear to do so at

the cost of decreased survival because they may make males more conspicuous to predatory grackles. However, male conspicuousness led to relatively higher predation rates only when grackles ran past crabs then turned back to strike one that did not descend into its burrow. Crabs took fewer risks when grackles approached them directly. They entered their burrows and disappeared from view early enough so that grackles did not target males as prey even though they must be visually more conspicuous than dark and mottled females. Hence, males may pay a predation cost of conspicuousness, but only in a highly specific context. This cost evidently has not exceeded the benefits to males of developing large claws, bright colours and exuberant courtship displays.

Acknowledgments

We thank M. Matsumasa, M. Jennions and two referees for helpful advice. The work was supported by a grant from the Japanese Ministry of Education, Science and Culture (No. 10041175). T. K. was also partly supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists and the Japan Science and Technology Corporation.

References

- Backwell, P. R. Y. & Passmore, N. I.** 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab *Uca annulipes*. *Behavioral Ecology and Sociobiology*, **38**, 407–416.
- Backwell, P. R. Y., O'Hara, P. D. & Christy, J. H.** 1998. Prey availability and selective foraging in shorebirds. *Animal Behaviour*, **55**, 1659–1667.
- Bildstein, K. L., McDowell, S. G. & Brisbin, I. L.** 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. *Animal Behaviour*, **37**, 133–139.
- Christy, J. H.** 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology*, **12**, 169–180.
- Christy, J. H.** 1988. Pillar function in the fiddler crab *Uca beebei* (I): effects of male spacing and aggression. *Ethology*, **78**, 53–71.
- Christy, J. H. & Salmon, M.** 1984. Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biological Review*, **59**, 483–509.
- Crane, J.** 1975. *Fiddler Crabs of the World. Ocypodidae: genus Uca*. Princeton, New Jersey: Princeton University Press.
- Darwin, C.** 1871. *The Descent of Man, and Selection in Relation to Sex*. London: Murray.
- Ens, B., Klaasen, M. & Zwarts, L.** 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour. *Netherlands Journal of Sea Research*, **31**, 477–494.
- Jennions, M. D. & Backwell, P. R. Y.** 1995. Fighting behaviour in the fiddler crab *Uca annulipes*: body size, residency and weapon size. *Biological Journal of the Linnean Society*, **57**, 293–306.
- Koga, T., Backwell, P. R. Y., Jennions, M. D. & Christy, J. H.** 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society of London, Series B*, **265**, 1385–1390.
- Land, M. & Layne, J.** 1995. The visual control of behavior in fiddler crabs. II: Tracking control systems in courtship and defence. *Journal of Comparative Physiology A*, **177**, 91–103.
- Magnhagen, C.** 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution*, **6**, 183–186.
- Martin, J. & Lopez, P.** 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology*, **10**, 487–492.
- Montague, C. L.** 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. *Contributions in Marine Science*, **23**, 25–55.
- Wolf, P. I., Shanholzer, S. F. & Reimold, R. J.** 1975. Population estimates for *Uca pugnax* (Smith, 1870) on the Duplin Estuary Marsh, Georgia, USA (Decapoda, Brachyura, Ocypodidae). *Crustaceana*, **29**, 79–91.
- Zwarts, L. & Blomert, A.** 1990. Selectivity in whimbrels feeding on fiddler crabs explained by component specific digestibilities. *Ardea*, **78**, 193–208.