

Prey availability and selective foraging in shorebirds

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Abstract. Accurate measurements of prey availability are vital to our understanding of foraging behaviour, particularly prey selectivity. In the present study, observations of shorebirds foraging for fiddler crabs on intertidal mudflats demonstrate that prey availability depends both on the temporal variation in crab activity and on the crabs' responses to the presence of foraging shorebirds. Our results suggest that measurements of prey availability that do not specifically account for prey activity patterns and their responses to predators are necessarily inaccurate. Furthermore, our results also show that tests for foraging selectivity are extremely sensitive to the way in which prey availability is measured and can even indicate active prey selectivity when more accurate measures of prey availability show predators to be non-selective. Because inaccurate measures of food resources greatly reduce our ability to detect food preferences, greater care must be taken to account for prey activity patterns and their responses to predators in measurements of prey availability.

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Food availability plays a crucial role in virtually every aspect of animals' lives, including their geographical distribution, reproductive success, habitat selection, migration and territoriality (Dodge et al. 1990; Hutton 1990; Terrill 1990; Wolda 1990). Our understanding of these biological patterns depends fundamentally on accurate measurements of food availability, a notoriously difficult task (Hutton 1990; Wolda 1990; Luo et al. 1996). Our sensory limitations and strengths can prevent us from perceiving the environment in the way our study animals do (Blake et al. 1990; Dodge et al. 1990; Hutton 1990; Dusenbury 1992; Lovette & Holmes 1995). Furthermore, prey availability may depend not only on the predator's perceptual abilities, but also on the behavioural responses of prey animals to the presence of predators (Charnov et al. 1976; Kersten et al. 1991; Ens et al. 1993).

The accuracy of prey availability measurements is probably most vital in selective foraging tests because here the prey availability to predators is the standard against which the predators' apparent preferences are judged. Selective forag-

ing implies that predators do not take prey as it is encountered but sometimes reject prey items with relatively low profitability (see Goss-Custard 1984). Profitability depends on the offset of handling costs (e.g. time, energy, danger) against gross energy gain (dependent on prey size, digestibility, etc.).

Shorebirds are ideal subjects for studies of selective foraging, and many attempts have been made to relate their prey preferences to prey availability (e.g. Rands & Barkham 1981; Piersma et al. 1993; Kalejtja & Hockey 1994; McNeil et al. 1995; Thibault & McNeil 1995). Several studies have shown that prey availability depends not only on the total number of prey present, but also on behavioural interactions between predator and prey (Zwarts 1985; Kersten et al. 1991; Ens et al. 1993). These interactions are particularly important when prey animals, such as fiddler crabs (*Uca* spp.), are able to detect and evade potential predators. The availability of fiddler crabs to shorebirds has usually been estimated by counting either the number of open burrows in an area, or the number of crabs active on the surface when a predator is not present (Zwarts 1985, 1990; Ens et al. 1993; Thibault & McNeil 1995). These simple measures of prey availability have been intuitively

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accepted despite mounting evidence of their inaccuracy (Goss-Custard 1984; Zwarts 1985, 1990; Ens et al. 1993; Kalejta 1993; Thibault & McNeil 1995). If earlier studies incorrectly estimated the relative abundance of different size and sex classes, this may have led to incorrect assessments of foraging selectivity by shorebirds and sex-biased predation on fiddler crabs (see Boshe 1982; Zwarts 1985, 1990; Ens et al. 1993).

Fiddler crabs are especially interesting prey because their profitability (net energy per unit time gained by the predator) is closely linked to their pronounced sexual dimorphism (Bildstein et al. 1989; Zwarts & Blomert 1990). Males have a greatly enlarged, sexually selected claw that is used in courtship and inter-male conflicts (Crane 1975; Greenspan 1975; Christy 1980; Jennions & Backwell 1996). The claw may confer some protection against avian predators because of the high handling costs associated with this potentially dangerous weapon (Bildstein et al. 1989). If predators avoid male fiddler crabs because their enlarged claws make them less profitable prey, then such prey selectivity may affect the evolution of this sexually selected trait. Survival is generally thought to decrease with the increased exaggeration of traits under sexual selection. The fiddler crab claw, however, may confer an advantage in both competition for mates and in predator-prey interactions.

We studied shorebird-fiddler crab predatory interactions: (1) to assess the adequacy of simple prey availability measures for tests of foraging selectivity; (2) to introduce a new technique for measuring prey availability; and (3) to present a more realistic account of foraging selectivity in these animals. Although the empirical work was conducted on shorebirds and fiddler crabs, our theoretical arguments apply generally to the measurement of prey availability for any visual predator of mobile prey.

METHODS

We conducted the study on a large, unvegetated, intertidal mudflat at La Playa el Agallito, Chitre, Republic of Panama. The study site consisted of the opposite banks of a stream. One bank was steep and sandy and supported a large population of *U. stenodactylus* (area 35×75 m). The other bank was flat and muddy and supported a large

population of *U. princeps* (area 30×50 m). Both areas were exposed for 7–8 h each low tide. During diurnal low tides, fiddler crabs were present in large numbers, as were the shorebirds that fed on them. We collected data over an 8-week period, during October 1995 and January 1996. Large numbers of shorebirds used the mudflats over this period with both resident and over-wintering migratory species present. Focal samples of bird behaviour were made over the first 2 weeks of each month, and we documented crab responses to bird predators during the second half of each month. We collected data during a daily 6-h period centred around diurnal low tides.

Uca stenodactylus is considerably smaller (adult carapace width 1–2 cm; claw length 2–3 cm) than *U. princeps* (adult carapace width 2–5 cm; claw length 6–8 cm). Shorebirds eat both species. Although the birds used several foraging tactics, this study is confined to visual-search foraging, whereby the birds walk or run in a straight line for 1–4 m across the mudflat and attempt to pick prey off the surface (run/walk and grab tactic). Birds foraging in this way continually move into new areas of the mudflat and encounter previously unseen prey. This is the most common method shorebirds use to prey on fiddler crabs (Zwartz 1985; Bildstein et al. 1989; Thibault & McNeil 1995). Each of the other foraging tactics have different prey availabilities associated with them, and therefore require different methods of investigation. Thirteen shorebird species regularly foraged in the study area. We studied six species, all of which appeared to feed almost exclusively on fiddler crabs while they were at the study site. Whimbrel, *Numenius phaeopus*, and willet, *Catotrophorus semipalmatus*, were the larger species; ruddy turnstone, *Arenaria interpres*, and black-bellied plover, *Pluvialis squatarola*, were of medium size; and Wilson's plover, *Charadrius wilsonia*, and semi-palmated plover, *C. semipalmatus*, were the smaller species.

Prey Availability

Avian predators elicit escape responses from fiddler crabs at distances that greatly exceed the strike distance of the predator (Land & Layne 1995). Crabs attempt to escape by running to a burrow opening, or into a burrow if the threat persists. Crabs that enter burrows become unavailable as prey to those birds using a

run/walk and grab foraging tactic. Our method of measuring prey availability was specifically designed to account for the effects of these responses on predator-prey encounter rates.

We used a semi-realistic model of a medium-sized shorebird to elicit crab escape responses. The model had a plastic foam body, wooden legs and bill, feather wings, and was painted and sized realistically. Two vertical poles with a monofilament guide line between them were set in the sediment 3 m apart. The model was suspended by a hook to the guide line so that it just cleared the surface. It was moved by pulling two control lines that led from the model, through guide-holes in the poles, to the investigator. The model moved over a distance of 2.5 m in a straight line. Since zigzag movement was rarely seen in the study species, and the investigation was limited to the run/walk and grab foraging tactic, the model's movement accurately represented the natural movement of foraging birds. Fiddler crabs use movement-sensitive vision to detect predators (Land & Layne 1995), so the lack of odour and vibrational cues are unlikely to affect the efficiency of the model.

We positioned predator models on poles and placed them in study plots of *U. stenodactylus* and *U. princeps*. Plots for *U. stenodactylus* and *U. princeps* differed in size (1×0.5 m and 1×1 m, respectively) to accommodate the differences in crab densities. The effectiveness of the model was not influenced by the difference in plot size. We delimited study plots with pegs and twine well within the boundaries of each crab species' distribution. We initially positioned models 2 m from a plot edge then moved them to the edge at a rate that simulated either a walking or a running bird. We used the following protocol to record crab responses. Five minutes after set-up, we counted (using binoculars) the number of male, female and juvenile crabs that were present on the surface of the plot. We then moved the model at either the walking or running rate to the edge of the plot and immediately counted the number of male, female and juvenile crabs that did not retreat down a burrow. These crabs would have been available on the surface as prey to a real predator. We moved the model to the starting position and repeated the sequence at the alternative approach rate after a 5-min acclimation period. Hence, for each plot we recorded male, female and juvenile responses to a walking and a running predator.

We divided the tidal exposure interval into three 2-h periods that spanned the peak times of crab activity: 3–1 h before low tide (ebb tide), 1 h before to 1 h after low tide (low tide); 1–3 h after low tide (flood tide). On a given day, we set up five plots for one of the crab species. During each period, we moved the models at each of the five plots sequentially for each rate. We then delimited new plots for the next period. We used each plot only once. We completed a total of 25 plot set-ups at each of the three periods for each of the two crab species, yielding 150 statistically independent experiments. Each experiment consisted of before (model at rest) and after (model moved) counts of males, females and juveniles to running and walking models, resulting in a total of 1800 observations.

We analysed fiddler crab responses using a repeated measures design mixed MANOVA (SAS Institute 1996). We measured crab responses as the proportion of crabs still present after the approach of the shorebird model relative to the number before approach (relative crab abundance). Response variables were crab type (male, female, juvenile) and approach speed (fast or slow). We treated plots as non-repeated measures when used in species and period comparisons and as repeated measures in all other cases.

Prey Selectivity

The number of focal samples per species were as follows: whimbrel, $N=29$; willet, $N=23$; ruddy turnstone, $N=26$; black-bellied plover, $N=27$; Wilson's plover, $N=30$; semi-palmated plover, $N=25$. We observed each bird through a spotting scope for a 10-min period or less if it flew away (minimum=5 min). We documented all successful captures of fiddler crabs by birds that used the 'run/walk and grab' foraging tactic. For each capture, we noted the crab species, sex (male, female, juvenile) and size (large, medium, small).

We used our bird-focal sample data to test for foraging selectivity. We compared the evidence for selective foraging that resulted from a 'pre-approach' and a 'post-approach' measure of prey availability. The pre-approach measure was used to estimate the number of crabs above-ground when no predator was present. The post-approach measure was equal to the number of crabs above-ground after they had responded to the approaching predator (as described above). Both tests

Table I. Number of fiddler crabs present above-ground before and after exposure to a model predator

Crab species	Period	Crab type					
		Male		Female		Juvenile	
		Before	After	Before	After	Before	After
<i>U. princeps</i>	1	88	8	58	7	74	4
	2	120	18	37	5	61	11
	3	138	23	9	3	41	7
<i>U. stenodactylus</i>	1	49	4	85	6	93	11
	2	123	17	86	4	166	17
	3	111	23	54	7	127	7

Experiments were conducted over three time periods, on two crab species. Values represent total counts for 50 trials, 25 with a walking and 25 with a running model.

compared the ratio of crab classes (male, female and juvenile) that were caught with those that were available using a log-likelihood ratio chi-square test for contingency tables.

RESULTS

Prey Availability

Fiddler crabs responded differently to the approach of a model predator depending on their sex, age, species, and the tidal phase (Tables I and II; Fig. 1). The relative abundance of male, female and juvenile crabs present before we introduced a model predator differed from those remaining above-ground once a model predator had approached. Prey responses were also temporally dependant, and differed between fiddler crab

species. There was no difference in crab responses to walking versus running bird models, and it therefore appears justifiable to ignore the predator's speed in a measure of prey availability.

There were three significant higher-order interactions between pairs of factors (Table II; Fig. 1). The first of these interactions (tide and crab type) indicated that males were more likely than females to risk detection on a flooding tide. The second interaction (tide and species) showed that both species took equal risks on ebb tides, but *U. princeps* were more cautious than *U. stenodactylus* during low and flood tides. The third interaction (crab type and species) showed that male *U. princeps* were more likely to risk detection than females or juveniles of this species.

Prey Selectivity

Table III presents the numbers of crabs caught by all six bird species during 160 focal samples. These counts were used in two tests of prey selectivity: first using the pre-approach measure of prey availability (number of crabs above-ground) and then using the post-approach measure suggested here (see Methods). The measure of prey availability used did not affect the results of the prey selectivity tests for *U. stenodactylus* when all bird species were included in the analysis. In both tests, the ratio of male, female and juvenile *U. stenodactylus* caught did not differ from the ratio of those available (pre-approach test: $\chi^2_2 = 5.26$, $P = 0.07$; post-approach test: Table III). Therefore there was no evidence, by either

Table II. Mixed MANOVA on the responses of fiddler crabs to a model predator

Source	<i>F</i>	<i>df</i>	<i>P</i> (two-tailed)
Approach speed	2.63	1	0.11
Tide	6.31	2	<0.01
Crab type	9.94	2	<0.01
Species	49.65	1	<0.01
Tide and crab type	14.27	4	<0.01
Tide and species	13.90	2	<0.01
Crab type and species	33.42	2	<0.01

$N = 25$ counts in each smallest sub-category (total = 1800 counts). First- and second-order interactions are presented. Higher-order interactions were non-significant.

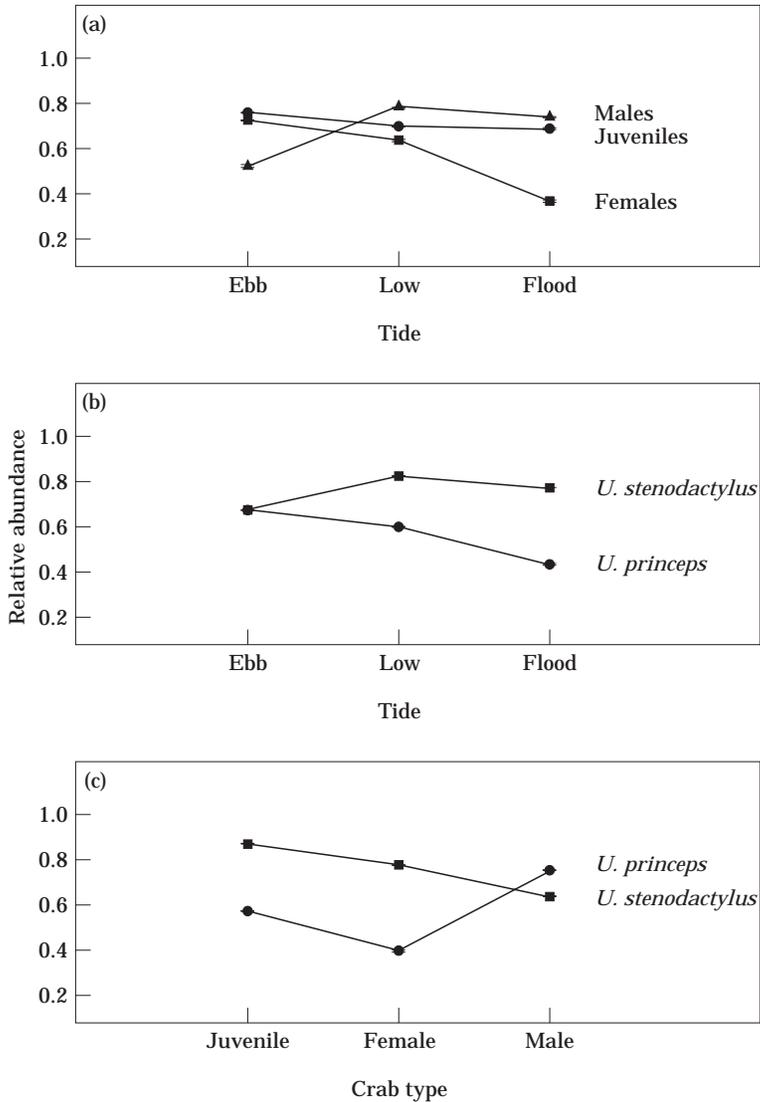


Figure 1. Second-order interactions showing the changes in relative crab abundance (proportion of individuals remaining on the surface after model approach) with respect to (a) tide and crab type, (b) tide and species and (c) crab type and species.

measure, of selective foraging on this species. However, this was not the case for *U. princeps*: both the pre- and post-approach tests indicated a significant difference between the ratios of caught and available crabs (pre-approach test: $\chi^2_2=97.23$, $P<0.01$; post-approach test: Table III). Male *U. princeps* were under-represented in the population of caught crabs, and were therefore sometimes being passed over when encountered by birds.

It is possible that male *U. princeps* were avoided in favour of more profitable prey. However, because they were the largest crabs available to the birds, it is equally possible that they were avoided because some birds were physically incapable of consuming them. By examining the data on all *U. princeps* that were caught (Table IV), it is clear that the smaller bird species were not eating male *U. princeps*. The two largest bird species, willets and whimbrels, ate male *U. princeps*. It was

Table III. Number of fiddler crabs caught by all bird species during 160 focal samples; and chi-square test results for the number of crabs caught against the number available using post-approach prey availability measures (Table I)

Crab species	Period	Crab type			χ^2	df	P
		Male	Female	Juvenile			
<i>U. princeps</i>	1	4	15	44	18.44	2	<0.01
	2	12	20	38	13.86	2	<0.01
	3	11	10	21	14.55	2	<0.01
<i>U. stenodactylus</i>	1	4	2	12	1.91	2	0.39
	2	6	2	10	0.70	2	0.71
	3	6	2	5	1.90	2	0.39

therefore possible to test for selective foraging by these two species. The test based on the pre-approach measure of prey availability indicated that willets and whimbrels did not catch male, female and juvenile *U. princeps* in the proportions at which they were available ($\chi^2_2=11.07$, $P=0.004$); they sometimes overlooked males. When using the post-approach measure of prey availability, however, we found no evidence for foraging selectivity: willets and whimbrels caught crabs in the proportions at which they were available (Table V).

Table IV. Number of *U. princeps* caught by each bird species during 160 focal samples

Bird species	Crab type		
	Male	Female	Juvenile
Willet	16	10	11
Whimbrel	7	10	11
Black-bellied plover	0	3	12
Ruddy turnstone	3	6	12
Wilson's plover	1	15	32
Semipalmated plover	0	1	25

DISCUSSION

Prey Availability

Shorebirds foraging on intertidal mudflats are clearly not surrounded by the enormous number of prey items superficially apparent. Because we lack a shorebird's perception (Hutton 1990), we cannot reliably determine how it experiences its world (Wolda 1990). Recent work, however, is yielding a more realistic picture of prey availability. This is largely due to the recognition, by a number of authors, that prey availability is a dynamic, changing property of the predator's environment (e.g. Charnov et al. 1976; Zwarts 1990; Ens et al. 1993; Kalejta 1993; Anholt & Werner 1995; Skutelsky 1995; Luo et al. 1996). The importance of viewing prey availability from the perspective of the prey has also improved our understanding of selective foraging (Zwarts & Wannink 1989; Wolda 1990; Kersten et al. 1991; Ens et al. 1993; Thetmeyer & Kils 1995). A particularly significant contribution was that of Ens et al. (1993), who equated prey availability with the performance of risky behaviour by fiddler crabs. The present study adds

Table V. Number of fiddler crabs caught by willets and whimbrels during 52 focal samples; and chi-square test results for the number of crabs caught relative to the number available (χ^2 ; Table I)

Crab species	Period	Crab type			χ^2	df	P
		Male	Female	Juvenile			
<i>U. princeps</i>	1 (ebb)	4	6	4	0.68	2	0.71
	2 (low)	9	9	12	4.01	2	0.14
	3 (flood)	10	5	6	3.16	2	0.21

to previous work by (1) providing the first empirical evidence showing how misleading foraging-selectivity test results can be when inaccurate measures of prey availability are used and (2) providing a practical method for measuring prey availability in prey animals, such as fiddler crabs, that are able to detect and evade predators.

Fiddler crabs need to leave the safety of their burrows for feeding and courtship, thereby exposing themselves to predators. When a predator approaches, most crabs run to their burrow entrances. Some individuals descend to the terminal burrow chamber, some retreat to just within the burrow shaft, and others remain on the surface thereby risking detection and attack. Any response to a potential predator is costly for a fiddler crab because it represents lost time for feeding and courting: time that is already limited by the tidal inundation cycle. Shorebirds are often constantly present on the mudflat, and it is therefore not surprising that some fiddler crabs will risk detection by a predator in order to limit the time they spend in their burrow. The balance an individual strikes between the costs and benefits of retreating into its burrow when it detects a potential predator determines its availability to foraging shorebirds (see [Ens et al. 1993](#)).

The present study demonstrates that prey availability depends on the responses of prey animals to the presence of their predators. Consequently, any measure of prey availability in the absence of predators is inaccurate. The study also indicates that prey availability depends on a complex set of prey behaviour. First, males were more likely than females to risk detection on a flooding tide. Because mate choice occurs during the flooding tide ([Zucker 1976](#); [Christy 1980, 1983, 1988](#); [Backwell & Passmore 1996](#)), the benefit to males of sexually displaying is greatest at this time. It therefore appeared that males took more risks when the potential benefits from risky behaviour were greatest. Second, there were important behavioural differences between crab species. Both species studied here took equal risks on ebb tides, but *U. princeps* were more cautious than *U. stenodactylus* during low and flood tides. Third, male *U. princeps* were more likely to risk detection than females or juveniles of this species, which is not surprising given the low profitability of these individuals (see below).

Prey Selectivity

Selective foraging is indicated when there is a discrepancy between the prey that is available to the predator and the prey it actually eats. It is possible, however, for such a discrepancy to arise in the absence of selective foraging. When predators consistently avoided prey animals above a certain size, we were unable to determine whether rejection was due to the inability of predators to handle and swallow such large prey, or because their profitability was comparatively low. An animal that is too large for a predator to consume cannot strictly be considered potential prey. Our inability to determine the upper limit of prey size that a predator is capable of consuming thus restricts our ability to detect foraging selectivity in those cases where the largest prey items are the ones avoided. The present study clearly demonstrates this point. Male *U. princeps* were seldom eaten by small and medium sized birds, giving them an overall advantage in terms of lowered predation probability. Because they were the largest prey animals available to the foragers, the test was unable to determine whether the small- and medium-sized birds selectively avoided male *U. princeps* due to their low profitability, or whether these birds were unable to kill and eat such large prey. However, the two largest bird species, willets and whimbrels, ate all classes of *U. princeps*, and all bird species were capable of consuming all classes of *U. stenodactylus*. These two prey-selectivity tests could therefore potentially detect the selective rejection of crabs based on their low profitability. Both tests, however, failed to show selectivity: willets and whimbrels caught male, female and juvenile *U. princeps* in the proportions at which they were available; and the ratio of male, female and juvenile *U. stenodactylus* caught by all bird species did not differ from the ratio of those available. There is therefore no compelling evidence for selective foraging on *U. stenodactylus* by any of the bird species, or on *U. princeps* by the two largest bird species we studied. Male *U. princeps* clearly have an advantage in terms of vulnerability to predation. The smaller birds are either incapable of killing and eating male *U. princeps*, or are avoiding doing so because of their low profitability. Those bird species large enough to be able to kill and eat male *U. princeps* do so in proportion to their availability.

Sex-biased Predation on Fiddler Crabs

In fiddler crabs, profitability is thought to be closely linked to their pronounced sexual dimorphism. Males are generally larger than females (Crane 1975), have thicker, less digestible exoskeletons (Zwarts & Blomert 1990), and have an enlarged claw which can be a powerful weapon. Furthermore, many shorebirds do not eat the claws of large fiddler crabs (Bildstein et al. 1989; Ens et al. 1993), and therefore need to expend time and energy in shaking the claw loose before consuming the crab body. Bildstein et al. (1989) suggested that the fiddler crab claw conferred some protection against predation. Captive ibises were given a simultaneous choice between male and female crabs, or between a male with its claw removed and an intact male. Birds showed a preference for the crabs without the claw. Choosing between two simultaneously presented prey items, however, is clearly not equivalent to choosing whether or not to catch a prey item encountered on the mudflat (see Backwell & Jennions 1993). Rejecting an encountered crab while foraging naturally on the mudflat involves a cost (in terms of lost foraging opportunity). Rejecting a prey item in favour of one presented simultaneously has no such associated cost. While birds may prefer to eat clawless crabs (Bildstein et al. 1989), this preference does not appear to outweigh the costs of rejecting an encountered prey item in the species studied here.

The enlarged claw of male fiddler crabs is considered a classic, sexually selected trait (Darwin 1871; Anderson 1994) that benefits individuals both in courtship and territorial conflicts (Crane 1975; Christy 1980; Backwell & Passmore 1996; but see Murai et al. 1996). Sexually selected traits offer their bearers a reproductive advantage, often at the expense of survival (Darwin 1871; Zahavi 1975; Gould & Gould 1989; Anderson 1994). This, however, may not be the case in fiddler crabs. The results of our study do not indicate that the enlarged claw reduces a male's fitness in the predation context. Hence predation risk probably does not influence the size of male fiddler crab claws.

Conclusion

The availability of fiddler crabs to foraging shorebirds has been inaccurately measured in the

past, and this may have led to the incorrect assessment of foraging selectivity studies. This work is the first to show that foraging selectivity tests are so sensitive to measures of prey availability that they can indicate active selectivity when there is no evidence of this using a more accurate measure of prey availability. This paper is also the first to provide a practical method of measuring fiddler crab availability for future studies.

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