

COMPETITIVE MATING, MATE CHOICE AND MATING ASSOCIATIONS OF BRACHYURAN CRABS

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ABSTRACT

The mating associations of brachyuran crabs are reviewed and classified according to apparent modes of competition among males for mates. Males obtain mates in three general ways: they may compete directly for females and then defend them for relatively long periods before mating (female centered competition), they may compete for resources females use during breeding or refuges they occupy (resource centered competition), or they may search for or intercept receptive females but defend neither females nor resources (encounter rate competition). Male modes of competition for females are influenced by patterns of predation, competitor density, female density, distribution, mobility, habitat requirements for breeding and mate choice. Some form of mate guarding, multiple copulations and sperm plugs occur in nearly every type of mating association. Sperm competition may be common in brachyurans and may have a pervasive influence on male competitive tactics.

A major goal of those interested in the evolution of mating behavior is to understand how sexual selection leads to differences in mating associations (the spatial and temporal relationships between the sexes that result from social interactions and lead to mating) in different species. Classification of the mating associations exhibited within a group is useful for summarizing the diversity of mating behavior and for spotting trends in how sexual selection operates. Choice of a classificatory scheme is important as the criteria used to sort species' mating associations into types reflect judgments about which differences are superficial and which arise from fundamental contrasts in the way males compete for females and how females choose mates.

In this paper I will review and classify mating associations in brachyuran crabs. The scheme employs criteria which focus attention on ecological and social determinants of male mating behavior (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977). It is appropriate to stress male mating behavior because how males compete for mates largely determines the spatial and temporal relations between the sexes. Female interests, as reflected in female mate choice and control of receptivity, can have profound effects on how males compete (Borgia, 1979; Knowlton and Greenwell, 1984; Parker, 1984; Thornhill and Alcock, 1983). Therefore, I will also discuss how female crabs may choose among competitors in each type of mating association.

Reviews of courtship and mating behavior in crabs by Hartnoll (1969), Hazlett (1975a), Ridley (1983) and Salmon (1983), each with a slightly different focus, stimulated many of the ideas I develop here and provided numerous references. Field studies of sufficient depth and scope to permit clear judgments about modes of mating are few or lacking for most families. I will focus on these (mostly recent) studies when possible.

MATING ASSOCIATIONS IN BRACHYURAN CRABS

I distinguish eight kinds of mating associations in brachyuran crabs that fall into three general categories (Table 1). Males may (1) search for or attract individual receptive females that they defend directly from other males, (2) defend resources that females require for breeding or survival and mate with the females

Table 1. A classification of mating associations of brachyuran crabs based on modes of competition among males for females with comments on modes of female choice

I. Female centered competition
A. <i>Defense of mobile females following free search.</i> Males search for and aggressively defend mobile females that release water-borne pheromones. Prolonged (days) mate guarding. Females advertise their sexual receptivity for long periods leading to intense competition among males for females and resulting in female choice of large dominant males that may provide protection or genetic benefits.
B. <i>Defense of sedentary females following restricted search.</i> Males patrol but do not exclude other males from limited areas that contain refuges (or hosts for symbionts) occupied by females. Large (dominant) males temporarily defend receptive females for one or more days. Females may avoid patrolling males or resist courtship attempts, thereby controlling the timing of mating and which males they accept as mates.
C. <i>Capture, carrying and defense of females at protected mating sites.</i> Males may guard females for several days. Females may avoid or aggressively resist capture and thereby choose large aggressive males that search effectively.
D. <i>Attraction and defense of females at protected mating sites.</i> Guarding may last several days. Females are free to choose males on the basis of location and courtship signals.
II. Resource centered competition
A. <i>Defense of breeding (mating and incubation) sites.</i> Males compete directly for sites (burrows) where females mate and incubate eggs. Males also compete indirectly by using signals to attract mobile receptive females. Resource defense while the sexes are associated is functionally equivalent to mate guarding and may last one or more days. Females choose mates on the basis of resource quality and courtship signals.
B. <i>Defense of refuges.</i> Males defend areas containing refuges (or hosts) which are occupied by females. Males may guard females directly during brief mating associations. Females may resist copulation attempts and thereby exercise some choice of mates.
III. Encounter rate competition
A. <i>Neighborhoods of dominance.</i> Mobile males interact aggressively with others in shifting areas (neighborhoods) where they search for, court and mate with females. Males may defend their mates during copulation. Females may avoid males or resist copulation attempts by some males.
B. <i>Pure search and interception.</i> Males seek mates freely or establish temporary sites from which they intercept and court mobile females. Temporary mate guarding may occur. Females may end courtship sequences by fleeing or resisting aggressively.

associated with these resources, or (3) compete in ways that maximize the rate they encounter females but neither defend females nor resources. Certain kinds of mating associations appear to be typical of certain families of the Brachyura while other families may exhibit diverse associations (Table 2). I next describe the eight kinds of mating association and give selected examples of each.

Female Centered Competition

Direct Defense of Mobile Females.—Male portunid and cancrinid crabs typically search for and aggressively defend females for several days immediately before a female's seasonal molt (Cancridae) or her molt to maturity (Portunidae). Mating occurs soon (minutes to hours) after the female molts. Males may continue to guard their mates for several days after mating. Females may use sperm from a single mating to fertilize their seasonal or lifetime production of eggs. There is strong evidence for the portunids (Ryan, 1966; Christofferson, 1978; Gleeson, 1980; Gleeson et al., 1984; but see Teytaud, 1971) and indirect evidence for the cancrinids (Kittredge et al., 1971; Eales, 1974) that females release a water-borne pheromone in their urine several days before they molt which stimulates search and courtship behavior in males. Males typically pass seminal products during

copulation that form sperm plugs which disappear from the female's vulvae and vaginae days or weeks later when ovulation occurs.

This kind of mating association has not been studied in the field. Aspects of the general ecology and breeding biology of the species that mate in this way suggest the following speculations regarding the ecological and social contexts leading to direct defense of mobile females by males.

Portunid and cancrid crabs are relatively large, mobile, aggressive, predators or omnivores. Female mobility, infrequent mating, sperm storage and the production of more than one clutch from a single mating may make receptive females a rare and unpredictable resource in space and time. This may preclude most modes of mate competition other than free search. In the field, males probably find sexually receptive females by moving up-current when they detect the pheromone that females begin to release several days before they copulate. The pheromone has not been identified for any species. Kittredge et al. (1971) presented evidence that crustecdysone stimulates search or premating behavior in *Pachygrapsus crassipes*, *Carcinus antennarius* and *C. anthonyi*. Methodological problems with this study (Dunham, 1978) make this conclusion equivocal. In addition, Eales (1974) found that the sex pheromones of *Carcinus maenas* and *Macropipus holsatus* are species specific. Finally, Gleeson et al. (1984) found no evidence that crustecdysone or structurally related compounds are effective as sex pheromones in *Callinectes sapidus*.

Grafen and Ridley (1983) presented a model of the selective dynamics leading to mate guarding in crustaceans from the male's point of view that would seem to explain why portunid and cancrid crabs mate as they do (Ridley, 1983). The model begins with the assumption that mating is possible only during a brief period. Two kinds of males compete for females: those that stay and mate with females only during their short period of anatomical receptivity and those that can sense when a female will mate in the future and then wait with the females they encounter for a period of time before mating. Males that follow the "wait and mate" strategy usually will mate more often than those that don't because they will spend less time searching to find an acceptable female. The time spent waiting with and guarding a female will be a function of the density of females, how often they mate, the degree of reproductive synchrony among them, and the density and behavior of competitors (Grafen and Ridley, 1983). While attractive, this model ignores how selection on females due to the possible costs and benefits of being guarded may lead to female control of which males guard them, when and for how long.

The adaptive value to females of releasing pheromones that attract potential mates is not known. Such signaling may function to ensure that a searching male will have found the female when she is ready to copulate. But females begin to attract males from about one to three weeks before they mate. Why do females become sexually attractive so long before they mate? When several crabs of both sexes are held together in tanks, males compete aggressively for receptive females. Large males win fights for females and do most of the mating [e.g., *Cancer pagurus*, Edwards (1966); *Carcinus maenas*, Berrill and Arsenault (1982)]. Prolonged advertisement of behavioral receptivity before mating may be a mechanism leading to female choice of particularly large and aggressive males as mates. What might females gain by mating with large males? While it seems obvious that a large male might better protect a female during and after her molt than a small male, field observations indicate that molting and mating in some species may occur in places that provide considerable physical protection [*Carcinus oregonensis* (Knudsen, 1964); *Carcinus maenas* (Berrill and Arsenault, 1982)] making additional pro-

Table 2. Mating associations of brachyuran crabs sorted according to the probable mode of competition among males for females (Table 1)

Mating association	Taxon	References	
Female centered competition			
<i>Search and defend</i>	Corystidae		
	<i>Corystes cassivelaunus</i>	Hartnoll (1968).	
	Portunidae		
	<i>Carcinus maenas</i>	Crothers (1967, 1968); Eales (1974); Berrill (1982), Berrill and Arsenault (1982); Jensen (1972).	
	<i>Portunus sanguinolentus</i>	Ryan (1966); Christofferson (1978).	
	<i>Portunus pleagicus</i>	Fielder and Eales (1972).	
	<i>Callinectes sapidus</i>	Van Engle (1958); Teytaud (1971); Gleeson (1980, Gleeson et al., 1984).	
	Cancridae		
	<i>Cancer oregonensis</i>	Knudsen (1964).	
	<i>Cancer productus</i>	Knudsen (1964).	
<i>Cancer magister</i>	Butler (1960); Knudsen (1964); Snow and Neilson (1966).		
<i>Cancer irroratus</i>	Elnor and Stasko (1978); Elnor and Elnor (1980).		
<i>Cancer borealis</i>	Elnor et al. (1985).		
<i>Cancer pagurus</i>	Edwards (1966).		
<i>Patrol and defend</i>	Majidae		
	<i>Inachus phalangium</i>	Wirtz and Diesel (1983); Diesel (1986a, 1986b).	
<i>Capture and defend</i>	Xanthidae		
	<i>Cataleptodius floridanus</i>	Hazlett (1975b); Hazlett et al. (1977); Engstrom and Lucenti (1984)	
	<i>Neopanope sayi</i>	Swartz (1976a, 1976b, 1978).	
	Ocypodidae		
	<i>Dotilla mictyrodies</i>	Tweedie (1950).	
	<i>Scopimera globosa</i>	Yamaguchi and Noguchi (1979); Wada (1981, 1983).	
	<i>Uca deichmanni</i>	Zucker (1983).	
	<i>Uca stenodactylus</i>	Crane (1975); Christy (unpublished).	
	<i>Attract and defend</i>	Ocypodidae	
		<i>Macrophthalmus japonicus</i>	Wada (1984).
<i>Ilyoplax pusillus</i>		Wada (1981, 1983).	
<i>Ocypode ceratophthalmus</i>		Barrass (1963); Hughes (1966, 1973); Jones (1972); Brooke (1981).	
<i>Ocypode saratan</i>		Linsenmair (1967).	
<i>Ocypode ryderi</i>		Vannini (1976, 1980a, 1980b).	
<i>Ocypode kuhlii</i>		Jones (1972).	
<i>Ocypode guadichaudii</i>		Crane (1941).	
<i>Uca musica</i>		Zucker (1984).	
Resource centered competition			
<i>Breeding site defense</i>	Gecarcinidae		
	<i>Gecarcoidea natalis</i>	Hicks (1985).	
	<i>Gecarcinus lateralis</i>	Abele et al. (1973); Klassen (1975); Bliss et al. (1978).	
	<i>Cardisoma guanhumi</i>	Gifford (1962); Henning (1975).	
	Ocypodidae		
	<i>Uca pugilator</i>	Salmon (1965); Hyatt (1977); Christy (1980, 1982, 1983).	
	<i>Uca rapax</i>	Greenspan (1980).	
	<i>Uca tangeri</i>	Muller (1983).	
	<i>Uca lactea</i>	Yamaguchi (1971); Murai and Goshima (1987).	

Table 2. Continued

Mating association	Taxon	References
Refuge defense	Xanthidae	
	<i>Trapezia</i> sp.	Huber (1985).
	<i>Menippe mercenaria</i>	Cheung (1968); Savage (1971); Sinclair (1977).
	Grapsidae	
	<i>Pachygrapsus transversus</i>	Abele et al. (1986).
	<i>Sesarma reticulatum</i>	Seiple and Salmon (1982).
Encounter rate competition		
Neighbor- hoods	Grapsidae	
	<i>Helice crassa</i>	Beer (1959); Nye (1977).
	<i>Aratus pisoni</i>	Warner (1967, 1970).
	<i>Goniopsis cruenata</i>	Schöne and Schöne (1963); Warner (1970).
	Ocypodidae	
	<i>Hemiplax latifrons</i>	Griffin (1968).
	<i>Heloecius cordiformis</i>	Griffin (1968).
	<i>Uca vocans</i>	Nakasone et al. (1983); Salmon (1984).
	<i>Uca thayeri</i>	Salmon (1987).
Search/inter- ception	Grapsidae	
	<i>Hemigrapsus oregonensis</i>	Knudsen (1964); Lindberg (1980).
	<i>Hemigrapsus nudus</i>	Knudsen (1964).
	<i>Grapsus grapsus</i>	Kramer (1967).
	<i>Sesarma cinereum</i>	Seiple and Salmon (1982).
	<i>Pachygrapsus crassipes</i>	Hiatt (1948); Bovbjerg (1960).
	Ocypodidae	
	<i>Macrophthalmus hirtipes</i>	Beer (1959).
	<i>Scopimera proxima</i>	Silas and Sankarankutty (1967).

tection by the male redundant or unnecessary. *Corystes cassivelaunus* do not mate when the female molts and is vulnerable (Hartnoll, 1968). Yet there appears to be especially strong sexual selection favoring mate guarding and associated male behavior and morphology (large chelae). Perhaps male size and aggressive ability in these crabs are correlated with genetic determinants of reproductive or general fitness; females that mate with large dominant males may produce especially fit offspring.

Costs to females of being guarded before mating have not been documented in the field. They might include a reduction in mobility and, hence, foraging efficiency and the ability to escape predators (Parker, 1984). Such costs would produce selection on females to control the ability of males to predict when they will mate. The length of precopulatory guarding periods would reflect a balance between the time dependent increase in the costs to females of being guarded and in any fitness gains due to an increase in the probability that the female is guarded by a dominant (high quality?) male when ready to mate.

Two features of courtship signaling in portunid crabs indicate that pair formation and the duration of precopulatory mate guarding may be largely controlled by females. First, Christofferson (1978) demonstrated that female *Portunus sanguinolentus* can control release (under unnatural conditions) of their sex pheromone and attractiveness to males. Regulation of pheromone release may also occur in *Callinectes sapidus* (Gleeson, 1980). Second, visual displays by one or both sexes precede pair formation in both *P. sanguinolentus* (Ryan, 1966) and *C. sapidus* (Teytaud, 1971) suggesting that females may be able to control which among the males that find them they accept as guards and mates. When field studies of mating in portunid and cancrid crabs have been done, a modification

of Ridley's "male interests" model that includes some of the "female interests" outlined here probably will be most useful.

Patrolling and Direct Defense of Sedentary Females.—A recently completed study of the breeding ecology and mating behavior of the spider crab *Inachus phalangium*, a symbiotic associate of the anemone *Anemonia sulcata*, has provided an exceptionally clear and complete description of this kind of mating association (Wirtz and Diesel, 1983; Diesel, 1986a; 1986b). Other spider crabs may exhibit similar reproductive behavior (e.g., *Libinia emarginata*, Hinsch, 1968). This kind of mating association may be relatively common among symbiotic crabs and other species in which females have a very limited home range.

At Diesel's study site on the Mediterranean coast of France *Anemonia sulcata* occurs in clumps or as single large individuals among boulders on a sand bottom. Following their terminal molt to maturity female crabs move only rarely among anemones, while males move frequently. During their 8 months of adult life, females produce about six clutches of eggs, ovulating immediately after each clutch hatches. Large males patrol areas containing two to eight adult females but do not defend territories. When a male encounters an adult female he probes her clutch with his chelae. If her eggs will hatch within 1 to 2 days, the male copulates, aggressively guards the female, copulates a second or third time immediately before the eggs hatch and then leaves. Sperm from the last copulation before the female ovulates fertilizes her eggs. Males apparently learn both the locations of the females in the area they patrol and the timing of the reproductive cycle of each, arriving at each female about 1 day before her eggs hatch.

Large males aggressively displace small males from females, are more often found with females about to release larvae than are small males, and obtain about 80% of all matings. Females are anatomically capable of mating any time. They do not advertise their sexual receptivity as a way of choosing mates but they may aggressively resist attempted copulations by smaller males that try to mate when dominant patrolling males are elsewhere.

Females occur in spatially predictable patches, move little, and breed asynchronously and continuously. Male competitive ability is largely determined by size. There is a large size range of adult males due, presumably, to individual differences in growth before the terminal molt. Large adult males have, locally, relatively few equally competent competitors for a spatially and temporally predictable resource. Together, these features favor direct aggressive monopolization of females in both space and time by dominant males. Intense predation has probably favored patrolling over territoriality due to the high risks associated with the behavior necessary for males to exclude all others from anemones containing females within their home range.

Capture and Direct Defense of Females.—Males of at least one xanthid and four ocyropodid crabs (Table 2) obtain mates by aggressively overpowering passing or nearby females and carrying them into burrows where they may guard them for a time before mating. Male *Scopimera globosa* will attempt to capture juvenile and adult crabs of all sizes and either sex, and even other species (Yamaguchi and Noguchi, 1979). Males of the other species seem to be more discriminating but do not distinguish receptive from non-receptive females. Females usually attempt to avoid capture and they struggle aggressively when caught, perhaps leading to female choice of relatively large and aggressive males. Male *S. globosa* fight for females carried by other males and may win both the female and the other male's burrow.

The conditions favoring this kind of mate acquisition behavior are unclear. All species tend to occur at high densities. Female *Scopimera*, *Dotilla*, *Uca deichmanni* and *U. stenodactylus* are highly mobile but female *Cataleptodius floridanus* are not (Hazlett, 1975b). Female *C. taboganus*, a close relative of *C. floridanus* that occurs on the Pacific coast of the tropical Americas, breed synchronously (Christy, 1986). The same may be true of *C. floridanus* and the ocypodids since other intertidal estuarine species in the family have strong reproductive cycles (Forward, 1987). Synchronous sexual receptivity among the females in a local population may reduce the chance that a male will find a second receptive female after mating with a first each breeding cycle. If only a portion of the female population breeds each cycle, then this might lead to intense selection on males to find receptive females and to guard them, thus assuring their paternity for at least one clutch. Still, it is not clear why males forcibly capture and carry females rather than use courtship signals to attract females to mating sites, as do some fiddler crabs that share these reproductive characteristics.

Attraction and Direct Defense of Females at Mating Sites.—Several species of ghost crabs (*Ocyopode*) mate in burrows males dig on open sand beaches. Males in some species mark the location of their burrow entrance with a pile (“pyramid”) of sand (Vannini, 1980a) which may be an optical courtship signal (Linsenmair, 1967). Males may also produce acoustic signals to attract females to their burrows (Horch and Salmon, 1969). Male *O. ceratophthalmus* compete for burrows located high on the beach, presumably because burrows there persist longer than those closer to the water (Brooke, 1981). Large males win fights for burrows and court for longer periods from high burrows and where burrows are most dense. Burrow construction, competition for burrows, courtship and breeding follow a lunar cycle. No successful courtships have been seen despite intensive study of this and other species. Few pairs have been found in burrows. Females apparently do not incubate eggs in the burrows in which they mate. The basis of mate choice is unknown but probably includes differential responses by females to courtship signals.

Female ghost crabs are highly mobile, sometimes moving hundreds of meters during a single feeding bout. They also seem to mate only rarely. To a male ghost crab, receptive females must be highly unpredictable in space and time. Territoriality, patrolling, free search, or interception strategies apparently are all too dangerous and/or costly in time and energy for males. Instead they advertise their readiness to mate with signals sent from a fixed position—a mating site. There is no evidence that defended mating sites differ qualitatively in ways that might affect female reproductive success leading to choice based on burrow characteristics or location. Males apparently do not compete for burrows females prefer. This mode of mate competition appears to be centered on females rather than resources. Surface matings have been seen in some species (Hughes, 1973) (their frequency relative to matings in burrows is not known) which indicates mating burrows are not an important resource for females.

Resource Centered Competition

Defense of Breeding Sites.—Males of some species of fiddler crabs (genus *Uca*) dig, court from and defend burrows to which females come for mating and in which they oviposit and may remain to incubate their eggs. Males guard their mates underground for one to several days until they have produced a clutch of eggs. Sexually receptive females respond sequentially to visual and acoustic courtship signals of several males before choosing their mates. Female choice appears

to be based primarily on the quality of the burrows males defend as breeding sites. Some gecarcinids also use burrows constructed by males as mating and breeding sites (Table 2).

I have discussed the selective factors that may lead to this kind of mating association elsewhere (Christy, 1980; 1983; Christy and Salmon, 1984). In brief, male defense of breeding sites arises when females require access to specific microenvironments in order to breed successfully and when they are unable to create or defend such sites themselves because they must move freely to maintain their foraging efficiency. High population (competitor) densities coupled with female mobility and breeding site requirements has led to resource-defense behavior in males. Males fight for the opportunity to court females from burrows they will choose as breeding sites. Male competitive ability is largely determined by size. Large males court for longer periods from high quality burrows than do small males and when most females will choose mates. Male size and mating frequency are correlated. Males also compete indirectly for females through courtship signaling. The importance of competitive courtship signaling as a selective context contributing to differential reproductive success among males has not been well studied. This kind of mating association is known only for terrestrial and semi-terrestrial species. Perhaps sites suitable for oviposition and egg development are especially rare in intertidal and terrestrial habitats.

Defense of Refuges.—This kind of mating association differs from the former in two important respects. First, males defend sites that may be used by both breeding and non-breeding females as refuges from predators and environmental extremes and as feeding sites. Second, female choice of mates is only contingent upon choice of refuges. Abele, Campanella and Salmon's study (1986) of the breeding ecology and behavior of *Pachygrapsus transversus* provides the best example of this kind of mating association.

Pachygrapsus transversus shelters in cracks in intertidal rock surfaces during high tide and during low tide when predators threaten and when rocks are hot and dry. Crabs graze algae adjacent to their crevices and on rocks located lower in the intertidal zone while they are wet during the beginning of the crabs' activity period. Large males maintain territories that include crevices used by several adult females. Territorial males attempt to exclude other adult males from their territories but they are not always successful. Large dominant males obtain about 88% of the matings with the females that occupy crevices on their territory. Females may aggressively resist copulation attempts by some males and thereby exercise mate choice. The identities of females on territories change frequently but crevices are nearly continuously occupied by females that can, anatomically, mate at any time. The location of females is highly predictable to males. These conditions can lead to male monopolization of mates through territorial defense of areas containing refuges and females. But such a strategy of mate acquisition is only possible when males are able to move freely and displace competing males and defend territorial boundaries. *P. transversus* has the behavioral capacity to detect and quickly repulse territory invaders and to avoid predators while doing so.

In general, relaxation of selection pressures that restrict male mobility in patrolling and direct female defense associations could lead to male defense of refuges. I expect this kind of mating behavior may occur when females are relatively sedentary but only when males can behaviorally control access of others to refuges. (Extremely heavy predation pressure might lead patrolling and refuge defense polygyny to female and refuge defense monogamy respectively, which would be difficult to distinguish.)

Table 3. Characteristics (as males may experience them) of the distribution of receptive females for each mating association

Mating association	Spatial distribution			Temporal availability		Comments
	Density	Pattern	Mobility	Individual receptivity	Synchrony	
Female centered						
Search and defend	low	dispersed	high	seasonal, once/life	low	aquatic
Patrol and defend	high	clumped	low	continuous	low	symbiont or movement of females otherwise limited
Capture and defend	high	clumped	low or high	limited (?)*, frequent	high (?)	
Attract and defend	low	dispersed	high	limited, infrequent	moderate	open intertidal habitat
Resource centered						
Breeding site defense	high	dispersed	high	limited, frequent	high	intertidal, female access to breeding sites important
Refuge defense	high	clumped	low or high	continuous, frequent	high (?)	males capable of excluding others from areas containing females
Encounter rate competition						
Neighborhoods	high	dispersed	low	continuous, frequent or limited, infrequent	high or low	breeding sites defensible by females or not important
Free search	low or moderate	dispersed	low or high	limited (?)	high (?)	

* Probable characteristic but no data are available.

Encounter Rate Competition

Mating associations that result from competition among males that maximizes the rate at which they encounter females often are brief and can occur at a variety of locations. This makes them difficult to study. It is likely that I have mistakenly classified some species as encounter rate competitors because so little is now known about how their mating associations form in the field.

Shifting Neighborhoods of Dominance.—Some male grapsid and ocypodid crabs interact aggressively with other males as they move about. Temporary dominance relations may be established wherein small males simply avoid or are displaced from the immediate vicinity of larger aggressive males. Male *Uca vocans* (Salmon, 1984) and *U. thayeri* (Salmon, 1987) appear to compete for mates in this way, though it is unclear exactly how male reproductive success is related to aggressive behavior in either species.

Females of both species defend burrows for several days to weeks around which they feed and in which they breed. Males also fight for and defend burrows. To obtain mates they either "sally" from their own burrows or wander freely and court and mate with females on the surface. Female *U. vocans* are continuously receptive behaviorally and anatomically. On the average about 50% of the females in a local colony mate at least once per fortnight. Female *U. thayeri* can mate

only during brief periods when their vulvar opercula are decalcified; they also mate only rarely as Salmon saw only 5 copulations following 508 courtships during a 3-month study. Males are not territorial but they do displace other males and temporarily defend their mates during copulation. However, females may mate multiply and with several males. Females may aggressively resist attempted copulations but this does not result in choice of large males as mates. Female choice may be based on male courtship tactics.

Pure Search and Interception. — Males of a few species of brachyuran crabs appear to search for or intercept females and attempt to mate with those they encounter. Differences among males in mating success probably result from differences in search efficiency, not from differences in ability to control the access of others to mates through aggressive interactions. Mate guarding, except during copulation, does not occur and females do not advertise their sexual receptivity. These features distinguish this kind of mating association from that exhibited by many portunid and cancrid crabs. Less is known about this mode of competition for mates than any other. *Scopimera proxima* is a possible example.

Silas and Sankarankutty (1967) provide detailed field notes on interactions among *Scopimera proxima* leading to mating. This small (4–6 mm carapace width) ocypodid crab occurs at low densities (2–3 adults per m²) in burrows near the high water mark on protected sand beaches. It feeds on organic mater in the sand around its burrow. Males are slightly smaller than females and are more lightly (cryptically) colored. Males seek mates by wandering and briefly entering the burrows they encounter. Courtship may include touching with the walking legs, grasping with the chelae and rapid movements by the male into and out of the burrow. Mating occurs on the surface near or in the entrance of the female's burrow. Crabs may mate more than once, each copulation lasting up to 6.5 minutes. After mating, males either leave and continue to wander or they dig a burrow close to that of the female where they may remain for an unknown time.

DISCUSSION

I have attempted to identify categories of mating associations in brachyuran crabs that reflect qualitative differences in how males compete for females. Males can, through aggressive interactions, potentially limit access of others to females in both space and time. Modes of competition for mates appear to be related to characteristics of the spatial and temporal distribution of receptive females as they may be experienced by males (Table 3).

When receptive females are relatively uncommon, dispersed, mobile, and mate infrequently and not in tight synchrony, males either search for and defend females that release pheromones or attract them to and defend them at mating sites. Differences in habitat may explain, in part, why these two very different modes of competition have evolved under similar conditions of female abundance and distribution. The attract-and-defend mode occurs in ocypodid crabs that burrow in open sand beaches while the search-and-defend mode occurs in aquatic families that are found in structurally more complex environments. While female ocypodid crabs could advertise their receptivity with visual signals, high predation rates on males that might search for (rare) receptive females on the surface of an exposed beach may have prevented the evolution of search-and-defend behavior in these crabs. The risks of searching for females that release pheromones may be less for the aquatic cancrid and portunid crabs and the benefits of finding and successfully defending a receptive female may be exceptionally great since most females may mate only once per lifetime or reproductive season.

Females appear to be similarly distributed in space in the patrol-and-defend

and capture-and-defend modes but their temporal availability differs greatly. Frequent clutch production by individual females coupled with close breeding synchrony among females may be necessary conditions leading to capture-and-defend behavior. It may pay a male to capture and guard any adult female near the time of a mating peak because there will be a high probability that the guarded female will soon reproduce. Females also are abundant, occur in clumps, breed frequently and (probably) are relatively synchronous in refuge-defense mating associations. As discussed above, the behavioral capacity of males to control access of others to areas containing refuges probably is the key feature that leads to this mode of competition rather than patrol- or capture-and-defend behavior.

Differences in the mobility of females and their ability to gain access to and defend sites suitable for breeding clearly separates breeding-site-defense and neighborhoods-of-dominance mating associations [Christy and Salmon (1984) for a discussion of how these modes of competition differ in fiddler crabs]. Free-search modes of competition are too poorly known to identify relationships between the distribution and abundance of receptive females and male competitive behavior.

The list of kinds of mating associations in brachyuran crabs will surely expand as more field studies of the breeding ecology and behavior of crabs are done. For example, lekking behavior and male resource gathering, kinds of mating associations known in most other major taxonomic groups, are as yet unknown in crabs. The categories themselves will change as understanding of how sexual selection affects modes of mate competition and choice in crabs improves (e.g., for birds, compare Selander, 1972; Brown, 1975; Wittenberger, 1981).

Research on crab mating associations has the potential to contribute importantly to two topics I have only touched on here: how sperm competition affects the competitive tactics of males that obtain mates in different ways and the evolution of conditional (Dawkins, 1980) mating strategies. Most female brachyuran crabs may have the capacity to store sperm and produce more than one fertile clutch from a single mating. The extent to which they do so in the field is poorly known. If common, this would tend to skew the operational sex ratio (Emlen and Oring, 1977) toward males and intensify competition among males for mates. It may also explain why multiple copulations, postcopulatory mate guarding and sperm plugs, all male tactics that may increase assurance of paternity, are relatively common among crabs.

Studies of mating behavior of *Uca* and other ocypodid crabs suggest a level of flexibility in how mating associations are formed that challenge any classificatory scheme. For example, male *Uca vocans* search for and mate with females on the surface near their burrows in relatively low density colonies in Australia (Salmon, 1984). In Japan, at sites where crabs are dense, males may either court from, defend and attract females into burrows for mating or mate on the surface as they do in Australia (Nakasone et al. 1983). *Macrophthalmus japonicus* (Wada, 1984), *Scopimera globosa* (Yamaguchi and Noguchi, 1979), *Uca lactea* (Yamaguchi, 1971; Murai and Goshima 1987) and *U. beebei* (Christy, unpublished) may also mate on the surface or in burrows males defend at the same time and site. Local ecological conditions and relative male size and competitive ability both appear to affect how males compete for females. Questions about how selection might lead to flexibility in the criteria females use to choose mates, which must underlie flexibility in male mating behavior, have yet to be asked.

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