The Effect of Cannibalism on the Demography and Activity of a Natural Population of Desert Scorpions

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Summary. 1. Cannibalism was studied over a five year period in a natural population of the scorpion, *Paruroctonus mesaensis*. Conspecifics are the fourth most frequent prey item and represent about nine percent of the diet; however when prey are ranked according to biomass captured, conspecifics are the number one diet item and constitute over twenty-five percent of all diet biomass. Cannibalism is a function of age, sex, size, time of year, scorpion density and level of available interspecific prey.

2. Several features of the population dynamics of *P. mesaensis* can be explained by cannibalism. Under natural conditions and in experimental enclosures, the mortality rate due to cannibalism increases with density and thus cannibalism is capable of producing population regulation.

3. Several behavioral characteristics function to decrease cannibalism: temporal and spatial aggregation of newborn animals; differential foraging phenology of subordinate scorpions; use of micro-habitat refuges by young animals; and components of male mating behavior.

4. It is suggested that cannibalism is potentially the most effective and homeostatic self-regulatory agent. There are several individual and group benefits which accrue to a population of cannibalistic individuals. Cannibalism is capable of contributing to the long term stability and persistence of populations.

Introduction

The potential for density-dependent regulation of population numbers by intraspecific interference has been long recognized (Nicholson and Bailey 1935;

Solomon 1949; Nicholson 1957; Chitty 1967; Williams 1975). Various intraspecific mechanisms have been proposed for the control of density: territoriality (Rand 1967; Brown 1969), social-dominance hierarchy (Watson and Moss 1970), stress (Christian and Davis 1964), migration (Wellington 1960; Lidicker 1962), genetic feedback (Chitty 1967), and habitat fouling (Barbosa and Peters 1970; Ikeshoji and Mulla 1970).

For many populations, intraspecific predation (cannibalism) may be an effective and homeostatic self-regulatory agent (Fox 1975a; Polis, to be published). Several studies indicate that it is important in population regulation, as a key-factor mortality agent, and as a determinant of age structure, sex ratio, and success of recruitment.

However, the role of cannibalism in the dynamics of natural populations is not widely recognized. This situation has arisen because some of the best-known examples are from the laboratory or under unnaturally crowded conditions: *Tribolium* cultures (Mertz and Davies 1968; Mertz 1969), laboratory mammals (e.g., Renshaw et al. 1975), cultures of protozoans (Giese 1973), rotifers (e.g., Gilbert 1977) and guppies (e.g., Silleman 1968), in mariculature (Ryther and Bardach 1968; Hanson 1974), and with economically important insects (e.g., Salt 1931; Brown 1972). The significance of cannibalism in the population dynamics of natural aquatic systems has been investigated often, but its role in population limitation of terrestrial organisms is largely unstudied (Fox 1975a). This is due, in part, to the inherent difficulties of observation and manipulation of terrestrial organisms. It is frequently difficult to collect large numbers of terrestrial animals and antibody-reaction prey identifications cannot detect cannibalism.

Populations of scorpions are good terrestrial systems for the study of cannibalism. In some species of scorpion, the existence of strong regulatory agents

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is suggested because they exhibit many characteristics of an equilibrium species (stable year-to-year population size, density-dependent mortality, survivorship intermediate between a type I and II curves, low r_{max}, and long generation time and life span) (Polis and Farley, to be published). Since scorpions are well-known 'inveterate' cannibals (Cloudsley-Thompson 1968), cannibalism may be important in the maintenance of equilibrium densities. Although scorpions are nocturnal, their behavior and surface density are easily monitored because they fluoresce under ultraviolet (UV) light (Stahnke 1972). Populations are sometimes dense (3,000–5,000/ha; Polis and Farley, to be published,), and their diet is readily determined because scorpions digest their prey externally in a process that often lasts hours.

Material and Methods

A population of desert scorpion, *Paruroctonus mesaensis* Stahnke (Vaejovidae), was studied at a sand dune 9 km northwest of Palm Springs, California (Riverside Country). Information on climate and vegetation are given elsewhere (Polis and Farley 1979b).

The entire study area was about 75 ha. Within this area, a grid 28 × 50 m was constructed by placing marker stakes 2 m apart in 15 rows. Each row was also separated by 2 m. Portable lights (Coleman Charger 3,000 and Burgess Safarilight) with UV bulbs (Sylvania F8T5) were used to locate and observe scorpions. All data were gathered from May 1973 through September 1977 during 900 field hours on over 225 different nights. In the four years of this study, over 850 scorpions in the grid were individually color-coded. Unique markings were achieved by using fluorescent paints of different colors in various dot combinations. Individual burrows were marked with coded stakes. Individual activity, forage range from burrow, and the distance scorpions moved between successive sightings were tabulated from repeated surveys of the grid area. Grid surveys were conducted on the average of once per week for the entire period. Population size within the grid was estimated by methods discussed elsewhere (Polis and Farley, to be published). Data obtained by surveying the entire study area include sex and age of the population, mating observation, feedings, cannibalism, and percent moving when first observed.

Overlap coefficients are used to quantify age-specific differences in food and phenology. Pianka's (1973) symmetric measure of overlap is used.

Relative abundance of insects was determined by trapping from spring 1974 through fall 1976. Details are presented elsewhere (Polis and Farley 1979b).

Field Experiments. I conducted a field experiment to determine the role of starvation to mortality of newly born scorpions. Second instar scorpions ($n=33$) were collected on their first night of surface appearance (3 August 1977). They were placed individually into bottles and then buried at the depth of-an average burrow (25 cm). Scorpions could freely move about as the bottles were relatively large (25 ml). Scorpions were excavated weekly and the number dying within that week's interval was determined.

A set of field experiments was established in summer 1976 to test whether the rate of cannibalism was density-dependent. Using aluminum sheet metal and wooden stakes, 28 field enclosures (each 30 m^2) were built. Using 348 marked newborn scorpions,

five densities were established: 3, 6, 12, 24, and 48 scorpions per enclosure. Enclosures were monitored at one- to three-day intervals; surface density and cannibalism were recorded. I was unable to complete these experiments because the heaviest rainfall in at least 15 years occurred in the study area (U.S. Environmental Data Service 1960–1976). However, some important data were tabulated before the storm occurred and these data are included since they help clarify the significance of cannibalism in the regulation of population density.

Related Life History Information. On the average, adult scorpions weigh 2 g and are 72 mm in total length (Polis and Farley 1979b). For five consecutive years, first appearance of newborn animals throughout the population was synchronous and occured in early August. Maturity is achieved at 19–24 months of age and growth is determinant. Because of the discrete birth period, three age groups can be identified in the field: young animals zero to one year of age, intermediate animals one to two years of age, and adult animals older than two years of age are precisely known. Since females can live at least five years, the adult age group includes animals from differently aged cohorts. Adults are grouped because animals older than two years of age are similar in size and appearance.

Analysis of foraging activity (Polis 1980) suggests that this scorpion is a time minimizer (Schoener 1971). On the average, individual scorpions emerge from their burrows to the surface on only about half the nights of the year.

Results

Characteristics of Cannibalism

Diet Compositon. These scorpions detect prey by monitoring substrate vibrations produced by movement of prey species (Brownell 1977). They will attack any object in the appropriate size range. Ninety-five prey species were recorded in the field. The large proportion of conspecifics in the diet is very probably a by-product of this mode of hunting.

Conspecific scorpions are a large component of the diet of *P. mesaensis*. Numerically, they are the fourth most common diet item and represent 9.1% of the total diet (Table 1). In certain bimonthly periods, scorpions constituted 40%–60% of the total number of prey items. When prey items are ranked by wet weight of each prey species, conspecifics are the single most important prey item, and account for 28% of the total prey biomass (Table 1). This is because they are one of the heaviest prey species.

The percent of *P. mesaensis* in the diet was significantly higher with increased scorpion surface density (Fig. 1). Surface densities in the 1,400-m^2 plot were grouped into a series of regular density classes (0–25, > 25–50...). For each density class, all feeding data were summed and the percent conspecifics in the diet was calculated. Feeding data were summed because of the irregular and sometimes low number of scorpions observed on different survey nights. The
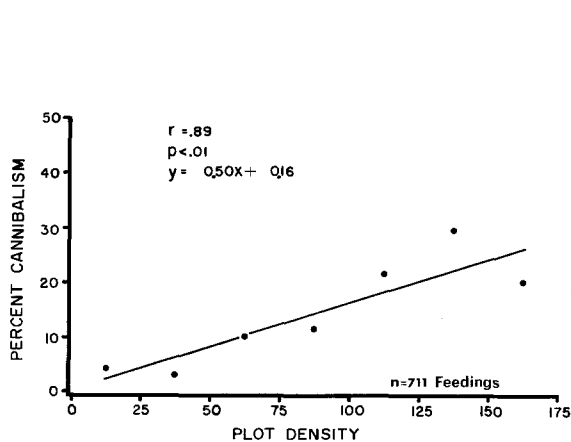
Table 1. Major prey species. The biomass (%) of prey species i in the diet is (relative frequency)$_i$ (weight)$_i$/Σ (relative frequency)$_i$ (weight)$_i$ × 100. Prey weight is the average wet weight (whole body) of 10–30 adults

Prey species	Frequency	Rel. freq. (%)	Weight (g)	Biomass (%)
Chilometopon sp. (Tenebrionidae)	127	16.0	0.025	1.9
Eussatus muricatus (Tenebrionidae)	107	13.5	0.234	14.7
Arenivaga investigata (Blattidae)	90	11.4	0.430	22.9
Paruroctonus mesaensis (Vaejovidae)				
(0–1 year)	45	5.7	0.166	
(1–2 year)	14	1.8	1.074	
(Adults)	13	1.6	2.000	
Total	72	9.1		28.4
Telabis sp. (Tenebrionidae)	40	5.1	0.015	0.6
Solenopsis xyloni (Formicidae)	35	4.4	0.006	0.1
Macrobaenetes valgum (Gryllidae)	29	3.7	0.756	13.1
Paruroctonus borregoensis (Vaejovidae)	23	2.9	0.250	3.4
Batulius sp. (Tenebrionidae)	21	2.7	0.010	0.1
Vaejovis confusus (Vaejovidae)	16	2.0	0.150	1.4
85 Other prey species	232	29.3	0.100[a]	13.7
Total	792	100		100

[a] Estimated weight. Data collected from 1973–1977

percent of *P. mesaensis* in the diet also increased with decreased abundance of insect prey (Fig. 2).
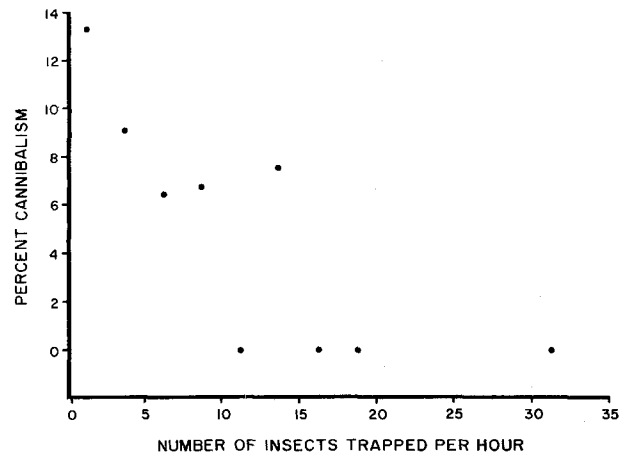
Traits of Predators and Prey. For *P. mesaensis,* relative size is paramount in the outcome of a cannibalistic encounter. In the 105 observations of cannibalism (74 natural field cases, 14 in the field enclosures, and 17 in the laboratory), larger scorpions were the predator in all cases but one (both animals were adult females of the same length) (Fig. 3). During a fight, each antagonist used one chela (pincher) to hold the metasoma (tail) of its opponent. The larger scorpion with the longer metasoma eventually stings its opponent. Paralysis results and the victim is consumed.

Cannibalism occurred both within and between each age class (Table 2). Scorpions less than one year of age were the most common prey, while adults were the predominant predators. Adults constitute a disproportionately high percentage of the predators: although they represent only 9% of the surface population, they are the predators in over 50% of all cannibalism. Adults also constitute a significantly larger percentage of the prey (18%) than their surface population. This is because adult males are commonly cannibalized by adult females (see below).

At all ages, there was a sex bias in cannibalistic encounters. A significantly greater fraction of the prey scorpions ($n = 56$ sexed) were male (males = 69%, fe-

Fig. 1. Percent of observed feedings that were cannibalistic as a function of surface density of scorpions in 1,400-m² gridded plot. *Points* are plotted at midpoint of each density interval. There were 711 feedings observed on nights when the plot was surveyed. A least-squares *regression line* was calculated for the two variables

Fig. 2. Percent of observed feedings that were cannibalistic as a function of insect abundance. There were 573 feedings observed during the periods when insects were trapped. The best curve fit is logarithmic ($y = 0.15 - 0.04 \ln x$) ($r = -0.87$, $P < 0.01$)
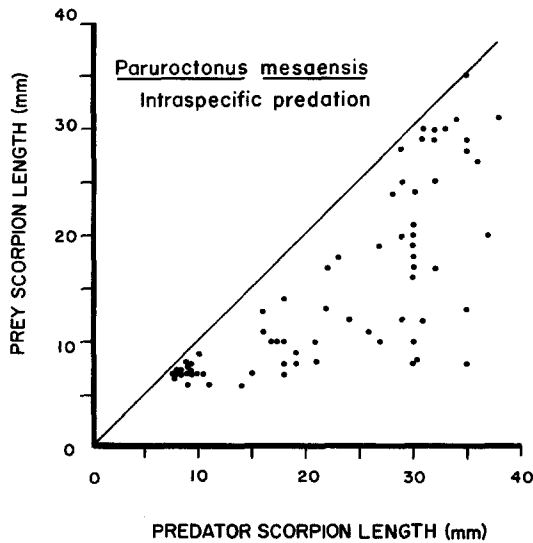
Fig. 3. Size of cannibalistic predators and their prey from encounters in the field. Scorpion length is measured from anterior edge of prosoma to the posterior edge of the last mesosomal segment and does not include the metasoma

Fig. 4. Percent of observed feedings that were cannibalistic as a function of time

Table 2. Analysis of cannibalism by age. (*Top*) Matrix of predator-prey interaction. (*Bottom*) Comparison of surface composition with composition of cannibalistic prey and cannibalistic predators. Percentage surface population determined from grid surveys conducted 1973–1977. The test statistic is the χ^2 goodness of fit using numbers, not percentages

		Predator			
	Age (years)	0–1	1–2	>2	Total
Prey	0–1	29.2	18.1	15.3	62.6
	1–2	0	0	19.4	19.4
	>2	0	0	18.1	18.1
	Total	29.2	18.1	52.8	100.0%

Age (years)	Surface composition (%)	Prey (%)	χ^2	Predator (%)	χ^2
0–1	70.74	62.6	0.7	29.2	17.3**
1–2	20.22	19.4	0.02	18.1	0.3**
>2	9.04	18.1	6.2*	52.8	143.1
n	6777	72	6.92*	72	160.7**

* $P<0.05$, ** $P<0.001$

males = 31%, t-test for differences in proportion, $t=$ 3.1, $P<0.001$). Further, a significantly greater fraction of the predator scorpions ($n=55$ sexed) were females (males = 31%, females = 69%, $t=2.9$, $P<$ 0.001). A frequent predator-prey combination (18.1% of all cannibalisms) was mature females eating mature males during the breeding season. These predations were observed during mating and during activity not directly associated with mating.
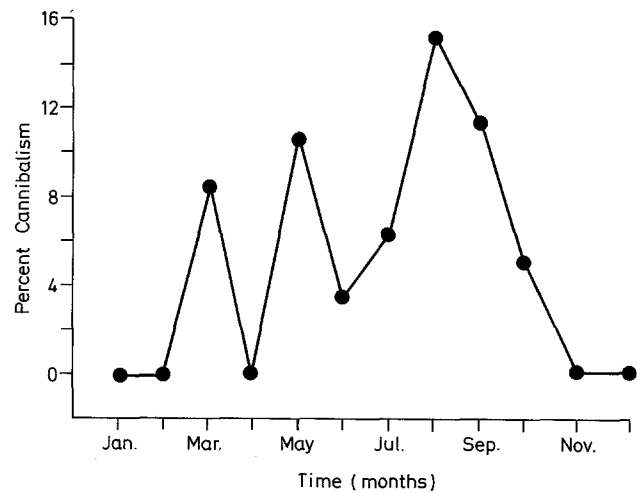
Seasonality. Although cannibalism was observed throughout the year, it occurred most commonly in spring, then again in late summer through early fall (Fig. 4). During late summer, the relative surface density of adults and newborn scorpions was much higher than that of intermediately aged animals (Polis 1980) and consequently most of the prey scorpions were young (67%) rather than intermediate animals (14%) or adults (19%). In spring, however, the relative surface density of each age group was high and intraspecific predation was distributed more evenly among each age class (young: 50%, intermediate: 31%; adults: 19%). By their absence in late summer, intermediate scorpions experienced significantly lower cannibalism than that occurring during periods of high temporal overlap with the adults in spring ($t=$ 1.89, $P<0.05$).

The high incidence of cannibalism in the spring is associated with factors not present during other seasons. At this time, overwintering animals emerge from their burrows to the surface and the percentage of animals observed moving is greater at this time ($2.7\pm4.0\%$, $n=24$ bimonthly periods) as compared with the rest of the year ($1.3\pm1.3\%$, $n=46$ bimonthly periods) ($t=2.01$, $P<0.01$). Further, on the average, marked scorpions move a significantly greater distance between successive sightings at spring emergence (15.4 ± 15.1 m, $n=29$) as compared with other time periods (6.2 ± 3.3 m, $n=634$) ($t=10.8$, $P<0.001$). Movement appears to be requisite for cannibalistic encounters. In the six instances that I observed the onset of a cannibalistic attack, the attacked individual
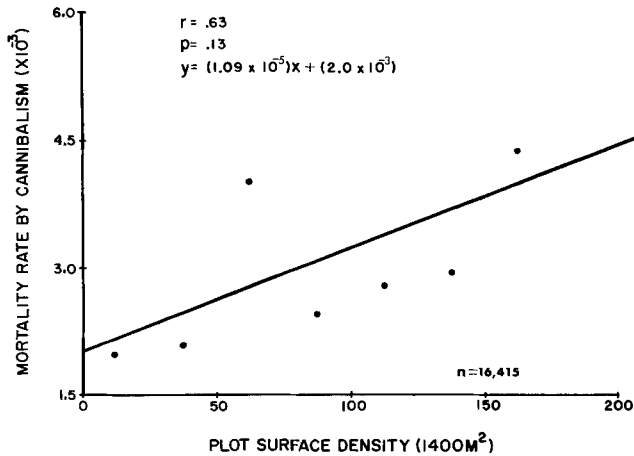
Fig. 5. Daily mortality rate (no. cannibalized animals/total no. animals) produced by cannibalism as a function of natural surface density in the 1,400-m² gridded plot. *Points* are plotted at the midpoint of each density interval. In total, there were 16,415 scorpions scored to determine these daily mortality rates. A least-squares *regression line* was calculated for the two variables

was moving. Smaller scorpions were never observed to attack larger moving scorpions.

Effect of Cannibalism on Population Dynamics

Population Regulation. The mortality of *P. mesaensis* is significantly density-dependent and the population fluctuates around an equilibrium size (Polis and Farley, to be published). I tested to determine whether cannibalism was density-dependent (i.e., increased rates at higher densities) and thus capable of contributing to population regulation.

The proportion of scorpions killed by cannibalism (no. cannibalized/total no. of scorpions) was determined for each night by a survey of the entire study area. Plot densities were again grouped into a series of regular density classes (as in Fig. 1). For each density class, all cannibalistic observations were summed and the average daily mortality rate caused by cannibalism was calculated. The individual nightly rates of mortality were summed because the number of scorpions observed on different survey nights was irregular and, on some nights, relatively few scorpions were observed. This procedure was particularly important because the nightly mortality rates due to cannibalism are relatively low and a low nightly sample size would introduce much random error. Mean mortality rates varied from 0.002 to 0.005/night, i.e., 2–5 scorpions cannibalized/night/1,000 scorpions on the surface.

The mortality rate caused by cannibalism increased with density (Fig. 5): all successively higher

densities (except one) were subject to higher rates of cannibalism. However, because the rate of cannibalism at surface densities of 50–75 scorpions per 1,400 m² was disproportionately high, the relationship is not statistically significant ($P=0.13$) (without this point, the relationship would be highly significant, $P=0.01$). This density occurs primarily in spring of each year and the concurrent high rate of cannibalism is partially a function of the significant increase in movement of individuals at this time.

Data from the experimental field enclosures also suggest that cannibalism is a positive density-dependent mortality factor. The rate of cannibalism (no. of observed cannibalisms/no. of scorpions at each density treatment) was correlated with log density ($r=0.89$, $P=0.05$). The rate of cannibalism in the most-dense enclosures (48 animals) was 6.3%; the rate was 4.1% in the 24 animal enclosures and there were no cannibalisms observed at the three lowest densities (3, 6, and 12 animals).

Thus, both under experimental and natural conditions, the rate of cannibalism is a positive function of density and could contribute to population regulation.

Newborn Mortality. In each of the five years of this study, absolute population density of scorpions less than one year old is highest in the period after birth in late August. By late September, the population is greatly diminished (Polis and Farley, to be published). During this period, temperatures reach an annual maximum and abundance of insect prey drops to an annual minimum (Polis and Farley 1979b).

Cannibalism appears to be the mortality factor responsible for the decline of the newborn population. At this time, cannibalism reached the highest levels (1 August to 16 September: 16.0% of the total diet) and produced much absolute mortality.

To test the hypothesis that cannibalism is the major mortality factor responsible for the population decline of newborn scorpions, I determined the relative contributions of alternate factors that could produce a decline in density (starvation, interspecific predation, and migration).

Since levels of insect prey are low during the post birth period, starvation might have accounted for the observed mortality. The results of the starvation experiment show that an average newborn scorpion could live about three months in the field on embryonic food reserve ($\bar{x}=85.5\pm31.9$ days; range: 28–143 days). Since most newborn mortality occurred within about 90 days after first surface appearance, the contribution by starvation can explain little of the observed mortality. These results possibly could slightly overstimate the period a 'free' scorpion could

survive without food, because the experiment inhibits normal nocturnal surface activity (burrowing and foraging behavior — but 'free' animals can feed).

Evidence suggests that interspecific predation could produce little absolute mortality (unpublished data). The surface density of five other species of scorpion that could prey on *P. mesaensis* was low (maximum surface density: 62.5/ha; average surface density 1975–1977: 10.4/ha) as compared with the surface density of *P. mesaensis* (maximum surface density: 2,064/ha; average surface density: 289/ha). These other species of scorpion were observed to eat newborn on only eight occasions over the five years of the study. Although predation by seven species of vertebrates probably accounts for much of the adult mortality (Polis and Farley, to be published), newborn scorpions are apparently too small (0.03 g) for these predators.

Migration cannot account for the decline in the population. No marked newborn ($n > 1,000$) was observed to travel more than 30 m away from the plot and the average distance moved between successive sightings was 2.7 ± 1.5 m ($n = 169$). Further, net migration was probably zero, as the study site is centrally located in a large, homogeneous sand dune.

Thus, evidence suggests that cannibalism is the only major factor that can produce the population decline of newborn scorpions.

Differential Sexual Mortality. Cannibalism may produce observed differences in age-specific survivorship of males and females. At all ages, males die faster than females (Polis and Farley, to be publsihed) and cannibalism is sexually biased. The sex ratio (males/total) significantly declines from birth (51%) to the onset of maturity (42%) to mature animals of all ages (35%). Further, the annual survivorship of mature males (5.5%) is significantly less than that of mature females (18.9%). For immature animals, cannibalism is the only reasonable explanation for the observed differential mortality. Results of the starvation experiment indicated that there is no sexual difference in mortality due to starvation (t-test $= 0.7$, $P = 0.24$). Intraspecific predation on mature males occurs during mating and as a result of behavior associated with mating. Mature males are vagrant and mobile during the breeding season (Polis and Farley 1979a) and this movement predisposes them to a disproportionately high incidence of cannibalism when compared with mature females. Although cannibalism produces much of the observed mortality of mature males, other factors associated with breeding also contribute to the mortality of adult males (Polis and Farley 1979a).

Behavioral Adaptations That Reduce Cannibalism

If cannibalism is an important mortality factor, natural selection should favor adaptations that decrease its effects.

Newborn scorpions do not disperse randomly. They exhibit a highly significant aggregated distribution, since they are found most abundantly under the canopy of large shrubs (Creosote, *Larrea divaricata;* and salt-bush, *Atriplex canescens*) (Poisson distribution: $\chi^2 = 118$, $P < 0.001$). Large shrubs occupied 8.9% of the grid area; one-third of the newborn ($n = 1,094$ scored) were located in these shrub areas. This association is significant (t-test for differences in proportion: $t = 16.8$, $P < 0.001$).

Large shrubs physically protect young animals from cannibalism. Branches and roots provide microhabitat refuges. I tested the effectiveness of prey capture by adult scorpions in such microhabitats. When vibration is produced in the sand, adults orient and then travel to the source of the vibration and seize the vibrating object. Under shrubs, adults can detect and move toward the vibration, but they sometimes cannot capture the object because of the difficulty in traveling through and over branches.

Adult distribution is spatially random ($\chi^2 = 0.4$) and is random in relation to large shrubs ($t = 0.2$, $P > 0.5$). Spatial aggregations of young may saturate localized intraspecific predators and thus decrease the average probability of cannibalism. The synchronous appearance of great numbers of newborn animals on the surface functions to produce further saturation.

The foraging phenology of young and intermediate scorpions serves to decrease cannibalism by adults. Intermediately aged scorpions exhibit maximum surface activity during the cooler periods of the year (fall through spring) when adults are generally inactive (Polis 1980). The temporal overlap of surface activity between intermediate and adult animals is the lowest of all combinations (0.676). Young animals are particularly subject to cannibalism by adults, as both of these age groups exhibit maximum activity from spring to summer; their temporal overlap (0.777) in surface activity is highest of all combinations. Young animals must forage after birth in August in order to ingest sufficient energy so they can successfully overwinter. However, the young manifest a within-night separation from adults during this period: young significantly increase their relative surface activity in the late evening while adults significantly decrease their activity during this time.

Mature males are sometimes cannibalized by mature females immediately after mating. After females are inseminated, male scorpions exhibit an escape be-

havior that serves to decrease mate cannibalism by the female. If successful, they quickly disengage from the female. Since males apparently can mate more than once (Polis and Farley 1979a), this behavior directly increases fitness.

Expansion of Adult Food Base via Cannibalism

Under certain conditions, young animals function as de facto grazers, and cannibalism can effectively increase the carrying capacity of the population of reproductive animals. The required conditions are: (a) immature animals feed on resources unaccessible or unutilized by the adults, (b) adults feed on these immature animals and thus indirectly incorporate these previously unavailable resources, and (c) food is limiting to the adult population so that an increase in food intake can be converted into a higher carrying capacity. Analysis of age-specific prey of other cannibalistic species shows that 'grazer' systems may be widespread (Polis, to be published).

Immature scorpions utilize different food resources than adults. The overlap in prey size between young and adult scorpions is only 0.399, while the overlap between young and intermediate scorpions is 0.639 (Table 3). More important, the overlap in actual prey species is also low. Further, each age group eats many prey species that are not used by the other two age groups: young animals consume 29 prey species not eaten by other ages and intermediates consume 20 unique prey species. Therefore, when adults cannibalize young or intermediate animals, they expand their resource base by indirectly incorporating several prey species that are not part of their diet.

Table 3. Age-specific prey overlap and diet composition. For the matrix of prey size overlap, prey were divided by body length into successive size categories, each encompassing 5 mm. Prey species overlap are in parenthesis

Overlap: prey size

Age (years)	0–1	1–2	>2	Total prey species	Unique prey species
0–1	1.0 (1.0)	0.639 (0.714)	0.399 (0.380)	57	29
1–2		1.0 (1.0)	0.933 (0.837)	50	20
>2			1.0 (1.0)	40	14

Discussion

Density-Dependent Regulation

In general, cannibalism is a self-regulatory process that has inherent advantages over other regulatory agents. Mortality should be a precise function of density and food because the density and feeding history of the regulatory population and regulated population are the same. Increased (decreased) density results in decreased (increased) Lebensraum (intraspecific space), which increases (decreases) the probability of encounter and thus cannibalism. Density-dependent cannibalism occurs in many populations (Fox 1975a; Polis, to be published).

Cannibalism is responsive to changes in the level of ambient prey. It increases during periods of low interspecific prey availability and decreases when the density of prey increases. Therefore, cannibalism acts to adjust the population size to the community resource base and thus functions as an adaptation to a variable food supply. The inverse relationship between food and cannibalism also occurs in many species (see Fox 1975a; Polis, to be published).

Two feedback loops exist between cannibalism and ambient food: as individuals are cannibalized, the population of intraspecific competitors declines and the per capita food level increases; and as animals are satiated by cannibalism, there will be a decrease in those activities related to food stress that predispose active individuals to cannibalism. It is generally accepted that food stress will cause increased movement and foraging activity. In proposing the 'resource concentration hypothesis,' Root (1975) argued that organisms will remain in a particular area only as long as the food supply can be profitably exploited. For arthropods, hunger lowers attack threshold (e.g., Holling 1966; Istock 1966), increases foraging time (Haynes and Sisojevic 1966; Miyashita 1968), causes changes in the location of foraging stations (Turnbull 1964; Wise 1975), and increases locomotion (Istock 1966; Brown 1972; Dethier 1976). Each of the behaviors can result in a higher incidence of cannibalism.

Further, the population does not escape regulation by reaching densities that may saturate some regulatory agents (negative density-dependence: Howard and Fiske 1911). Since mortality is direct and immediate, there is a minimal time lag effect and subsequent population oscillations will be dampened (Nicholson and Bailey 1935; Nicholson 1957; but see Mertz and Davies 1968); limited resources are not used by (dead) surplus animals; and additonal food in the form of surplus animals is available to the population.

Additional advantages accrue to members of a population that are self-regulated by cannibalism. Cannibalism functions in the same manner as territory and social dominance to maintain the size of the population below the carrying capacity of the environment (Fox 1975a; Polis, to be published). Therefore population eruptions are dampened before high densities can produce overexploitation and mass starvation. Further, the survivors of a population reduced by cannibalism are relatively more fit than survivors of a population reduced by exploitation (scramble) competition. Cannibalistic survivors would be well fed and capable of contributing more offspring to the next generation than those hungry survivors that have competed for a limited food supply.

In spite of all these characteristics, it is obvious that cannibalism is not an important strategy for all populations and is not perfectly homeostatic under all demographic and environmental conditions. Population oscillations can occur in some cannibalistic systems. As long as any regulatory mechanism affects younger animals instead of adults, there will be a time lag before this mechanism becomes effective and there is the possiblity of cycling (Mertz 1969). This time lag is a function of the relative proportion of the age-specific mortality rates that occur to immature animals as compared with mature animals. For *P. mesaensis*, adult mortality rate is comparable to the high mortality rate experienced by newborn animals, and adults actually constitute a higher proportion of cannibalistic prey than the adult proportion of the surface population (Table 2, bottom). Therefore, any time lag produced by a differential age-specific mortality should be negligible. However, the existence of a satiation effect introduces a component of inverse density dependence into the scheme and could contribute to cycling. Satiation and cycling occur in *Tribolium* (Mertz and Davies 1968).

Finally, it must be noted that in order to demonstrate that cannibalism is the regulatory factor that operates in this population of *P. mesaensis,* cannibalism must be shown to be both necessary and sufficient for regulation. These requisites are almost impossible to demonstrate under field conditions and were not satisfied in the present research. It is likely that several factors, (e.g., predation, starvation) contribute to the regulation of this population, but evidence strongly suggests that cannibalism is a major mortality factor and that it can contribute to regulation.

Spatial and Temporal Patterns
Associated with Cannibalism

Spatial distribution of young scorpions may be an adaptation to decrease cannibalism by adults. Large shrubs function as microhabitat refuges. Several other studies suggest that temporal and spatial separation among age groups are two factors that reduce cannibalism (Polis, to be published).

For scorpions, predator saturation is a likely result of the spatial and temporal aggregations of the young. Satiated scorpions become less active and remain in their burrows (H. Stahnke, personal communication). Further, Taylor (1976) predicts that for the prey of ambush predators (such as *P. mesaensis*), spatial and temporal aggregations are particularly effective in reducing the average probablitiy of death by predation. Hamilton (1971) and others (see references in Bertram 1978) argue that prey aggregations theoretically should be an effective strategy in reducing the individual's probability of predation. Although predator saturation appears to be a common phenomenon (see Taylor 1976), to my knowledge it was only once previously reported in the context of cannibalism (Mertz and Davies 1968).

Temporal and spatial aggregations of newborn scorpions produce a trade-off that could decrease the advantages accrued by clumping. Young scorpions are capable of eating other young scorpions only a little smaller than themselves (Fig. 3). Aggregations of young increase the risk of predation by other newborn scorpions. The important consideration is whether somewhat smaller scorpions gain more than they lose in aggregating, since the probability of predation by older scorpions (and any other predator species) is reduced. This situation is further complicated by possible benefits that may occur via sibling cannibalism (see Transitory Food Cache in the next section). I do not have data to address this complex problem adequately.

Differential patterns in seasonal and daily activity among the scorpion age groups may reflect long-term selection against those animals that exhibited activity during periods when adults were on the surface. For all age groups, the proximal (ecological) cue of activity appears to be differential response to temperature (Polis 1980). The distal (evolutionary) cue for young and intermediately aged animals may be avoidance of adults. Schoener (1971) suggests that predation is the paramount force which produces temporal separation. However, a trade-off exists: the avoidance of adults by subordinate animals places them on the surface during periods of suboptimal prey availability. Only adults exhibit a seasonal activity pattern that is significantly correlated with prey abundance (Polis 1980).

Overall Significance of Cannibalism

Empirically, several de facto benefits accrue to the individual cannibal and to the population of cannibals. Cannibalistic individuals benefit by obtaining

additional food while concurrently decreasing potential intraspecific competition by eating a putative competitor. Animals become spaced in the environment and successful cannibals may be assured a sufficiently large forage area in which to obtain requisite resources. By killing other cannibalistic conspecifics, a cannibal can also decrease potential intraspecific predation on itself and its future offspring. Further, a cannibalistic meal increases the probability of survival of the individual cannibal by decreasing the probability that the winner will be cannibalized: the risk of being eaten will decrease both with increased size and with decreased forage activity that accompany a meal.

Mate competition may favor the evolution of cannibalism. For *P. mesaensis,* males represent only one-third of all adults. There should be selection by females to cannibalize mature males after insemination. Removal of reproductive males directly increases the fitness of the cannibalizing female by decreasing the probability that other females will encounter a mate.

The population or group benefits are a consequence or effect of cannibalism by individuals and may be considered simple 'statistical by-products' of individual selection (Williams 1966 p 237). An obvious group benefit is self-regulation of the population. Effective homeostatic regulation decreases the probability of population extinction and increases the probability of persistence. Another group benefit occurs in those systems where the carrying capactiy of the population is effectively increased when older age groups eat younger animals and incorporate food resources otherwise unavailable to these older groups. Two additional groups benefits are discussed below.

'Lifeboat Strategy'. Cannibalism can serve as a 'lifeboat strategy' to decrease the probability of population extinction. The term lifeboat strategy was used by Giese (1973) in describing cannibalistic morphotypes of the protozoan, *Blepharisma.* Individuals in a population of cannibals could survive periods of food deprivation whereas individuals in noncannibalistic populations starved to death. Cannibal *Blepharisma* ate one another and the population was able to persist during periods of food stress. Ullyette (1950) obtained similar results for three species of sheep blowfly. Under conditions of very high densities and inadequate per capita food, the populations of the two cannibalistic species survived while the population of the noncannibalistic species became extinct. Thus, cannibalism can contribute to the long-term persistence and stability of a population that lives in an environment characterized by large fluctuations in food resources.

During prolonged periods of food shortage, this lifeboat strategy may operate within populations of

P. mesaensis. In its sand dune habitat, the levels of prey vary greatly according to season (Polis and Farley 1979 b). Average growth rates are actually negative during annual periods of minimum prey abundance in mid-summer (July). Further, deserts often are characterized by nonpredictable patterns of good years (high precipitation, plant growth, and insect densities) and bad years (low precipitation, plant growth, and insect densities) (Reiten and Green 1968).

Transitory Food Caches. Surplus animals that are cannibalized serve as transitory food caches, storing energy from periods of resource abundance for periods of food stress. For *P. mesaensis,* this is the de facto situation. Most embryonic growth occurs during the period of maximum insect abundance in spring (Polis and Farley 1979b). At this time, young are partitioned with 85 days of reserve food supply. In the period after August birth, food is at its lowest level (Polis and Farley 1979b), but the density of energy-rich young is maximum and cannibalism is at its maximum rate. Since newborn are highly aggregated, there is a high probability of sibling cannibalism (it was frequently observed at this time). Under these circumstances, siblings functually serve as packages of live meat for their kin. Consequently, there is a decreased probability of starvation and the potential for an increased probability of survival for the average individual of a clutch over the first winter.

The observed sibling cannibalism may represent either a case of kin selection (O'Connor 1978) that increases the inclusive fitness (Hamilton 1964) of the average offspring, or a case of parental manipulation (Alexander 1974) that increases successful parental reproduction (=number of offspring that survive to breed). Eickwort (1973) worked with chrysomelid beetles and calculated the change in average fitness of individuals that were sibling cannibals. She concluded that, even at low levels, sibling cannibalism should be favored by kin selection as the average fitness of the clutch was increased. In birds, the larger sibling of many species commonly eat smaller siblings if food shortages arise (Lack 1968; O'Conner 1978). O'Conner proposed a simple model of inclusive fitness that may explain the widespread evolution of brood reduction by sibling cannibalism.

There are many examples of sibling cannibalism on eggs and newborn animals (references in Wilson 1971; O'Connor 1978; Polis, to be published). An extreme case of this straegy occurs in animals that normally produce infertile 'nurse' or 'trophic' eggs, which serve as the first food of their newborn (references in Wilson 1971; Polis, to be published). Brood aggregation is an essential characteristic of this strategy and occurs in all the cited examples.

An alternate strategy to the sibling cannibalism/

food cache strategy would be to produce fewer but better partitioned young. For *P. mesaensis,* newborn mortality is high partially because of cannibalism by older animals that eat any smaller animal (even if it is a 'bigger' smaller animal). Thus, under a mortality regime that does not always distinguish the size of the young, a strategy that produces fewer young would be less successful than the food cache strategy. Further, there may be a limit to embryonic growth. Although females are gravid for 10–14 months, most growth occurs during peaks of insect prey abundance in spring (Polis and Farley 1979b). Adult females are absent from the surface for the 5–7 cold months of the year (Polis 1980) and the size of young at birth may be a simple reflection of the short periods of favorable embryonic growth. Under these conditions where there is no easy way for the female to convert her body resources into food, the sibling cannibalism/food cache strategy may increase the inclusive fitness of the female and her offspring.

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